Walla Walla River Bull Trout Ten Year Retrospective Analysis and Implications for Recovery Planning

September 30, 2014

Study funded by:

U.S. Fish and Wildlife Service
and
U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit,
Department of Watershed Sciences, Utah State University

Prepared by:

Howard Schaller[1], Phaedra Budy[2], and Courtney Newlon[1]

Contributing Authors:

Steve Haeseker[1], Julie Harris[1], Marshall Barrows[1], Darren Gallion[1], Ryan Koch[1], Tracy Bowerman[2], Mary Connor[2], Robert Al-Chokhachy[2], Joe Skalicky[1], and Don Anglin[1]

[1] U.S. Fish and Wildlife Service, Columbia River Fisheries Program Office, Vancouver, WA
[2] Utah State University, Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, Logan, UT

Table of Contents

List of Figures

List of Tables

Executive Summary

- We completed a multi-year synthesis of the data and analyses for the Walla Walla River to help broadly prioritize conservation actions and inform the conservation of bull trout.

- The assessment provides fundamental and critical information on bull trout growth, movement patterns, and survival rates. At the population level we assess abundance, structure, and growth rate. We characterized habitat quality, suitability, and availability for the Walla Walla River and Mill Creek that was formerly lacking.

- Protection of South Fork Walla Walla River spawning and rearing habitats and improvement of the lower Walla Walla River migratory and foraging corridor will allow bull trout to complete their lifecycle, express life-history variability, potentially serving as a donor population for other local populations (e.g., Touchet River and Mill Creek populations), or core areas (e.g., Umatilla Core Area) in less desirable habitat, and improve the resiliency of the entire Walla Walla River Core Area.

- Walla Walla River migratory fish appear to reach larger sizes and approach their maxima faster than do residents (i.e., migrants exhibit faster growth rates), although considerable overlap between the two life-history expressions appears to occur. Growth at juvenile life stages before emigration may be slightly higher for migratory fish than for resident fish.

- Generally, fish that migrated as sub-adults and small adults moved farther downstream and remained in lower parts of the watershed longer than juveniles and large adults. It appears that environmental factors and/or individual intrinsic growth influence transition to a migratory life-history. The consequences of the migratory life-history expression appear to involve complex tradeoffs between the benefits of increased growth and fecundity, but at a cost of lower survival.

- Larger bull trout size classes showed the greatest tendency to migrate downstream out of the headwater area. Since the lower river demonstrates a longitudinal trajectory of habitat degradation, migratory bull trout in the sub-adult and small adult size classes may be the most susceptible to lower river mainstem mortality. If this is the case, reduced survival for the sub-adult and small adult size categories could reduce the potential reproductive contribution of the migratory component of the population and the opportunity for dispersal.

- Several lines of evidence demonstrate that bull trout in the Walla Walla River Core Area still attempt to disperse among the local populations and between core areas (e.g., genetic and movement data). Providing for dispersal, by improving habitat conditions that restore connectivity among local populations and between core areas, is vital to maintaining and enhancing viability of the Walla Walla River Core Area local populations of bull trout and could be vital to long term maintenance of adjacent core area populations.

- The bull trout population of South Fork Walla Walla River appears stable; however, there is some indication that large migratory individuals may be in decline (e.g., mark-recapture trend analysis; redd counts) and there is high variability in survival for this size group. However, given the declining trend in large adults, the long term stability of the population structure is uncertain and may not reflect the historical population structure and evolutionary history of bull trout.

- Results from our life cycle viability model simulations indicate that at the metapopulation level, when individual local populations have different long term trends in abundance, connectivity and a continuum of suitable habitat conditions are important for maintaining smaller, declining populations (e.g., a rescue effect). This variability clearly relates directly to the Walla Walla River Core Area, where one local population is stable and the others appear to be declining. In order for dispersal to aid in maintaining persistence, connectivity and habitat conditions in the mainstem Walla Walla River will have to be restored and protected accordingly.

- Walla Walla River bull trout exhibit a continuum of life histories involving movements, migrations, spawning, rearing and foraging on time scales ranging from daily to annually or longer, and over different spatial scales.

- Collectively, this research and modeling demonstrate that diversity in life-history strategies can help stabilize demographic responses to environmental perturbations, which may help decrease the risk of extripation for both individual local populations and core area populations.

- Our study indicates that the migratory life-history strategy for South Fork Walla Walla River bull trout has been impacted by poor habitat conditions and lack of seasonal connectivity in the lower mainstem Walla Walla River. These mainstem bottlenecks appear to be associated with high summer water temperatures and numerous low flow barriers formed in the summer and fall. These factors impact the population in two ways: 1) reduce the reproductive contribution of the highly fecund migratory component of the population, and 2) limit dispersal of bull trout among the local populations.

- Our modeling of future climate conditions projects a greater loss of spawning and rearing habitat in the Touchet River and Mill Creek populations when compared to the losses projected for the South Fork Walla Walla River population.

- Protecting high quality spawning and rearing habitat in the South Fork Walla Walla River and improving migratory and foraging corridor conditions will allow bull trout to complete their life cycle, express life-history variability, potentially serving as a donor population for other local populations or core areas in less desirable habitat, and therefore improving the resiliency of the entire Walla Walla River Core Area.

- To provide as much demographic stability as possible, diversity within and among populations should be maintained along a continuum that emphasizes conservation of the full range of life-history traits expressed by bull trout. Maintaining life-history diversity will improve redundancy, increase representation and thus improve resiliency.

Acknowledgements

We would like to thank the following people and organizations for providing assistance and support throughout the duration of this project. Dave Crabtree (USFS), Glen Mendel (WDFW), Jackie Dougan (BLM), Bob Bower and Brian Wolcott (WWBWC), Phil Howell and Larry Boe (USFS), Bill Duke (ODFW), Tim Bailey (ODFW), Paul Sankovich (USFWS), Gabriel Brooks (NOAA), Gary Thiede (USU), Tom Krebs (City of Walla Walla), Mark Nelson (USFWS), Jim Gasvoda, Stuart Durfee (Gardena Farms Irrigation District), John Brough (Hudson Bay Irrigation District), from ACOE (Dave Parker, Chris Alford, Ben Tice, Jeremy Nguyen) from CTUIR (Brian Mahoney, Joelle Olsen, Ray Weldert, and Mike Lambert), William R. Brignon, David Hines (USFWS) and Nadia Jones. George Ehmer, Dwyane Wright and John Erhart helped maintain the upper Bear Creek PIT-tag antenna array provided assistance transporting gear to and from field sites. We also would like to thank the local land owners for allowing access to the river through their property: Brad Humbert, Tracy Larson, Dan Boch, Lance Bullock, Lynne Chamberlain, Joe Frazier, Walter Humbert, Clark Lampson, Jerry Larson, and Dale McKain. We would also like to thank Marci Koski, Don Anglin and Christina Wang for comments and feedback while reviewing the report.

Chapter 1 : Introduction, Synthesis and Management Recommendations

authored by

Howard Schaller
Phaedra Budy
Courtney Newlon

U.S. Fish and Wildlife Service
Utah State University

Introduction

In 1998, the U.S. Fish & Wildlife Service (FWS) listed the Columbia and Klamath River Distinct Population Segments (DPSs) of bull trout (*Salvelinus confluentus*) as threatened under the Endangered Species Act (ESA) (63 FR 21647, 63 FR 42757, and 63 FR 42757). Subsequently three more DPSs were identified and combined with the previously listed DPSs to be listed as threatened under one coterminous DPS in November 1999 (64FR 58910).

In 2002, the FWS published the 1st draft Recovery Plan for three of the DPSs (Columbia, Klamath and St. Mary Belly). In 2004, the FWS published a draft Recovery Plan for the remaining two DPSs (Jarbidge, Coastal-Puget Sound), which addressed and listed the entire coterminous DPS as threatened. The goal of the draft recovery plan was to remove threats and ensure sufficient distribution and abundance to improve the status of bull trout throughout their range in the coterminous United States so that protection under the ESA is no longer necessary. To recover bull trout the following objectives were identified in the draft plan (USFWS 2002):

1. Maintain and restore bull trout distribution within core areas as described in recovery unit chapters.
2. Maintain a stable or increasing trend in abundance of bull trout.
3. Restore and maintain suitable habitat conditions for all bull trout life-history stages and strategies (element of connectivity).
4. Conserve genetic diversity and provide opportunities for genetic exchange (element of connectivity).

The development of guidance on how to monitor and evaluate (M&E) recovery, specifically related to recovery criteria, was called for in the draft Recovery Plan. M&E was required to assess recovery action effectiveness and to assess the status of bull trout populations. Population distribution, abundance, habitat and connectivity (e.g., physical and genetic) are all considered important characteristics of bull trout population viability and recovery. However, the original draft recovery plans were unclear about: 1) how, where and when to monitor bull trout and their habitats (distribution and connectivity); and 2) which analytical techniques would provide adequate statistical soundness and rigor (abundance and trends). As a result of these information gaps, a Recovery Monitoring and Evaluation Group (RMEG) was established in 2003 to develop guidance on these questions, and the group has been working on these issues through 2012. The RMEG provided M&E guidance for bull trout to help reliably inform evaluation of bull trout recovery objectives (USFWS 2008).

One important clarification that RMEG identified is that connectivity refers to the maintenance of suitable stream conditions that allow bull trout to move freely upstream and downstream with habitat linkages that connect to other habitat areas. Two of the draft Bull Trout Recovery Plan objectives related to connectivity are: 1) conserve genetic diversity and provide opportunities for genetic exchange; and 2) restore and maintain suitable habitat conditions for all life-history stages and strategies. These objectives imply that measures and the associated monitoring of connectivity must be considered from two distinct perspectives: 1) connectivity among local populations (i.e., effective dispersal) and 2) connectivity to the migratory corridor associated with each local population (i.e., unrestricted migration opportunities and the full expression of life-history strategies). This clarification has helped focus many components of our research in the Walla Walla River (WWR).

In 2008, a 5-year status review was completed and the determination was made by the FWS that bull trout remained threatened throughout their range. As a result of the 5-year review, bull trout are still listed as a single coterminous DPS but have been organized into six recovery units that ultimately may be determined to represent individual DPSs (Figure 1.1). Each recovery unit is composed of a variable number of core areas. In general, core areas are defined as core habitat plus local populations. In most cases a core area is the closest approximation to a biologically functioning metapopulation and the basic unit on which to gauge recovery within a recovery unit. The FWS is in the process of finalizing the draft recovery plan and developing recovery criteria.

There was broad agreement among agency partners that the NatureServe (Faber-Langendoen et al. 2009) approach used by the FWS in 2008 for the 5-year status review was suitable for the purpose of assessing population status and can provide the basis for future assessments, including recovery. NatureServe applies an approach that uses information on demographics and threats to categorically rank relative conservation status. Feedback from our partners during the 5-year review process was that they were comfortable with the metrics and approach, and we should use the same approach and data for assessing recovery.

The goal of the FWS draft bull trout recovery plan was to remove threats and ensure sufficient distribution and abundance to recover bull trout throughout their range in the coterminous United States. In order to assess progress of recovery the FWS will be identifying criteria in the revised recovery plan. Recovery criteria are measurable and objective targets by which progress towards achievement of recovery objectives can be measured. The National Marine Fisheries Service (NMFS) and FWS (2010) Recovery Planning Guidance document recommends that recovery criteria be SMART: Specific, Measurable, Achievable, Realistic, and Time-referenced. It is recommended that recovery criteria be based in sound scientific rationale and reflect the biodiversity principles of resiliency, redundancy, and representation.

- Resiliency involves ensuring that each population is sufficiently large and maintaining within population life-history diversity to withstand stochastic events.
- Redundancy involves ensuring a sufficient number of populations to provide a margin of safety for the species to withstand catastrophic events.
- Representation involves conserving the breadth of the genetic makeup of the species to conserve its adaptive capabilities.

These biodiversity principles would take into account the physical and biological needs of bull trout throughout its range to meet range-wide recovery needs. The use of these biodiversity principles to develop recovery criteria should ensure adequate conservation of genetic diversity, life-history features, and broad geographical representation of bull trout populations. There are a number of approaches being explored to achieve these recovery criteria principles that rely on threats and demographics based criteria to determine the relative risk of extinction for each core area, and ultimately, the Recovery Unit as a whole.

The assessment that follows provides new and critical information on habitat, demographics and movement patterns in the Walla Walla Basin that should help establish recovery criteria for bull trout throughout the coterminous range. Before this study, there were some commonly held beliefs about the demography, behavior and life-history expression, and habitat requirements of bull trout that were not clearly defined and based on extremely limited empirical data (also identified in regional technical workgroups; USFWS 2002; Porter and Marmorek 2005; Al-

Chokhachy et al. 2008; USFWS 2008; USFWS 2012). In the South Fork Walla Walla River (SFWWR) and other similar systems, the common belief was that the population abundance was stable and existing population structure was representative of a healthy population. We generally assumed few bull trout migrated downstream and those that did, demonstrated limited migrations over discrete intervals (i.e., spring, fall). The extent of migration was unknown, including whether or not bull trout used the mainstem of the Columbia River. Previous to this analysis, almost all available information describing bull trout population ecology was from a few isolated studies concentrated largely on adfluvial forms (e.g., Fraley and Shephard 1989; Post et al. 2003). There were very few robust estimates of survival and no estimates of juvenile survival. In addition, the more pristine upper headwaters were thought to be high quality habitat and unlikely to be limiting for rearing and spawning. Also, it was unknown whether resident and migratory life-history forms assortatively mate, resulting in genetic distinction between the two forms. Lastly, the degree of individual fish dispersal among sub-populations and the role of dispersal in maintaining the genetic variability and persistence of each sub-population were unknown. This most basic population ecology information is crucial for monitoring population size and trends in order to determine population status as well as to evaluate opportunities for, and the effectiveness of, management activities aimed at bull trout recovery and their continued persistence.

The FWS's Columbia River Fisheries Program Office (CRFPO) and the U.S. Geological Survey, Fish and Wildlife Cooperative Research Unit at Utah State University (USU) have been conducting research, monitoring and evaluation on bull trout populations in the WWR over the past 12 years. The Walla Walla Basin is comprised of tow core areas and six local populations; three local populations in the Touchet River subbasin (Touchet River Core Area), and three local populations in the Walla Walla subbasins (WWR Core Area) (one local population in each of the Mill Creek and two in the Walla Walla River (Figure1.2). FWS and USU research is focused primarily on the WWR Core Area. In addition, we anticipated using the information and analysis from the WWR to help inform recovery evaluation for bull trout broadly across the range.

To that end we embarked on a multi-year synthesis of the data and analyses for the WWR to help broadly prioritize conservation actions and inform the conservation of bull trout. The retrospective information has been organized around key themes of habitat, life-history drivers, population trends and core area dynamics, and an overall synthesis. This information is derived from Chapters 3 - 9 and Appendices I - VIII. The synthesis for the habitat theme was derived from Chapters 3, 4, Appendices III and IV. The synthesis for the life-history drivers includes Chapters 5, 6, 7, 8 and Appendices V, VI, VII and VIII. The synthesis for the population trends and metopopulation dynamics includes Chapter 7, 9 and Appendix V. We provide an overall synthesis that integrates the summaries from these key themes. We also discuss the transferability of tools developed herein and lessons learned that can apply broadly across the range of bull trout and for recovery planning in general. Components of the study that are already published in peer-reviewed literature are provided as Appendices IV - VIII, as well as an Appendix describing sampling and tagging methodologies that apply across many chapters.

Synthesis and Management Recommendations

The FWS and USU have been conducting research, monitoring and evaluation on bull trout populations in the Walla Walla Basin over the past 12 years (2002-2014). Our assessment provides basic critical information on bull trout growth, movement patterns, and survival rates.

At the population level we assess abundance, structure, and growth rate. A large proportion of this information is derived from the PIT tagging of bull trout and the network of passive instream antenna (PIA) in the WWR (Figure 1.3). We characterized habitat quality, suitability, and availability for the WWR that was formerly lacking. We have synthesized those data and analyses to help prioritize conservation actions in the WWR and to provide range wide guidance for bull trout recovery and monitoring. This retrospective synthesis has been organized around key themes (i.e., habitat, life-history drivers (movement, growth, survival)) related to: identifying population status; assessing environmental and management influence; restoring and maintaining suitable habitat conditions for all bull trout life-history stages and strategies (element of connectivity); and conserving genetic diversity and providing opportunity for genetic exchange (element of connectivity).

To inform future recovery actions for bull trout, our study:

- Successfully implemented and evaluated extensive PIT tagging and detection studies to estimate bull trout abundance, survival, movement, distribution, trend, and life-history characterizations.
- Successfully implemented studies to assess bull trout occupancy and spawning and rearing habitat preferences.
- Provided information and analyses that were highly informative for guiding sampling strategies for estimating population trends.
- Developed an empirically based modeling framework that has the flexibility to evaluate future threats and to guide priorities for bull trout conservation.

The following is a synthesis of our work and how it relates to the biodiversity principles (resiliency, redundancy, and representation), limiting factors and threats, and corresponding management recommendations.

Habitat:

- Developed methods to assess aquatic habitat quality and quantity at the reach-scale in the SFWWR and mainstem WWR.
- Identified suitable and preferred habitat conditions at the microhabitat scale for spawning and rearing bull trout.
- Occupancy and movement analyses support the conclusion that seasonal timing of unfavorable habitat conditions in the middle/lower mainstem WWR may affect the ability of bull trout to move back upstream to rear and spawn. Collectively, results suggest that the migratory component of the population is primarily impacted by these unfavorable habitat conditions in the mainstem WWR (which are avoided by the resident component).
- Based on climate modeling within the WWR, we estimated a greater degree of spawning and rearing habitat loss for the Touchet River and Mill Creek local populations when compared with the SFWWR local population. Estimates of habitat loss associated with increased stream temperature varied considerably among populations, depending on the spatial arrangement of available habitat and the quality of habitat near a thermal boundary.
- Protecting high quality spawning and rearing habitat in the SFWWR is critical for enhancing and maintaining the resiliency of the Core Area population. Protection of these SFWWR habitats and improvement of the migratory and foraging corridor will allow bull trout to complete their life cycle, express life-history variability, and potentially

serve as a donor population for other local populations in less desirable habitat (e.g., Touchet River and Mill Creek populations) as well as adjacent core area populations (e.g., Touchet, Umatilla).

- Improving migratory corridor conditions is a key to improving the resiliency of the WWR Core Area bull trout population. Focusing on activities to improve stream temperature conditions in the mainstem WWR will be essential for restoring the foraging and migratory component of the bull trout population.

Life-history Drivers:

Growth:

- Based on synthesis of mark-recapture data, there is substantial individual variability in both growth rate and the maximum potential length. In addition, and perhaps more importantly, migratory fish appear to reach larger sizes and approach those maxima faster than do residents (i.e., migrants exhibit faster growth rates), although considerable overlap between the two life-history expressions appears to occur. Growth at juvenile life stages before emigration may be slightly higher for migratory fish than for resident fish.

Migration & Movement:

- Generally, fish that migrated as juveniles and large adults exhibited movements of shorter distances and duration relative to sub-adult and small adult migrators. Conversely, fish that migrated as sub-adults and small adults moved farther downstream and remained in lower parts of the watershed longer.
- The longer bull trout reared in the headwater area as juveniles and grew prior to migration, the farther they moved downstream.
- Fish tagged in the SFWWR, WWR, and Mill Creek have all been detected at the Oasis Road Bridge PIA, suggesting a migratory population is present in all of the local populations; and connectivity and dispersal has been documented between local populations with in the WWR Core Area. WWR tagged fish have also been detected at the mouth of the Umatilla River and at mainstem Columbia River locations (e.g., McNary Dam). During this study, two WWR tagged fish were detected completing downstream migrations into the Columbia River and subsequently detected at or above Harris Park in the SFWWR during the spawning season.
- Bull trout that were tagged in the SFWWR and WWR and migrated downstream had low survival rates. That is, of the SFWWR and WWR tagged fish, only 11 and 42% were subsequently detected again. Of these recaptures, only 18% and 31% were documented completing upstream movements after tagging. This pattern suggests that conditions in the lower and middle river may have substantial influence on survival and consequently affect the ability to move upstream and avoid unfavorable conditions.
- Although bull trout demonstrate differences in life-history expressions including resident and migratory forms, there were no significant differences in the genetic structure between presumed resident and migratory fish. Thus it appears that environmental factors and/or individual intrinsic growth potential influence transition to a migratory life-history.

- The consequences of the migratory life-history expression are determined by the complex tradeoffs of greater growth and fecundity, but lower survival; therefore, a fish that survives migration likely has a greater per capita contribution to population growth than a resident.

Survival Rate:

- Using return rates alone (without accounting for recapture or detection probability), the survival advantage of size varies dramatically with year; in some years being large provides a substantial benefit, whereas in other years survival is similar across size classes.
- Survival rate indices in the size range 150-300 mm appear to co-vary in the upper and lower river sections, while survival rates in the size range 300-420 mm do not. Survival rate indices for large adults are similar across years in both reaches.
- Lower river mortality appears to drive annual mortality (or survival) rates in the larger size classes of fish that demonstrate the greatest tendency to migrate downstream out of the headwater area.
- The lower river demonstrates a longitudinal trajectory of habitat degradation, which suggests migratory bull trout in the sub-adult and small adult size classes may be the most susceptible to lower river mainstem mortality.
- Reduced survival for sub-adult and small adult size categories resulting from poor habitat conditions in the lower river mainstem potentially reduces the reproductive contribution of the migratory component of the population and the opportunity for dispersal. Mainstem bottlenecks likely impact the resiliency of the WWR Core Area population.

Connectivity:

- During the study period we documented connectivity between local populations within the WWR Core Area. Additionally, a small number of individuals were observed migrating from one local population to the spawning area of another local population within the WWR Core Area.
- When considered within the context of the genetic structure, several lines of evidence demonstrate that bull trout in the WWR Core Area still attempt to disperse among the local populations (e.g., genetic and movement data).
- Providing for dispersal, by improving habitat conditions that restore connectivity among local populations, is vital to maintaining and enhancing viability of the WWR Core Area populations of bull trout.

Population Trend and Metapopulation Dynamics:

- The population of the SFWWR appears stable; however, there is some indication that large migratory individuals may be in decline (e.g., mark-recapture trend analysis; redd counts) and there is high variability in survival for this size group. Population growth rates estimated from mark recapture data suggest a stable population, but this is primarily due to the high proportion of small adults. However, given the declining trend in large adults, the long term stability of the population structure is uncertain and may not reflect the historical population structure and evolutionary history of bull trout. The time series is quite short, and if recent observations were compared to historical conditions, our conclusions on population status would likely be more dire.

- In life cycle viability model simulations, resident fish are more vulnerable to changes in reproduction and thus more susceptible to events that disrupt spawning success (e.g., inputs of fine sediment in spawning habitat). In contrast, migratory sub-populations (fish that tend to mature at larger sizes and demonstrate higher fecundity rates) are most sensitive to changes in survival rates of large adults (e.g., harvest, predation). As discussed above, there are several lines of empirical evidence that suggest that variability in survival rates for large fish may pose a threat to this population (e.g., survival rates of large, migratory fish are more variable and sensitive to habitat degradation in the lower river). In addition, high growth rates of migrants would be predicted to have a large impact on the population growth rates, due in part to the higher fecundity of larger fish.
- As we expect bull trout populations to have a significant response to changes in juvenile survival rates and individual growth rates, bull trout populations may be particularly susceptible to environmental changes that affect juvenile survival and bioenergetics, including stream productivity, food availability, and temperature.
- At the core area level, when individual local populations have different long term trends in abundance, connectivity is important for maintaining smaller, declining populations (e.g., a rescue effect). This variability in trends clearly relates directly to the WWR Core Area, where one core area is stable and the others appear to be declining. In order for dispersal to aid in maintaining persistence, connectivity of the mainstem will have to be protected and restored accordingly.

Overall Synthesis

- Walla Walla River bull trout exhibit a continuum of life histories involving movements, migrations, spawning, rearing and foraging on time scales ranging from daily to annually or longer, and over different spatial scales.
- Collectively, this research and modeling demonstrate that diversity in life-history strategies can help stabilize demographic responses to environmental perturbations, which may help decrease the risk of extinction for both individual local populations and core area populations (i.e., addressing redundancy and resiliency).
- Our study indicates that the migratory life-history strategy for SFWWR bull trout has been impacted by poor habitat conditions in the lower mainstem WWR. These mainstem bottlenecks appear to be associated with high summer water temperatures and low streamflows that result in numerous low flow barriers formed in the summer and fall. These factors impact the population in two ways: 1) reduce the reproductive contribution of the highly fecund migratory component of the population, and 2) limit dispersal of bull trout among the local populations.
- Our modeling of future climate conditions projected a greater loss of spawning and rearing habitat in the Touchet River Core Area and the Mill Creek local population when compared to the losses projected for the SFWWR local population.
- Our study synthesis indicates that protecting high quality spawning and rearing habitat in the SFWWR and improving migratory and foraging corridor conditions will allow bull trout to complete their life cycle, express life-history diversity, and potentially serve as a donor population to other local populations and core areas in less desirable habitat (e.g., Touchet River and Mill Creek populations).
- To provide as much demographic stability as possible, diversity within and among populations should be maintained along a continuum that emphasizes conservation of the full range of life-history traits expressed by bull trout. Maintaining life-history diversity will improve redundancy, increase representation and thus improve resiliency.

To provide the basis of support for the synthesis and management recommendations, we summarized the study findings from the chapters and appendices by key themes mentioned above and in some cases further divided key themes. Much of the detailed data on bull trout abundance, survival, movement, distribution, and life-history characterizations has been obtained from the extensive PIT-tagging effort in the WWR along with the instream PIT tag detection arrays deployed throughout the basin (Appendix I; Appendix II). Additional information on habitat quality, suitability, and availability has also been obtained from other fish sampling efforts throughout the basin.

Habitat:

<u>Spawning, Rearing, and Foraging Habitat (Chapters 3 and 4, Appendix IV)</u>

Bull trout typically prefer to spawn in relatively pristine habitat; however, there are basins where land development is encroaching on spawning habitat and where bull trout production is limited. Understanding spawning habitat relationships for resident and migratory bull trout is critical for guiding the recovery of the species. Recovery efforts can be guided by identifying suitable and preferred habitats for spawning, early rearing, foraging, and migration, as well as by quantifying the availability of these habitats within the Recovery Unit. This information could be used to ensure connectivity among populations, resilience within populations, and to identify habitat that may be limiting.

In the SFWWR, bull trout were associated with small gravel and pebble substrates across all three redd size classes (e.g., small, medium, large). As redd size class decreased, bull trout redds were increasingly associated with smaller substrates. In the SFWWR, medium to large gravel is more abundant but sand and smaller gravel are more limited. Therefore, if population growth for the SFWWR population relies heavily on the smaller resident fish spawning, spawning habitat could become limiting. For the medium and large redd size classes, slow water velocity was associated with increased spawning habitat suitability, with the highest suitability at locations with water velocity less than 0.5 m/s. Diel comparisons suggested that rearing bull trout use deeper microhabitats with cover during daytime periods, but shift into significantly slower habitats during nighttime periods; however, we observed no discrete differences in substrate use patterns across diel periods. Across life stages, we found that both juvenile and adult bull trout used slow velocity microhabitats with cover, but the use of specific types of cover varied.

Spawning and rearing habitat use and modeling in the SFWWR have provided data and tools that will be valuable for implementing and focusing restoration efforts not only in the Walla Walla Basin, but also in other basins. Spawning habitat suitability models developed in the SFWWR provide quantitative tools to assess the quantity, quality, and location of suitable spawning habitat by life-history form and are useful for identifying areas where habitat is compromised in order to focus restoration efforts. These models may also be useful for assessing spawning habitat conditions in other basins that have not been monitored intensively and for developing recovery objectives or criteria for other river basins. Our rearing habitat evaluations together with rearing habitat studies in other basins demonstrate that bull trout rearing microhabitat use patterns are generally consistent across systems, a pattern that parallels other observations at both similar and larger scales and across life-history forms. Thus, our results, in combination with previous bull trout habitat studies, provide managers with benchmarks for restoration of rearing habitat in highly degraded systems.

Climate change is projected to increase stream temperatures and disrupt hydrologic regimes which will likely impact bull trout across their native range given their thermal sensitivity (Isaak et al. 2010). Based on our climate modeling within the WWR Core Area, we estimated a greater degree of spawning and rearing habitat loss for the Touchet River and Mill Creek populations than for the SFWWR population. Estimates of habitat loss, associated with increased stream temperatures, varied considerably among populations depending upon the spatial arrangement of available habitat and the quality of habitat near a thermal boundary.

Protecting high quality spawning and rearing habitat in the SFWWR is critical for the resiliency of the core area population. By protecting SFWWR habitats and improving the mainstem migratory corridor of the WWR, bull trout should be able to complete their life cycle, express life-history variability, and potentially serve as a donor population to other local populations and core areas in less desirable habitat.

Connectivity (Foraging and Migratory Habitat; Chapters 3 and 4, Appendix III)

Effective management of threatened species requires a sufficient knowledge of fundamental habitat requirements, particularly for species occurring in intensively managed and modified landscapes. WWR bull trout exhibit a continuum of life histories involving movements, migrations, spawning, rearing and foraging on time scales ranging from daily to annually or longer, and over different spatial scales.

Identification of methods to restore and maintain suitable habitat conditions for all bull trout life-history stages and strategies (element of connectivity) is critical to address the conservation principles of resiliency and redundancy. We developed a practical and fundamentally straightforward approach to assess aquatic habitat quality at the reach-scale in the SFWWR, mainstem WWR, and Mill Creek subbasins to help inform future recovery actions explicitly for bull trout. Habitat quality model scores (HQS) suggest that habitat quality for most bull trout life stages, strategies and actions is generally better in headwater reaches and degrades incrementally downstream from the Umatilla National Forest boundary, as the severity and often cumulative anthropogenic modifications and other influences become more prevalent. While the resident component of the population only experiences the good quality headwater conditions, migratory bull trout are exposed to a spectrum of anthropogenic channel modifications, riparian habitat degradation, streamflow reductions, and other influences throughout the basin and in the mainstem Columbia River.

Water temperatures generally increased from the headwaters in the SFWWR to the lower mainstem WWR, making downstream habitats less thermally suitable for bull trout of most life stages, compared to headwater habitats, especially in the summer. The flows are largely diverted for agricultural purposes downstream of rkm 76. As temperatures become less tolerable and streamflows drop to summer base flows, sub-adult bull trout that recently migrated to middle and lower river reaches often retreated back upstream to escape intolerable conditions and find suitable habitat to over summer. With the onset of summer, elevated water temperatures and severe low flow conditions decrease habitat quality and modeled habitat quality scores (HQS) remain low throughout the summer months. Of the eleven habitat variables we used to model HQS, water temperature and surface flow heavily influenced the HQSs derived by our model for adult bull trout foraging and maintenance. Water temperature was the most influential variable on our model HQSs.

We evaluated occupancy of bull trout throughout the mainstem WWR and compared results with monthly stream temperatures. Surveys to determine foraging and migratory habitat preferences showed that stream temperatures increased moving downstream in the mainstem WWR in all months. However, the greatest rate of temperature increase occurred in July and August with temperature increasing at a rate of 2°C for every 5 rkms distance downstream. Across all years and months, we observed a decreasing probability of bull trout occupancy with distance downstream. During the July-September period, the average probability of occupancy was 3% (range: 0% - 10%) at rkm 76 (Cemetery Bridge), which is the point of main diversion for irrigation withdrawals. During the October-November period, the average probability of occupancy increased to 16% (range: 9% - 26%) at rkm 76. Across all years and months we observed a decrease in the probability of bull trout occupancy as stream temperatures increased and in any given month, bull trout occupied locations with the coolest water available.

Life-history Drivers:

Growth (Chapter 5, Appendix V)

Since survival and fecundity are often a function of fish size, individual growth rates can be necessary for population viability modeling, evaluating demographic changes, and effective conservation. In addition, estimates of individual growth are critical for assessing population change and population productivity over time and thus directly address the conservation principle of resiliency. Our goals were to evaluate individual variability and patterns in growth and to determine if growth varied between migratory and resident components of the population of bull trout that spawns in the SFWWR.

We integrated two data sources, mark-recapture data (i.e., measured change in length over time) and otolith aging (i.e., length at estimated age), to estimate growth and assess variability by individual bull trout of known life-history expression.

In previous analyses (Al-Chokhachy and Budy 2008), we determined that bull trout are relatively long lived in the SFWWR and live ≥ 9 years, similar to some adfluvial populations. However, bull trout in the SFWWR have been observed to reach sexual maturity at much smaller sizes (200 mm) and earlier ages than systems with adfluvial populations. Our results are relatively consistent with observations from Lowe Creek within the Mill Creek basin (i.e., maturity at <199 mm and as early as age 3; Sankovich et al. 2003).

Based on this synthesis of mark-recapture data, there is substantial individual variability in both growth rate and maximum potential length. In addition, and perhaps more importantly, migrants appear to reach larger sizes and grow faster than do residents, although considerable overlap between the two life-history expressions appears to occur. Growth at juvenile life stages before emigration may be slightly higher for migratory fish than for resident fish. Our study indicated that bull trout of similar sizes would move out of the headwater areas at the same times of the year and to similar areas downstream.

These results have important implications associated with connectivity and headwater spawning and rearing habitat. Larger fish have the potential to contribute disproportionately to reproductive success and population viability through their much greater fecundity (Al-Chokhachy and Budy 2008; Bowerman 2013; Chapter 9). In contrast, small, likely resident fish that spawn in the headwaters also contribute to population viability through their repeated spawning, potentially starting at earlier ages.

Movement (Chapter 6 and Appendix VI)

Migratory and dispersing bull trout require connectivity between suitable habitats to move long distances and express their full life-history. Migrations can result in individuals dispersing into new populations or habitats, therefore increasing genetic exchange between populations. For these reasons bull trout require connected habitats to persist; however, the integrity of these migration corridors is highly susceptible to disturbances from land practices, water diversion structures, and consumptive water use. Diminished connectivity limits the ability of full life-history expression (representation), dispersal from one local population to another within a core area (resiliency and redundancy), dispersal from one core area to an adjacent core area, and may result in the elimination of certain life-history strategies. Therefore diminished connectivity will lead to increased vulnerability to extinction of these bull trout populations. This and future work should determine movement behavior and spatial and temporal bottlenecks throughout the migration corridor for all life stages to assess actions to improve connectivity and effectively manage bull trout.

In previous related studies, we (Homel and Budy 2008) established that juvenile and sub-adult bull trout in the SFWWR exhibited downstream migrations year round, occurring mostly at night, and the greatest movement out of the headwaters occurred during August, however later analysis revealed that peak sub-adult out migration occurs in the spring. Migration response to environmental cues was assessed, and results suggested that minimum water temperature may influence migration timing. Bull trout appeared to migrate downstream out of the headwaters at similar sizes regardless of size at marking (i.e., surrogate for age at marking – cohort). Thus, it appears that environmental factors and/or individual intrinsic growth potential influence transition to a migratory life-history.

We evaluated the spatial and temporal movement of migratory bull trout in the SFWWR and mainstem WWR to determine if there is a life-history stage (i.e., age class) that limits population abundance and to better understand the migratory life-history diversity of the population. Generally, of the fish that migrate, the longer a bull trout reared in the headwater areas, the farther it moved downstream. Additionally, fish that migrated as juveniles and large adults generally exhibited movements of shorter distance and duration. Fish that migrated as sub-adults and small adults moved farther downstream and remained in lower parts of the watershed longer.

Adult bull trout primarily migrated upstream of Harris Park Bridge, presumably to spawn, from May through August. Adults exhibited movements downstream of Harris Park Bridge from early August through February, with the highest number of movements occurring during October. Of the bull trout that were tagged in the SFWWR and WWR, only a small number migrated downstream out of the headwaters. Of the SFWWR and WWR tagged fish that migrated, only 11% and 42%, respectively, were subsequently detected again. Of the recaptured migrating bull trout, only 18% and 31% were documented completing upstream movements after tagging. This pattern suggests that conditions in the lower and middle mainstem portions of the river may have substantial influence on survival rates and consequently affect the ability to move upstream and avoid unfavorable conditions.

Some individuals tagged in the SFWWR, WWR, and Mill Creek have been detected at the Oasis Road Bridge PIA, which suggests a migratory component in two of the five local populations. Further, PIA sites have documented connectivity and dispersal between local populations with in the WWR Core Area. WWR tagged fish have also been detected at the mouth of the Umatilla River and at mainstem Columbia River dam locations (e.g., McNary Dam). During this study, two WWR tagged fish were detected completing downstream migrations into the Columbia River and subsequently detected at or above Harris Park Bridge in the SFWWR during the spawning season.

Low flow or poor habitat conditions (Chapter 3) may compromise the ability of WWR bull trout to migrate, rear or disperse. Results suggest that the timing of unfavorable habitat conditions in the mainstem WWR may reduce the ability of bull trout that previously migrated downstream to move back upstream to rear (i.e., for juveniles migrating back to more favorable conditions) and spawn (i.e., after maturity). In particular, our movement results suggest that the migratory component of the population is primarily impacted by these unfavorable habitat conditions. The consequences of the migratory life-history expression are determined by the complex tradeoffs of greater growth and fecundity, but lower survival; fish that survive migration likely have a greater per capita contribution to population growth since they become large and likely highly fecund. Since migratory individuals likely have much higher fecundity, poor habitat conditions in migratory habitats and corridors likely impacts the resiliency of the WWR Core Area populations.

Survival

South Fork Walla Walla River Population Trend and Survival (Chapter 7, Appendices VII and VIII)

Population trend is an important vital rate that describes the cumulative effects of survival across life stages on the population. Understanding whether the trend of a population is stable, increasing, or decreasing across relevant temporal scales is key for recovery of most species listed under the ESA. Developing effective management strategies, however, also requires information regarding how extrinsic and intrinsic factors can influence population abundance and trends, preferably within a hypothesis-driven framework.

Our goal was to address this need by employing multiple years of mark-recapture data (Appendices I,II) to assess how biotic and abiotic factors influence bull trout vital rates (e.g., survival, emigration and fecundity) and ultimately population trends (e.g., population growth rates, population trend). We compliment these mark-recapture data with long-term, redd count data for a multifaceted assessment.

We estimated both survival and long-term population growth for the population of bull trout in the SFWWR based on ten years of capture-mark-recapture (CMR). We used a Pradel CMR trend model to estimate the annual rate of population change (λt) and other pertinent trend response variables for adult bull trout. When the population growth rate exceeds one, the population is increasing; when the population growth rate is less than one, the population is decreasing (noting the pattern of confidence intervals). For the Pradel model, we restricted our population of interest (potentially sexually mature) to bull trout >300 mm total length (TL). We used a Barker survival CMR model to estimate annual survival (and other pertinent vital rates) for all size classes of fish (i.e., juveniles, sub-adults, small adults, and large adults) and to test hypotheses of potential limiting factors.

Population growth rates (λt) for all adult fish combined (i.e., migratory, non-migratory, and unknown) were greater than one near the start of the time series, declined significantly until 2006-2007, but then increased for the last three years (with wide overlapping confidence intervals). There is a 1% chance the population decreased ≥ 50% (~endangered threshold), and a 5% chance the population decreased ≥ 30% (~threatened threshold). Similarly, the top Pradel population trend model for the time series including only migratory fish had an estimated median population growth rate of 0.99 (95% CI = 0.81-1.12), and this model predicted only a 5% chance the population decreased ≥ 50%, but a 22% chance they decreased ≥ 30%.

The number of bull trout redds varied considerably during the last two decades in the SFWWR, consistent with patterns from proximate populations of bull trout in the Blue Mountains, and the trend in bull trout redds during the period of our mark-recapture study (2002 to 2011), was λ = 0.97 (95% CI = 0.84-1.13). Previous studies suggested that redd counts were most similar to the abundance trends observed for large, adult bull trout; this pattern is consistent with the Pradel findings described above for migratory fish.

Survival (S) varied over time (across years) and among groups with no clear or consistent time trend. Specifically, in the top Barker models, survival rate (S) differed among three size groups of fish (< 150 mm, 150 mm-300, and > 300 mm). Based on the top-ranked models, survival (S) was the greatest for fish > 300 mm and ranged from a low around 20% in 2005-2006 to a high between 70-80% in 2007 and 2010. Survival for fish 150-300 mm bounced around 40% with highs in 2006 and 2010 and lows in 2007-2008. In previous analyses, we also estimated survival of 22% for age-1 bull trout and 23% for age-2 bull trout (Bowerman and Budy 2012). Survival rates of the smallest sized fish were the lowest, rarely exceeding 30%. The pattern of survival across time and age/size groups strongly suggests that different factors determine survival in the upper river, where small adults stay and migrate, versus the lower river, where most large fish attempt to migrate.

Bowerman and Budy (2012) observed juveniles emigrating from Skiphorton Creek, a tributary to the SFWWR, at almost all examined sizes (i.e., 80-170 mm TL) and throughout the year. Once they migrated, larger fish had a greater probability of survival in the mainstem WWR below Harris Park, than smaller individuals. Small (<200 mm TL) bull trout tagged in the SFWWR that became migratory initially exhibited growth similar to residents, but growth apparently increased as fish approached 200 mm TL. These results have important implications for assessing population status and management actions; while the population may be managed as a single reproductive unit, the phenotypic variation within this population may have fitness consequences and thus merits conservation.

From analysis of the limited time series of mark recapture data and redds, the population appears stable; however there is some indication that the population may be in decline. Redd counts are stable over the complete time series available, but appear to have declined over the more recent study period. Although Pradel model results suggest that the migratory component of the population is stable (Λ=0.99), the low proportion and low survival rates for large fish could suggest that the population is declining. Further, the time series is actually quite short and if we were comparing these observations to historical conditions, our conclusions of status may be quite different and likely more dire.

Survival Comparison for the SFWWR and WWR (Chapter 8)

Estimation of survival rates is a key element towards the development of effective conservation and recovery strategies. Evaluation of survival rates and associated variability within a population can provide critical information on how habitat conditions and phenotypic characteristics influence individual and population viability. Furthermore, increased understanding of how habitat biotic and abiotic factors (e.g., climate) influence bull trout vital rates such as survival is critical to develop effective conservation and restoration strategies.

The goal of this research was to quantify patterns of survival across size classes, locations, seasons, and years for bull trout in the lower WWR. We estimated the relative return rate, an index of survival, during two seasonal periods each year, and evaluated the effects of year, the number of days since tagging, fish length, and location on return rate. We also estimated the relative return rate on an annual basis, and made comparisons between fish that were tagged in the lower (mainstem WWR) and upper (SFWWR) sections.

Fish tagged in the spring-summer period were considerably smaller than fish tagged in the fall-winter period. Indices of survival increased with fish length and decreased with the number of days since tagging, and survival was similar across years and across locations in the lower river. Based on the size differences between the two groups and what we know from examining movement information, it appears the spring-summer fish are likely dominated by sub-adults moving downstream, rearing in the area or retreating back upstream to avoid unfavorable habitat conditions downstream. The fall-winter fish are larger sub-adults, small adults and large adults that are moving downstream to overwinter or rear in the lower river.

Within the SFWWR, tagging and recapture data were amenable to use of the Barker Model, a mark-recapture model that allows for separation of survival from detection probability and emigration rates (Chapter 7). However, for technical reasons the tagging and recapture data from the lower WWR were not amenable to use of the Barker Model. To make comparisons between the SFWWR and the WWR data sets, we calculated annual survival indices (return rates without accounting for recapture or detection probability). The advantage of the survival indices was that it allowed for comparisons between fish released in the upper and lower sections using a consistent analytical approach. The disadvantage of the survival indices is that they do not account for recapture probability and do not estimate emigration rates. As a result, the survival indices are known to be biased low to some degree. Despite this bias, the survival indices do provide a consistent analytical approach for quantifying and comparing patterns of survival for the lower (WWR) and upper (SFWWR) sections.

For both the WWR and SFWWR sections, annual survival indices generally showed a positive relationship between survival and size. However, the survival advantage of size varied across years. In some years being large provided a substantial benefit, whereas in other years survival was similar across size classes. During 2002-2010, survival rate indices for the SFWWR bull trout averaged only 9% for sub-adults and 16% for small adults. During the three years with survival rate indices throughout the river (2008-2010), the patterns of survival for fish tagged in the upper (SFWWR) and lower river were similar for fish in the sub-adult and small adult categories.

There are several important but potentially conflicting implications of these patterns in the lower river (WWR) survival indices compared to similar indices developed for the upper river (SFWWR). The lower river demonstrates a longitudinal trajectory of habitat degradation (i.e., habitat becomes more degraded farther downstream, Chapters 3 and 4) and hence it is expected that survival rate indices would be lower for fish in the lower WWR compared to fish in the SFWWR. But based on three years of data from both locations, annual survival rate indices were similar. In contrast, growth analyses (Chapter 5) indicate greater growth rates for fish from the WWR compared to fish from the SFWWR. Given the generally positive effects of fish length on survival (Chapter 8), favorable growth conditions in the lower WWR should improve survival for fish in this portion of the river. It may be that the positive effects of improved growth in the lower river (i.e., increased survival), alongside reduced survival due to habitat degradation in the lower river, cancel each other out resulting in similar survival rate indices between the upper and lower sections. Additional years of data will be required to better understand these apparently conflicting patterns of growth and survival. Although additional years of data would be useful for understanding these patterns of growth and survival, poor habitat conditions in the WWR potentially reduce the reproductive contribution of the migratory component of the population and the opportunity for dispersal. These migration and survival bottlenecks could impact the resiliency of the WWR Core Area population, and fish in these areas may also be the most likely to benefit from future management actions.

Connectivity (Biological and Genetic – Chapter 6, Appendix VIII)

With the expression of multiple life-history forms, resident and migratory bull trout from a single population tend to use a wider array of habitat types, thus reducing the risk of extirpation from local disturbances. In addition, this diversity of life-history expression affords bull trout the opportunity to access a greater amount of food resources. For bull trout, resident and migratory life-history forms co-occur in streams and demonstrate important differences in growth, movement patterns, and survival (as described above). Fish that migrate tend to grow larger, move farther stream distances, but have lower survival rates as compared to their resident form. Despite these differences in vital rates and behavior, there are no discernable differences in genetic structure between presumed resident and migratory fish within the SFWWR population were observed based on microsatellite loci (Appendix VIII). Moreover, environmental factors and individual intrinsic growth potential likely influence transition to a migratory life-history (Chapters 5 and 6) and the consequences of that behavior.

During the study we documented connectivity between local populations within the WWR Core Area (i.e., Mill Creek fish in SFWWR); a small number of tagged fish completed migrations into the Columbia River and subsequently returned to be detected in the spawning area of the SFWWR. Additionally, a number of individuals were observed migrating between local populations within the WWR Core Area. When considered within the context of genetic structure, there are several lines of evidence demonstrating that bull trout in the WWR Core Area still attempt to disperse among the local populations (e.g., genetic and movement data). Improving habitat conditions to restore connectivity among local populations is key to the maintaining redundancy and supporting resilency of bull trout in the WWR Core Area.

Population Trend and Metapopulation Dynamics (Chapters 6, 9, and Appendix V):

Information on growth, survival, reproductive rates, movement, and abundance was incorporated into a life-cycle model for both resident and migratory life-history strategies of bull trout. This model was used to evaluate how populations might respond to changes in demographic rates as a result of management actions, environmental variability, or climate change. Based on perturbations to this life-cycle model, changes in juvenile survival rates and maturity schedules had the largest influence on overall population trend. Bull trout populations composed of individuals that spawned earlier in their life cycle and grew more slowly (resident life-history strategy) were more vulnerable to changes in reproductive success (e.g., egg survival). In contrast, populations composed of late-maturing individuals that grew to larger sizes (migratory life-history strategy) were more vulnerable to changes in adult survival rates (e.g., via harvest or predation).

We observed a few instances of bull trout migrating from one population to another, from which we estimated rates of dispersal among distant patches. The potential for individuals to disperse, or move from one population into another to reproduce, was important to sustain declining populations when neighboring populations were stable. Improvements to the migration corridor are also required to allow for longer migrations and dispersal among sub-populations.

In sum, this research and modeling collectively demonstrate that diversity in life-history strategies can help stabilize demographic responses to environmental perturbations, which may help decrease the risk of extirpation for both individual local populations and core area populations (i.e., metapopulation). Maintaining a diversity of life-history expression requires preservation of headwater conditions in the SFWWR and improvements to the connectivity and habitat conditions in the migration corridor; thus allowing access to habitats throughout the entire watershed to maintain all complex life cycle components (contributing to redundancy and resiliency).

.

Literature Cited

Al-Chokhachy, R., and P. Budy. 2008. Demographic characteristics, population structure, and vital rates of a fluvial population of bull trout in Oregon. Transactions of the American Fisheries Society 137:1709-1722.

Bowerman, T. and P. Budy. 2012. Incorporating movement patterns to improve survival estimates for juvenile bull trout. North American Journal of Fisheries Management 32(6): 1123-1136.

Bowerman, T. 2013. A multi-scale investigation of factors limiting bull trout viability. Doctoral dissertation, Utah State University, Logan, Utah.

Faber-Langendoen, D., L. Master, J. Nichols, K. Snow, A. Tomaino, R. Bittman, G. Hammerson, B. Heidel, L. Ramsay, and B. Young. 2009. NatureServe conservation status assessments: methodology for assigning ranks. NatureServe, Arlington, Virginia.

Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology, and population status of migratory bull trout (Salvelinus confluentus) in the Flathead Lake and River system, Montana. Northwest Science 63:133-143.

Homel, K., and P. Budy. 2008. Temporal and spatial variability in the migration patterns of juvenile and subadult bull trout in northeastern Oregon. Transactions of the American Fisheries Society 137(3):869-880.

Isaak, D. J., Luce, C. H., Rieman, B. E., Nagel, D. E., Peterson, E. E., Horan, D. L., Parkes, S. and Chandler, G. L. 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. Ecological Applications 20(5): 1350-1371.

National Marine Fisheries Service (NMFS). 2010. Interim endangered and threatened species recovery planning guidance version 1.3. NMFS, Silver Springs, MD. Available from http://www.nmfs.noaa.gov/pr/pdfs/recovery/guidance.pdf.

Porter, M., and D.R. Marmorek. 2005. Bull Trout Recovery Monitoring and Evaluation Technical Working Group (RMEG) Workshop 3 (Dec. 16-17, 2004) USFS Regional Office, 333 SW

First Ave., Portland, Oregon – Workshop Report, Report prepared by ESSA Technologies Limited., Vancouver, BC for the US Fish and Wildlife Service, Vancouver, Washington. 113 pp.

Post, J.R., C.J. Mushens, A.J. Paul and M. Sullivan. 2003. Assessment of alternative management strategies for sustaining recreational fisheries: model development and application to bull trout, Salvelinus confluentus. North American Journal of Fisheries Management 23:22-34.

Sankovich, P. M., Gunckel, S. L., Hemmingsen, A. R., Tattam, I. A., & Howell, P. J. 2003. Migratory patterns, structure, abundance, and status of bull trout populations from subbasins in the Columbia Plateau. 2002 Annual Report. Project, 199405400.

U.S. Fish and Wildlife Service (USFWS). 2002. Chapter 10, Draft Umatilla-Walla Walla Recovery Unit, Oregon and Washington. In: U.S. Fish and Wildlife Service, Bull Trout (Salvelinus confluentus) Draft Recovery Plan. Portland, Oregon. 149pp.

U.S. Fish and Wildlife Service (USFWS). 2008. Bull Trout Recovery: Monitoring and Evaluation Guidance. Report prepared for the U.S. Fish and Wildlife Service by the Bull Trout Recovery and Monitoring Technical Group (RMEG). Portland, Oregon. version 1. 74 pp.

U.S. Fish and Wildlife Service (USFWS). 2012. Bull Trout Recovery: Monitoring and Evaluation Guidance, Volume II. Draft Report prepared for the U.S. Fish and Wildlife Service by the Bull Trout Recovery and Monitoring Technical Group (RMEG). Portland, Oregon. 126 pp.

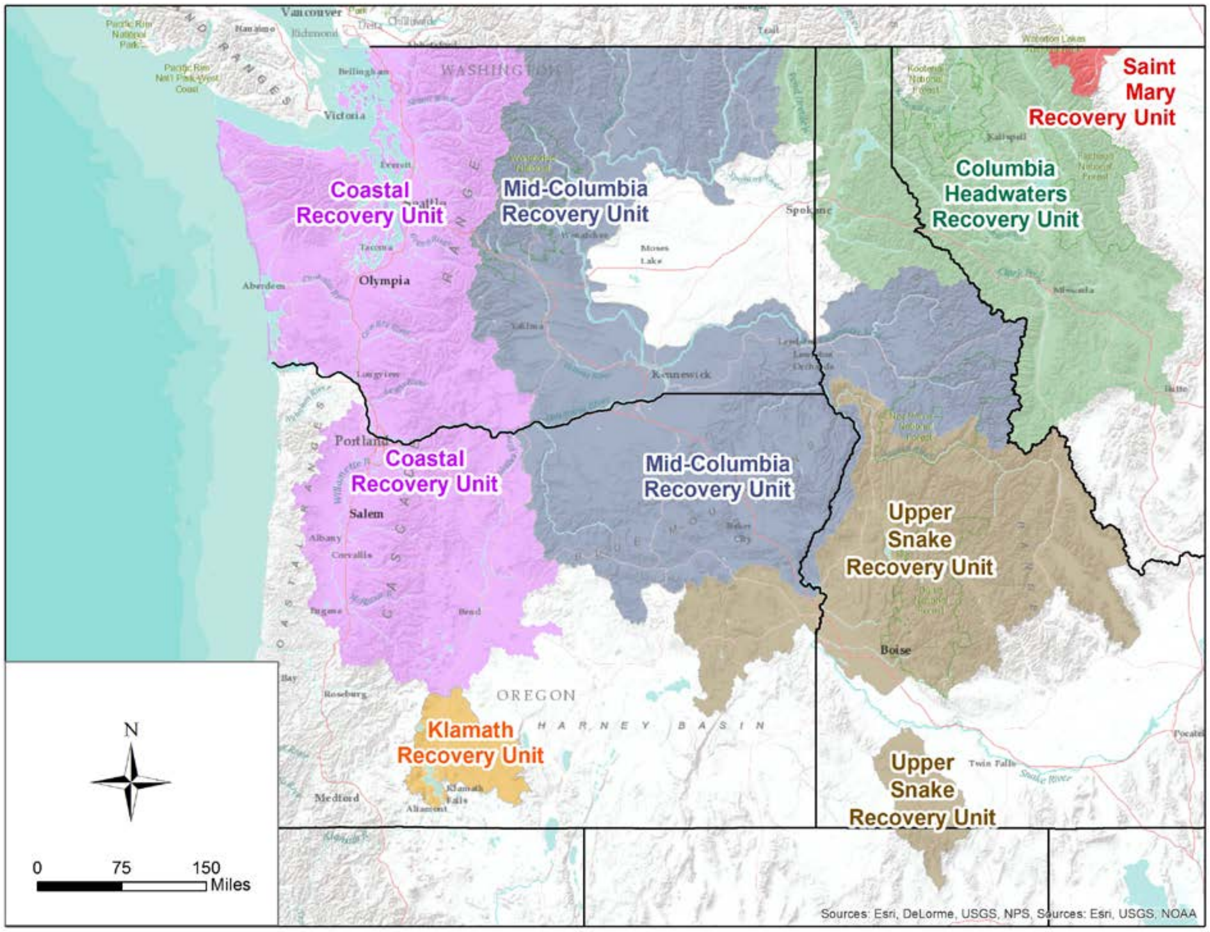

Figure 1.1. Coterminous distinct population segment (DPS) for bull trout and the six recovery units.

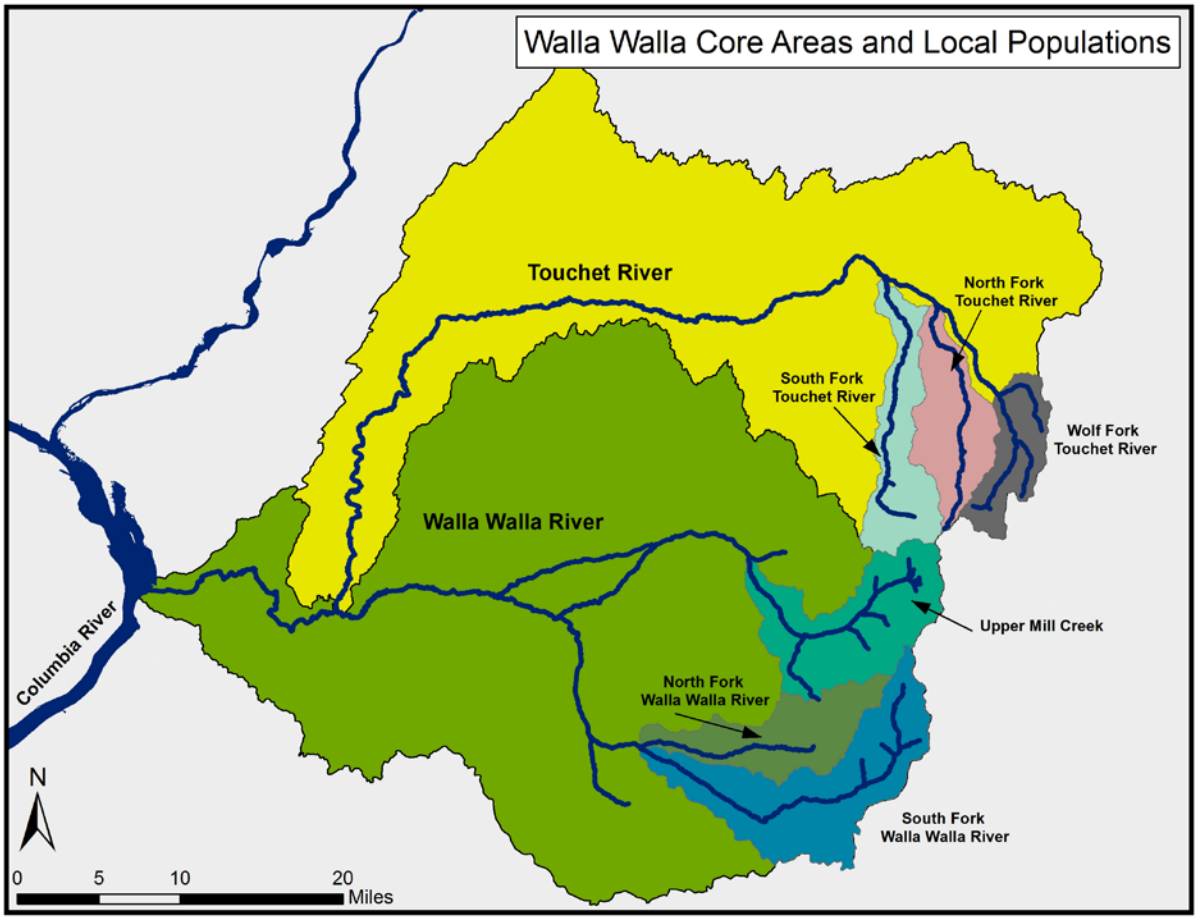

Figure 1.2. Walla Walla River Basin displaying the two identified core areas; the Touchet River (yellow) and the Walla Walla River (green). Each core area has three local populations.

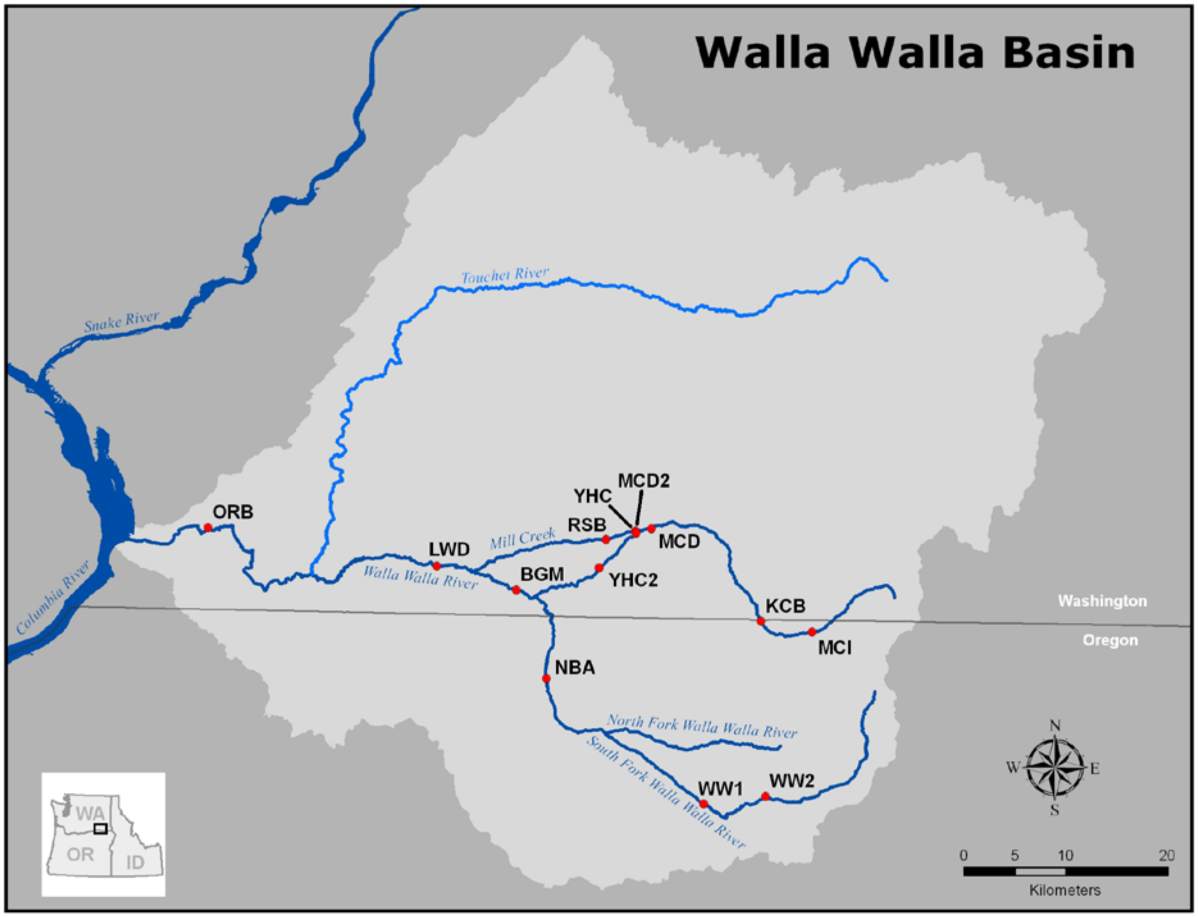

Figure 1.3. Walla Walla River passive instream antenna sites. Site locations are identified in Appendix I.

Chapter 2 : Chapter Summaries

Here we provide a more detailed summary for each of the chapters and appendices. Each of the following chapter summaries are organized by: 1) the draft recovery plan objectives they inform; 2) the study justification and how each topic addresses recovery criteria guidance; 3) goal and methods; and 4) key findings and considerations for applications to other basins.

Chapter 3: Walla Walla Basin Bull Trout Habitat Quality Assessment

Chapter 3 addresses this objective in the draft Recovery Plan:

- Restore and maintain suitable habitat conditions for all bull trout life-history stages and strategies (element of connectivity).

Effective management of threatened species requires sufficient knowledge of their fundamental habitat requirements and the ability to assess the quality of available habitat, particularly for species occurring in intensively managed and modified landscapes. Walla Walla River bull trout exhibit a continuum of life histories involving movements, migrations, spawning, rearing and foraging on time scales ranging from daily to annually or longer, and over different spatial scales. While the resident component of a population only experiences relatively pristine headwater conditions, migratory bull trout may be exposed to a spectrum of anthropogenic channel modifications, riparian habitat degradation, streamflow depletion and regulation, passage barriers, and other influences throughout the Walla basin and in the mainstem Columbia River.

Our goal was to develop a simple, adaptable and fundamentally straightforward approach to assessing aquatic habitat quality at the reach-scale in the SFWWR, mainstem WWR, and the Mill Creek subbasin to help inform recovery actions explicitly for bull trout.

- We developed a model to spatially and temporally identify and rate the quality of bull trout habitat at the reach-scale in the SFWWR and mainstem WWR as well as Mill and Yellowhawk creeks with respect to each bull trout life-history stage and strategy. The output from this model should be used as a “first cut” tool when determining potential sites for habitat restoration or the implementation of future management actions.

- Our approach can be used to help inform current and future recovery actions explicitly for bull trout within the Walla Walla Basin. In addition, our approach is widely applicable to other basins for informing bull trout recovery. Overall, our approach informs how and where to restore and maintain suitable habitat conditions for all bull trout life-history stages and strategies (element of connectivity) and addresses the conservation principles of resiliency and redundancy.

Model development included delineating the study area into 22 largely homogenous river reaches using specific attributes and relatively distinct breaks in channel morphology, hydrological channel junctions and habitat structure. We selected 11 variables to include in the model that we believed to influence the quality of bull trout habitat. We used the findings from recent studies, empirical data and professional opinion to make well-reasoned judgments toward crafting simple rating criteria to characterize the quality of each habitat variable monthly for each reach and in relation to each of eight life stages (Table 2.3), life-history strategies and behavior exhibited by bull trout in the WWR and its tributaries. A monthly habitat quality score

(HQS) was derived for each reach and for each of the life stages, strategies and actions. Habitat scores were compared with temporal and spatial bull trout occurrence information and used to help assess and describe the quality of habitat for bull trout throughout the study area. Habitat scores can be used to inform potential sites for habitat restoration, implementation of future management actions, or in conjunction with smaller scale (e.g., micro-scale) habitat models and empirical data to assess or quantify habitat within reaches.

Model scores suggest that the quality of habitat for most bull trout life stages, strategies and actions is generally better in headwater reaches and degrades incrementally downstream from the Umatilla National Forest boundary as the severity and often cumulative anthropogenic modifications and other influences become more prevalent. While the resident component of the population only experiences headwater conditions, migratory bull trout may be exposed to a spectrum of anthropogenic channel modifications, riparian habitat degradation, varying levels of streamflow depletion and regulations, and other influences throughout the basin and in the mainstem Columbia River. In the middle and lower WWR, as flows decrease and are largely diverted for agricultural purposes and water temperatures elevate, habitat conditions become progressively less favorable for most bull trout uses. We can use the analyses and model scores to summarize habitat conditions in the migratory corridor for each bull trout life stage. Poor and low quality habitat conditions for juvenile, sub-adult and adult bull trout movements, migrations, rearing and foraging develop seasonally in up to 79% of the linear distance of the migratory corridor and primarily downstream from reach WW6 (rkm 75) for up to 28% of the year (Table 2.1). The timing and severity of poor or low quality habitat conditions vary spatially and temporally and are relative to each life-history stage, strategy or action. Poor and low quality habitat conditions primarily develop due to extensive anthropogenic modifications to the riverscape and the over-allocation of water resources for agriculture between June and October and persist in some reaches for up to six months. Reaches downstream of WW6 in the mainstem WWR consistently were assigned scores indicating poor and low habitat conditions for most bull trout life stages and strategies from approximately July through October. Of these reaches, WW11 (rkm 55) consistently scored the lowest of all reaches in the mainstem WWR River during the summer and early fall months.

Table 2.1. Summary of poor and low habitat quality conditions for bull trout in the SFWWR and mainstem WWR. Habitat quality scores of ≤ 1.8 and > 1.8 - 2.6 are considered to be of poor and low quality respectively.

Reach	Length (km)	Proportion	Life Stage													
			Juvenile		sub-adult						Adult					
			Rearing		Rearing		DS Migration		US Migration		Rearing		DS Migration		US Migration	
			Score	Months	Score	Months	Score	Months	Score	Months	Score	Months	Score	Months	Score	Months
SFWW1	9.8	0.078														
SFWW2	20.1	0.160														
SFWW3*	12.6	0.100														
WW4*	4.8	0.038														
WW5*	3.0	0.024														
WW6*	2.0	0.016							2.44	1					2.60	1
WW7*	3.8	0.030			10.50	5	11.05	5	8.49	4	10.74	5	11.09	5	13.63	6
WW8*	6.4	0.051	6.79	3	4.29	2	6.55	3	6.05	3	4.40	2	8.92	4	11.02	5
WW9*	2.6	0.021	4.86	2	4.93	2	4.76	2	4.58	2	2.41	1	4.76	2	4.74	2
WW10*	5.6	0.045	7.13	3	4.67	2	4.60	2	4.41	2	4.79	2	4.60	2	6.99	3
WW11*	23.5	0.187	7.18	4	8.46	4	8.58	4	8.03	4	8.47	4	8.17	4	8.12	4
WW12*	23.3	0.186	8.94	4	6.69	3	2.41	1	7.37	3	6.84	3	7.57	3	2.49	1
WW13*	8.0	0.064	8.70	4	6.68	3	2.44	1	7.53	3	6.82	3	2.43	1	2.53	1
Mig. Corridor (Total)	**95.6**	**0.762**	**43.61**	**20**	**46.21**	**21**	**40.39**	**18**	**48.90**	**22**	**44.47**	**20**	**47.53**	**21**	**52.12**	**23**
WW Basin (Total)	**125.5**	**1.000**	**43.61**	**20**	**46.21**	**21**	**40.39**	**18**	**48.90**	**22**	**44.47**	**20**	**47.53**	**21**	**52.12**	**23**
Average Score for Low-poor Conditions (Migratory Corridor)			**2.18**		**2.20**		**2.24**		**2.22**		**2.22**		**2.26**		**2.27**	
% Migr. Corr. Exhibiting low-poor conditions (Linear Distance)			**73%**		**77%**		**77%**		**79%**		**77%**		**77%**		**79%**	
% of the Migr. Corr. in low-poor condition (% of the year)			**28%**		**25%**		**21%**		**23%**		**24%**		**25%**		**27%**	

* Indicates reach within the migratory corridor

We used datasets resulting from our extensive network of PIT tag detection arrays in addition to data from radio telemetry, snorkeling, acoustic telemetry, electrofishing, trapping and angling studies to summarize spatial and temporal occurrence with respect to the identified strategies and actions exhibited by the various life stages of bull trout within the WWR (Table 2.2). Juveniles rear during all months in the upper three percent of the basin while sub-adult and adult foraging is common during most months and in most reaches with the exception of summer months downstream of Nursery Bridge Dam (rkm 73). Sub-adults migrate downstream through most reaches during most months upstream of Nursery Bridge Dam, with notable peaks in the spring and fall. Both adult and sub-adult downstream migration commonly occurs incrementally into lower WWR reaches during the fall and winter months when streamflows increase from summer base flows and as water temperatures decline. Fluvial adult bull trout begin moving upstream from lower Basin reaches towards headwater spawning areas in March, continuing through June, and occasionally into July. Movement from mid-Basin reaches into the headwater spawning areas occurs from June through September. In addition, sub-adults that previously dispersed downstream during spring and early summer months to middle and lower WWR reaches often move back upstream to more tolerable habitat as conditions progressively deteriorate downstream of reach WW5 in the WWR.

Table 2.2. High, low and no occurrence for bull trout in the SFWWR and mainstem WWR. Reaches where monthly occurrence is high, low or no occurrence were assigned scores of 2, 1 and 0, respectively.

Reach	Length km	Proportion	Life Stage													
			Juvenile		Sub-adult						Adult					
			Rearing		Rearing		DS Migration		US Migration		Rearing		DS Migration		US Migration	
			Score	Months	Score	Months	Score	Months	Score	Months	Score	Months	Score	Months	Score	Months
SFWW1	9.8	0.078	24	12	24	12	20	12	0	0	24	12	5	3	4	2
SFWW2	20.1	0.160	24	12	24	12	20	12	0	0	24	12	5	3	7	4
SFWW3*	12.6	0.100	12	12	24	12	19	12	0	0	23	12	8	5	6	3
WW4*	4.8	0.038	0	0	24	12	19	12	0	0	23	12	8	5	7	4
WW5*	3.0	0.024	0	0	24	12	19	12	5	3	22	12	8	5	7	4
WW6*	2.0	0.016	0	0	24	12	20	12	5	3	21	12	9	6	6	3
WW7*	3.8	0.030	0	0	24	12	20	12	5	3	20	11	9	6	5	3
WW8*	6.4	0.051	0	0	23	12	19	12	5	3	20	11	10	6	5	3
WW9*	2.6	0.021	0	0	20	11	18	11	6	4	20	11	9	6	5	3
WW10*	5.6	0.045	0	0	19	10	14	10	8	5	18	10	9	5	6	4
WW11*	23.5	0.187	0	0	19	10	15	10	8	6	16	9	9	5	5	4
WW12*	23.3	0.186	0	0	18	9	10	5	6	4	16	9	9	5	5	4
WW13*	8.0	0.064	0	0	18	9	10	5	6	4	16	9	9	5	5	4
Migr Corr. (Total)	**95.6**	**0.762**	**12**	**12**	**237**	**121**	**183**	**113**	**54**	**35**	**215**	**118**	**97**	**59**	**62**	**39**
WW Basin (Total)	**125.5**	**1.000**	**60**	**36**	**285**	**145**	**223**	**137**	**54**	**35**	**263**	**142**	**107**	**65**	**73**	**45**
Average Score for Bull Trout Occurrence (Migratory Corridor)			**1.00**		**1.96**		**1.62**		**1.54**		**1.82**		**1.64**		**1.59**	
Bull Trout Occurrence in the Migratory Corridor (% of Linear Distance)			**13%**		**100%**		**100%**		**100%**		**100%**		**100%**		**100%**	
Bull Trout Occurrence in the Migratory Corridor (% of the year)			**9%**		**92%**		**86%**		**27%**		**89%**		**45%**		**30%**	

* Indicates reach within the migratory corridor

Poor and low quality habitat conditions may inhibit survival or compromise the ability of a bull trout of a given life stage to migrate, rear or disperse. By characterizing instream habitat by reach and identifying when and where poor and low quality habitat conditions interface with bull trout occurrence within the basin, we can provide managers with useful information to inform future conservation actions or initiate additional studies that target the particular bull trout life stage or strategy of concern. We found that mean HQSs are usually higher when bull trout occurrence is high and lower when occurrence is low for most life stages and strategies (Table 2.3). Mean HQSs are usually lowest for each life stage and action when there is no observed occurrence. For example, mean HQSs for high, low and no occurrence for adult bull trout foraging and maintenance in the SFWWR and mainstem WWR were 3.74 (95% CI, 3.67-3.82), 2.93 (95% CI, 2.66-3.20) and 2.30 (95% CI, 2.13-2.46), respectively (Figure 2.1). One exception was the inverse relationship between mean HQS and the level of bull trout occurrence for fluvial sub-adult upstream migration. The mean HQSs for fluvial sub-adult upstream migration were higher when there is no or low occurrence and HQSs were lowest when occurrence was high (Figure 2.1). This relationship was expected since sub-adults often move back upstream to more favorable habitat in response to deteriorating downstream habitat conditions.

We have documented that flows are largely diverted for agricultural purposes and water temperatures are elevated in the middle and lower WWR. The EPA has recommended water temperature standards to protect bull trout during various life stages and strategies that include upper optimum thresholds of 9°C (7 Day Average of Daily Maximum (7DADM)) for spawning, 12°C 7DADM for juvenile rearing and 16°C 7DADM for foraging and migration. Our modeling results demonstrate that thermal habitat conditions become progressively less favorable for most bull trout life stages; moving from the headwaters to the middle and lower mainstem sections of the WWR. As temperatures become less tolerable and stream flows drop to summer base flows, sub-adult bull trout that had recently migrated to middle and lower river reaches often retreat back upstream to escape intolerable conditions and find suitable habitat to over summer. Habitat quality scores for upstream sub-adult movement are primarily good from reach WW6 to WW13 during May, but scores decline to fair in June and to low and poor in July and August. With the onset of summer, elevated water temperatures and extreme low flow conditions decrease habitat quality and HQSs remain low throughout the summer months. Of the eleven habitat variables we modeled, water temperature and surface flow heavily influenced the HQSs derived by our model for adult bull trout foraging and maintenance. Water temperature was the most influential variable on our model HQSs. Declining instream surface flows during June and warmer water temperatures decrease HQSs to fair quality before habitat conditions deteriorate to low quality during July and August. In September, as water temperatures decrease, HQSs for reaches WW8 through WW10 increase to fair, but the quality of habitat remains poor from WW11 to WW13 until October and November.

Table 2.3. Mean HQSs for high, low and no bull trout occurrence when conceivable in the SFWWR and mainstem WWR, Mill Creek and Yellowhawk Creek for each life stage, strategy or action.

		High Occurrence		Low Occurrence		No Occurrence	
Bull Trout Life Stage, Strategy or Action	**Conceivable Occurrence (# Months)**	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**
SFWWR and mainstem WWR							
Spawning	Aug - Nov (4)	4.32	4.1 - 4.53	NA	NA	2.65	2.39 - 2.91
Juvenile Rearing, Foraging and Growth	Jan - Dec (12)	4.28	4.2 - 4.36	4.24	4.14 - 4.34	3.32	3.20 - 3.43
Fluvial Adult Upstream Migration	Mar - Oct (8)	3.70	3.49 - 3.91	3.28	2.90 - 3.65	3.17	3.0 - 3.35
Adult Foraging and Maintenance	Jan - Dec (12)	3.74	3.67 - 3.82	2.93	2.66 - 3.20	2.30	2.13 - 2.46
Fluvial Adult Downstream Migration	Aug - Feb (7)	3.69	3.5 - 3.89	3.78	3.55 - 4.00	3.34	2.99 - 3.68
Fluvial Sub-adult Downstream Migration	Jan - Dec (12)	3.82	3.69 - 3.95	3.62	3.4 - 3.83	3.09	2.74 - 3.44
Fluvial Sub-adult Upstream Movement	Mar - Aug (6)	2.93	2.55 - 3.31	3.41	2.94 - 3.87	4.04	3.86 - 4.22
Fluvial Sub-adult Rearing, Foraging and Growth	Jan - Dec (12)	3.45	3.36 - 3.53	2.25	2.02 - 2.48	2.37	2.15 - 2.59

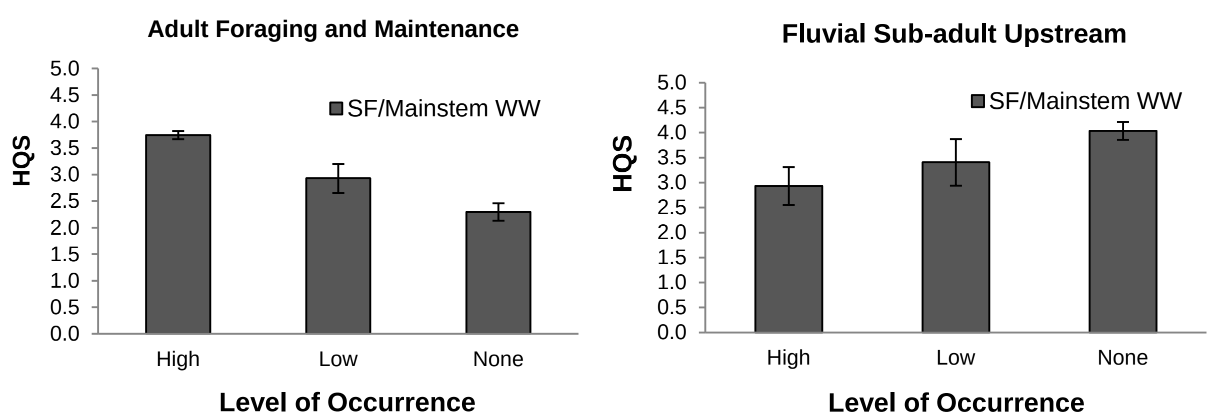

Figure 2.1. Mean habitat quality scores when occurrence of adult foraging and maintenance (left) and fluvial sub-adult upstream migration (right) are high, low and not observed during time periods when occurrence is conceivable in the SFWWR and mainstem WWR.

Habitat variation exists at a variety of spatial and temporal scales, requiring habitat quality to be assessed at multiple scales as well. Therefore, the output from this model should be used as a “first cut” tool when determining potential sites for habitat restoration or the implementation of future management actions to work toward bull trout recovery. Due to the simplicity of this approach, this model should be applicable to assess habitat for bull trout in other basins or river systems. The Umatilla River in northeastern Oregon is one example of many basins in the Pacific Northwest where the application of this habitat assessment approach may be useful for managers to help address similar population connectivity, water diversion and habitat modification issues that impact bull trout recovery.

Chapter 4: Spawning, Foraging, and Migratory Habitat Use of Bull Trout in the South Fork Walla Walla River

Chapter 4 addresses this objective in the draft Recovery Plan:

- Restore and maintain suitable habitat conditions for all bull trout life-history stages and strategies (element of connectivity).

Bull trout exhibit resident and migratory life-history forms. Although bull trout typically spawn in relatively pristine habitat, there are basins where land development is encroaching on spawning habitat and bull trout production is limited. Understanding spawning habitat relationships for resident and migratory bull trout is critical for guiding the recovery of the species and will allow managers to quantify the amount of suitable spawning habitat, identify locations of suitable and non-suitable spawning habitat, characterize the features of suitable spawning habitat, and determine if spawning habitat may be limiting production.

Similarly, the management and recovery of bull trout populations requires a comprehensive understanding of rearing habitat use across different systems, life stages, and life-history forms. Here, the goal was to develop predictive models to assess resident and migratory bull trout spawning and rearing habitat in the SFWWR. In addition, we assessed patterns of foraging and migratory habitat use in the lower WWR.

- We developed predictive microhabitat models to improve the understanding of spawning habitat needs for bull trout. The output from these models can provide quantitative tools to assess the quantity, quality, and location of suitable spawning habitat by life-history form, and help inform habitat restoration and future management actions. The development of predictive spawning habitat models can be useful for assessing spawning habitat conditions in other basins that have not been monitored intensively.

- We used empirical data to evaluate diel differences in microhabitat use, the consistency of microhabitat use across systems and size-classes based on preference, and our ability to predict rearing bull trout microhabitat use. Developing and testing predictive models across systems provides insight into the transferability of rearing microhabitat models and can inform effective restoration actions and management strategies.

- We quantified seasonal patterns of foraging and migratory habitat use and examined associations with water temperature and location (rkm) in the lower WWR. These analyses help quantify the thermal tolerances, streamflow limitation, and preferences of bull trout for foraging and migratory habitat.

We developed the predictive spawning habitat model using empirical data collected at bull trout spawning redds and at sites where redds did not occur in the SFWWR. We categorized redds into small, medium and large sizes to represent resident, a mix of resident and migratory, and migratory bull trout. We used logistic regression to predict the presence of each redd size class as a function of measured habitat variables (water depth, velocity, and substrate size). Next, we collected rearing microhabitat use and availability data in three fluvial populations of bull trout in eastern Oregon. We used a one-way analysis of variance to test for diel differences in microhabitat use. We used habitat use and availability data to calculate juvenile and adult bull trout habitat preference values. Lastly, we evaluated the influence of microhabitat factors on juvenile and adult bull trout presence using logistic regression.

Bull trout displayed high selection for small gravel and pebble substrates across all three redd size classes (e.g., small, medium, large; Figure 2.2). As redd size class decreased, bull trout increasingly selected smaller substrates. Locations with cobble or boulder substrates were unsuitable across all three size classes. For the medium and large redd size classes, slower water velocities were associated with increased spawning habitat suitability, with the highest suitability for large redds at locations with water velocity less than 0.5 m/s and for medium redds at locations with water velocities less than 1.0 m/s. Depth had little effect on spawning habitat suitability for both the medium and large redd size classes, although the medium redd size class did indicate a slight decrease in suitability at shallow locations less than 0.2 m.

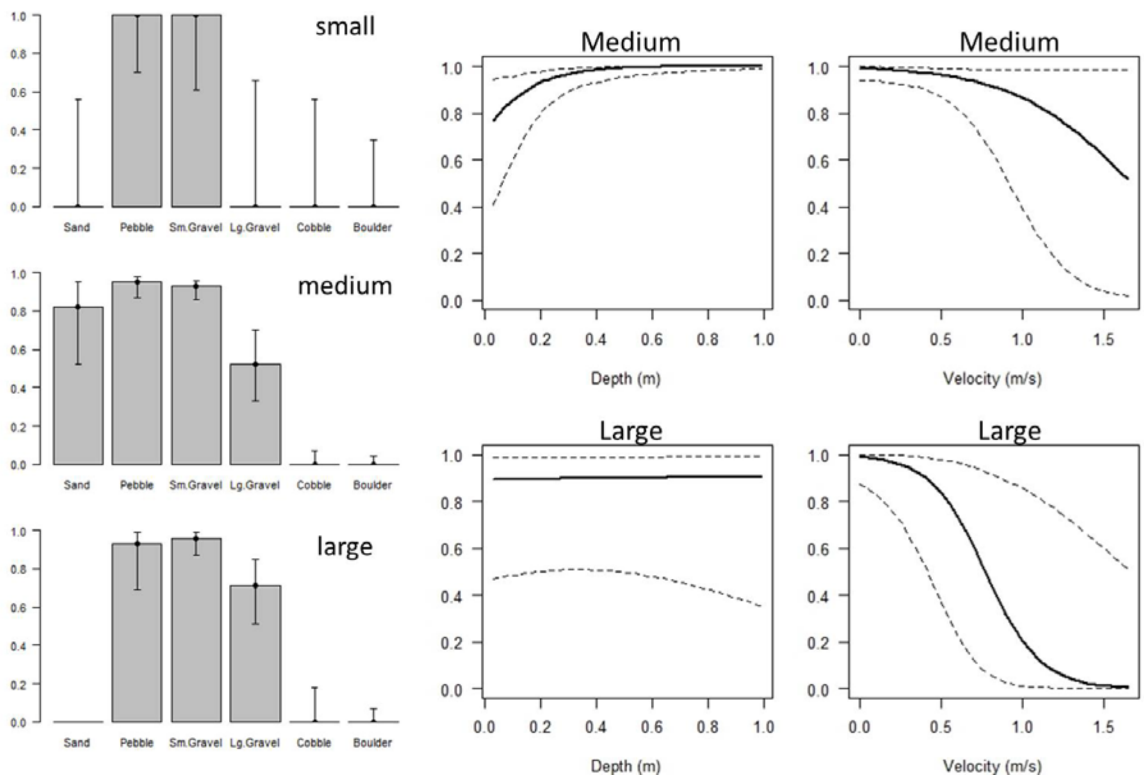

Figure 2.2. (Left panel) Relative probability of spawning habitat use by substrate category for small, medium, and large redd size classes. (Right panel) Relative probability of spawning habitat use for the medium and large redd size classes versus water depth and water velocity.

Diel comparisons suggested rearing bull trout use deeper microhabitats with cover during daytime periods but shift into significantly slower habitats during nighttime periods; however, we observed no discrete differences in substrate use patterns across diel periods. Across life stages, we found that both juvenile and adult bull trout used slow velocity microhabitats with cover, but the use of specific types varied. Both logistic regression and habitat preference analyses suggested that adult bull trout used deeper habitats than juveniles. Habitat preference analyses suggested that bull trout habitat use was consistent across the three populations we evaluated, where chi-square tests rejected the null hypotheses that microhabitats were used in proportion to those available. Validation analyses indicated that the logistic regression models (juvenile and adult) were effective at predicting bull trout abscence across all tests; however, our ability to accurately predict bull trout presence was limited.

Surveys to determine foraging and migratory habitat preferences showed that stream temperatures increased moving downstream in the mainstem WWR in all months. However, the greatest rate of temperature increase occurred in July and August with temperature increasing at a rate of 2°C for every 5 rkms distance downstream. Across all years and months, we observed a decreasing probability of bull trout occupancy with distance downstream. During the July-September period, the average probability of occupancy was 3% (range: 0% - 10%) at rkm 76 (Cemetery Bridge), which is the point of main diversion for irrigation withdrawals. During the October-November period, the average probability of occupancy increased to 16% (range: 9% - 26%) at rkm 76. Across all years and months we observed a decrease in the probability of bull trout occupancy as stream temperatures increased and in any given month, bull trout occupied locations with the coolest water available. These results indicate that focusing on activities to improve stream temperature conditions in the mainstem WWR will be integral for restoring the migratory component and improving the resiliency of the WWR Core Area bull trout populations.

Our results highlight the limitations of the models used to predict rearing microhabitat use for fish species like bull trout, which occur at naturally low densities. However, our results also demonstrate that bull trout microhabitat use patterns are generally consistent across systems, a pattern that parallels observations at both similar and larger scales and across life-history forms. Thus, our results, in combination with previous bull trout habitat studies, provide managers with benchmarks for restoration in highly degraded systems.

Chapter 5: Growth of Bull Trout from the South Fork Walla Walla River: an Assessment of Individual Variability and Differences between Resident and Migratory Life-history Forms

Chapter 5 addresses this objective in the draft Recovery Plan:

- Estimate rates and variability in growth for this population of bull trout.

Since survival and fecundity are often a function of fish size, growth rates can be necessary for population viability modeling, evaluating demographic changes, and effective conservation. Fish growth is commonly assessed using a von Bertalanffy growth model, which estimates two parameters (asymptotic length L_∞ and the growth coefficient k) that describe growth over the lifetime of a fish. Bull trout that spawn in the SFWWR exhibit variability in life-history, migratory patterns, and demographic rates. Both resident and migratory life-history forms are thought to be vital to the persistence of this bull trout population and the two forms appear to have differential growth rates. Accounting for variability (i.e., individual and by life-history form) is critical for estimating appropriate growth parameters with suitable uncertainty to be used as input values for population viability modeling.

Our goals were to determine if growth varied between migratory and resident components, to evaluate individual variability and patterns in growth, and to estimate von Bertalanffy growth parameters for the SFWWR local population of bull trout.

- We integrated two data sources (mark-recapture, otoliths) to estimate von Bertalanffy growth parameters and assess variability (by individual and life-history form) for this population of bull trout.

- Estimates of growth are critical for assessing population change and population productivity over time and thus directly address the conservation principle of resiliency. It is still unclear whether genetics, environmental factors, or both affect the probability of initiating a migratory life-history. Although studies have not detected a genetic link, it is thought that both life-history forms are needed for population persistence; thus, this work also addresses the conservation principle of representation.

Individual bull trout were PIT-tagged, detected at various locations in the WWR, and recaptured, from 2002-2011, allowing assessment of individual growth and growth as a function of life-history form. We examined growth by change-in-length overtime for migrants and residents, as well as by back-calculated length at age for otoliths from bull trout with unknown migratory status. We fit hierarchical von Bertalanffy growth models for both methods (i.e., mark-recapture and otolith data) separately and then using an integrated model. We evaluated the need to describe individual variability in growth parameters as well as differences between residents and migrants using an information theoretic approach. All models were fit using Bayesian methods with vague priors. We assessed growth and produced growth parameters to be used in future population modeling.

We included data from 253 recaptured individuals with known migratory status and 36 otoliths with unknown status. The selected model included individual variability in both growth parameters, but not differences between life-history forms. The two field methods assessed growth slightly differently, with mark-recapture data suggesting a lower population-level asymptotic length (UL_∞) and a higher population-level growth coefficient (Uk) than back-calculation by otoliths. In addition, mark-recapture data suggested substantial individual variability in both asymptotic length (σ_{L_∞}) and growth rate (σ_k), whereas, otolith data only suggested variability in asymptotic length. The combined model produced parameter estimates that were intermediate between the two methods (Table 2.4). Estimates of length-at-age can be calculated by the following equation: Length = $UL_\infty *$ (1-EXP(-Uk* (Age$-Ut_0$))), where length is in mm FL and age is in years.

Table 2.4. Von Bertalanffy growth parameter estimates from multiple data sources.

Parameter	Mark Recapture (n = 124 R, 88 M)	Otoliths (n = 36)	Combined (n = 289)
UL_∞	403 (378 – 431)	639 (545 – 766)	479 (443 – 536)
σ_{L_∞}	95 (82 – 110)	130 (95 – 182)	120 (102 – 143)
Uk	0.76 (0.61 – 0.95)	0.13 (0.10-0.16)	0.38 (0.27 – 0.47)
σ_k	0.28 (0.19 – 0.39)	0.01 (0.00 – 0.02)	0.12 (0.06 – 0.18)
Ut_0 or t_0	-0.05 (-0.05 – -0.04)	-0.37 (-0.54 – -0.22)	0.04 (-0.08 – 0.16)
σ_{t_0}	NA	0.20 (0.11 – 0.32)	NA

Migrants appear to reach larger sizes and approach those maxima faster than do residents, although considerable overlap appears to occur (Figure 2.3). The mean estimate of L_∞ for migrants (median: 559, 95%: 514-625) was over 100 mm FL higher than that for residents (median: 436, 95%: 405-491), and 95% credible intervals did not overlap. The mean estimate for k was also higher for migrants (median: 0.44, 95%: 0.29-0.55), than for residents (median: 0.36, 95%: 0.26-0.44), but 95% credible intervals did overlap. Migrants emigrated at lengths up to ~200 mm FL (expected ages >1 to 3) and may not return until reaching ~400 mm FL (expected ages 4-5). The average resident was not expected to reach 400 mm FL until age 8-9.

Growth for migrants just before emigration may be slightly higher than that for residents. During the migratory period, growth was rapid, resulting in a lifetime growth pattern that may not adhere to the von Bertalanffy model. Individual variability was high; thus, growth may truly vary based on genetics, migratory patterns, and habitat use.

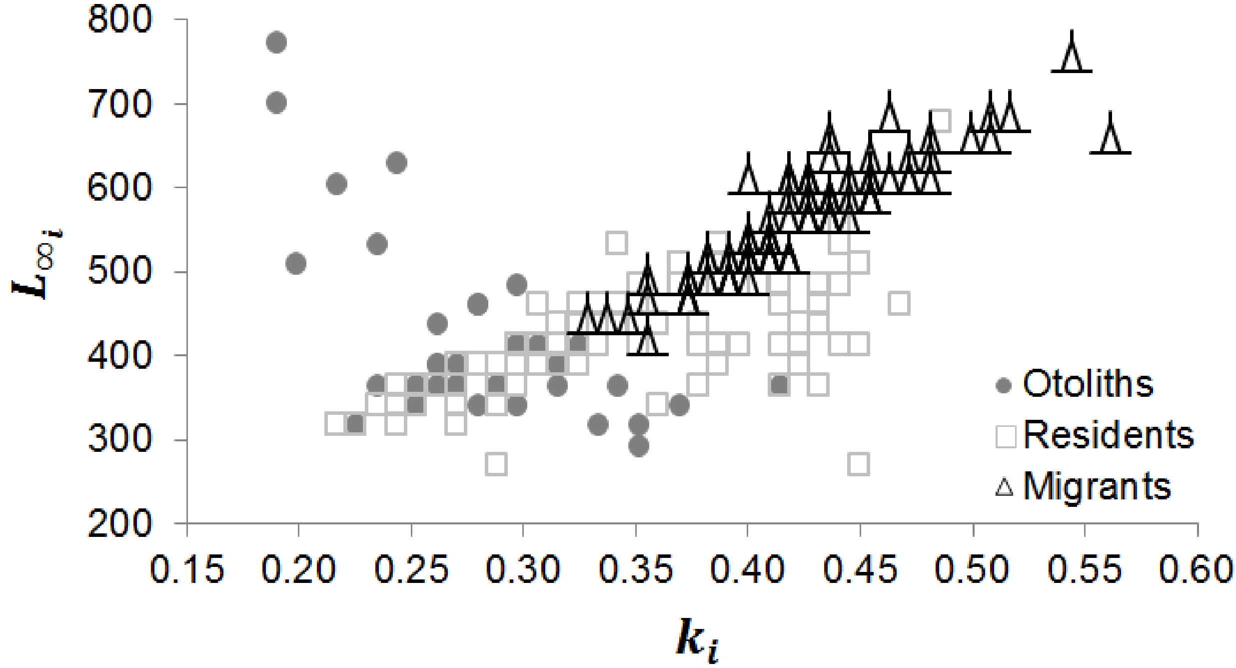

Figure 2.3. Asymptotic length L_∞ and growth coefficient (k_i) estimates for migrant and resident individuals and otoliths.

Estimates and uncertainty in growth rates, along with estimates of survival, fecundity and migration, could be incorporated into population modeling for the SFWWR, as well as compared to other systems to evaluate differences as a result of environmental conditions and land use patterns, which could be used to evaluate potential impacts of future conservation activities.

An integrated approach including individual variability using Bayesian methods would likely be useful for assessing growth for many bull trout populations, since it can easily account for population and individual variability, and can incorporate multiple data sources. The ability to incorporate multiple sources is beneficial for ESA-listed, rare, or relatively unstudied populations, since data from any one sampling technique could be limited.

Chapter 6: Characterizing Bull Trout Movement Patterns in the Walla Walla River

Chapter 6 addresses these objectives in the draft Recovery Plan:

- Restore and maintain suitable habitat conditions for all bull trout life-history stages and strategies (element of connectivity).
- Conserve genetic diversity and provide opportunity for genetic exchange (element of connectivity).

Movement is an essential part of a species' life-history strategy and has wide ranging consequences for growth, reproduction, survival and ultimately population sustainability. Bull trout require connected habitats to persist and are therefore highly susceptible to riverscape disturbances as a result of land use practices and consumptive water use. Resident, migratory (e.g., fluvial, adfluvial and anadromous), and dispersing bull trout require connectivity between suitable habitats to complete their life cycle. Migrations can result in individuals dispersing into new populations or habitats, therefore increasing genetic exchange between populations. The WWR is a highly altered and human influenced river system consisting of dams, irrigation canals, and leveed and channelized banks, resulting in barriers that compromise connectivity. If altered conditions occur during important bull trout movement periods (i.e., during pre-spawn migration), then there is potential to further limit connectivity. Diminished connectivity limits the ability of full life-history expression (representation), limits dispersal from one local population to another within a core area (resiliency), and may eliminate certain strategies. To effectively recover and manage bull trout, we need to describe their migratory behavior, determine factors limiting movement, and identify spatial bottlenecks in the migration corridor for all life stages.

Our goal was to describe movement patterns and timing for the migratory population of bull trout tagged in the SFWWR and the mainstem WWR. This migratory life-history strategy can provide larger, faster growing, more fecund adults and provide a greater recovery benefit to the meta-populations of the Walla Walla Basin. However, this portion of the population is more likely to encounter degraded and altered habitats, resulting in reduced survival and therefore may be less likely to contribute to the overall persistence of this population (resiliency).

- We evaluated the spatial and temporal movement of migratory bull trout in the SFWWR and mainstem WWR to determine if there is a life-history stage (i.e., age class) that limits population abundance. These results should be considered when determining flow, temperature, and passage criteria at various locations in the river system throughout the critical migratory times for these bull trout.

- We quantified and summarized the spatial and temporal movement patterns of migratory bull trout in the SFWWR and mainstem WWR to better understand the migratory life-history diversity of the population. This work is transferable to similar basins and can inform future recovery and population rebuilding strategies for populations that exhibit similar life histories (redundancy). These results provide metrics to evaluate the recovery criteria guidance of representation, resiliency and redundancy.

We used PIT tag detection and recapture data from 2002 to 2011 to characterize migratory bull trout movement patterns. For each fish, total distance, duration, and rate were calculated by downstream and upstream movements.

We found that from 2002 to 2011 only a small proportion (11%) of the 4763 bull trout PIT tagged in the SFWWR migrated downstream to the middle or lower WWR (Table 2.5). These data suggest that the remaining 89% of the tagged bull trout were either mortalities or never moved far enough to be redetected during the study (e.g., resident fish). Of the fish that migrated downstream out of the headwaters, only 18% were detected making subsequent upstream movements after marking during this study period, suggesting that conditions in the lower and middle river may have substantial influence on survival of the migratory population.

Table 2.5. Number of bull trout PIT tagged in the SFWWR by size class. Number of migratory fish, percent that migrated downstream, and percent detected migrating upstream.

Size Class at Tagging (mm)	Tagged	Migratory	Downstream Movement (%)	Upstream Movement (%)
Juveniles (< 144)	2657	211	8%	5%
Sub-adults (144 - 290)	1679	229	14%	10%
Small Adults (291 - 406)	249	30	12%	63%
Large Adults (> 406)	178	66	37%	67%

Of the 926 bull trout PIT tagged in the middle/lower WWR during 2007-2011, only 42% were subsequently detected moving either upstream or downstream (Table 2.6). The remaining tagged bull trout were either mortalities or never redetected during the study. Of the redetected migrating bull trout, only 31% were detected making subsequent upstream movements after marking during this study period, further suggesting habitat conditions in the lower and middle river impact the ability to move upstream to avoid unfavorable conditions.

Table 2.6. Number of migratory bull trout PIT tagged in the mainstem WWR by size class, the number that subsequently made downstream movements, and the percent detected moving both downstream and upstream.

Size Class at Tagging (mm)	Migratory Tagged	Migratory Moved Downstream	Downstream Movement (%)	Upstream Movement (%)
Juveniles (< 144)	35	10	29%	10%
Sub-adults (144 - 290)	657	266	40%	24%
Small Adults (291 - 406)	199	95	48%	45%
Large Adults (> 406)	35	21	60%	62%

Previous analyses (Appendix VI) found that within the headwaters, juvenile and sub-adult bull trout exhibited downstream migrations year round, movements occurred mostly at night, and the greatest movement activity occurred during August, however later analysis revealed peak outmigration of sub-adult bull trout occurred in the spring. Migration response to environmental cues was also modeled and results suggested minimum water temperature may influence migration timing. Bull trout appeared to migrate downstream out of the headwaters at similar sizes regardless of size (surrogate for age at marking – cohort) at marking. Our results suggested that generally, the longer a bull trout reared in the headwater areas, the further they moved downstream. Additionally, fish that migrated as juveniles or large adults typically moved shorter distances and durations relative to sub-adult and small adult migrators. Fish that migrated as sub-adults and small adults moved farther downstream and remained in the lower parts of the WWR longer.

Fish tagged in the SFWWR, WWR, and Mill Creek have all been detected at the Oasis Road Bridge PIA, suggesting a migratory population is present in all of the local populations; and connectivity and dispersal has been documented between local populations with in the WWR Core Area. WWR tagged fish have also been detected at the mouth of the Umatilla River and at mainstem Columbia River hydropower projects (e.g., McNary Dam). During this study, two WWR tagged fish were detected completing downstream migrations into the Columbia River and subsequently detected at or above Harris Park in the SFWWR during the spawning season.

We observed that poor and low habitat conditions (Chapter 3) may compromise the ability of WWR bull trout to migrate, rear or disperse. It is important to consider all life-history strategies (e.g., migratory, resident) when evaluating factors that limit population abundance and recovery plan actions. In particular, movement results suggest that the migratory component of the population is primarily impacted by these unfavorable habitat conditions. Since migratory individuals likely have much higher fecundity, poor habitat quality in the WWR likely impacts resiliency of the population. Many Columbia River basin bull trout populations exhibit similar life-history strategies (e.g., partially migratory population) and are faced with similar anthropogenic impacts to their habitat. These findings should be transferrable for managing rivers to promote range-wide species recovery of bull trout.

Chapter 7: Quantifying Survival and Population Trends in the Upper South Fork Walla Walla River

Chapter 7 addresses these objectives in the draft Recovery Plan:

- Maintain stable or increasing trend in abundance of bull trout.
- Restore and maintain suitable habitat conditions for all bull trout life-history stages and strategies (element of connectivity).

Population trend is an important vital rate that describes the cumulative effects of survival at multiple life stages on the population as a whole. Understanding whether the population is stable, increasing, or decreasing across relevant temporal scales is a key component for recovery of most species listed under the ESA. Developing effective management strategies, however, also requires information regarding how extrinsic and intrinsic factors can influence population abundance and trends, preferably within a hypothesis-driven framework.

Our goal was to estimate bull trout vital rates (survival, emigration, recruitment) and population trends (e.g., population growth rates). We use a multifaceted approach to specifically evaluate: 1) life-stage (juvenile, sub-adult, adult, and large adult) and life-history expression (migratory, resident, and unknown) specific trends in bull trout abundance; 2) bull trout survival and emigration rates across life stages and life-history expressions (as above); and 3) hypotheses of how biotic and abiotic factors influence such patterns.

- We employed 10 years of capture-mark-recapture (CMR) data to assess how biotic and abiotic factors influence bull trout survival at specific life stages and overall population trend in the SFWWR local population. Developing life-stage specific vital rates and identifying factors influencing these rates is integral to understanding bull trout population dynamics.

- Linking biotic and abiotic factors to survival and population trends can help direct and understand the effects of different management and restoration actions within the WWR. Life-stage and life-history specific vital rates also provide a framework for planning in other basins where such data are limited.

We used CMR data collected from 2002-2010 (Appendices I,II) to estimate long-term growth and survival rates for the local population of bull trout in the SFWWR. We used a Pradel CMR trend model to estimate annual rates of population change (λ_t) and other trend response variables for adult bull trout. For the Pradel model, we restricted our population of interest to bull trout > 300 mm total length (TL). We integrated existing redd count data for the SFWWR to provide a comprehensive assessment of population trends and allow for transferability of our results to other populations, which predominantly utilize redd count data for trend monitoring. We used a Barker CMR model to estimate annual survival (and other pertinent vital rates) for all size classes of bull trout and to test hypotheses of potential limiting factors.

In the top Pradel population trend model for the analysis including all adult fish (≥ 300 mm), there was an interaction between group and time for population growth rate. Based on the top model, both population growth rates (λt) and realized population change (Δt) for all adult fish combined (migratory, non-migratory, and unknown) were greater than 1 near the start of the time series, declined significantly though 2006-2007, but then increased for the last three years, albeit with wide confidence intervals that overlap 1 (i.e., stable population trend) in all years except 2006-2007 (Figure 2.4). There is a 1% chance the population decreased ≥ 50% (endangered threshold), and a 5% chance the population decreased ≥ 30% (threatened threshold). Similarly, the top Pradel population trend model for the analysis that included only fish that migrated (data not shown here) had a similar model structure but the estimated median λ_{MCMC} for the time series was 0.988 (95% CI = 0.81-1.12). There is a 5% chance the population decreased ≥ 50% (endangered threshold), but a 22% chance the population decreased ≥ 30% (threatened threshold).

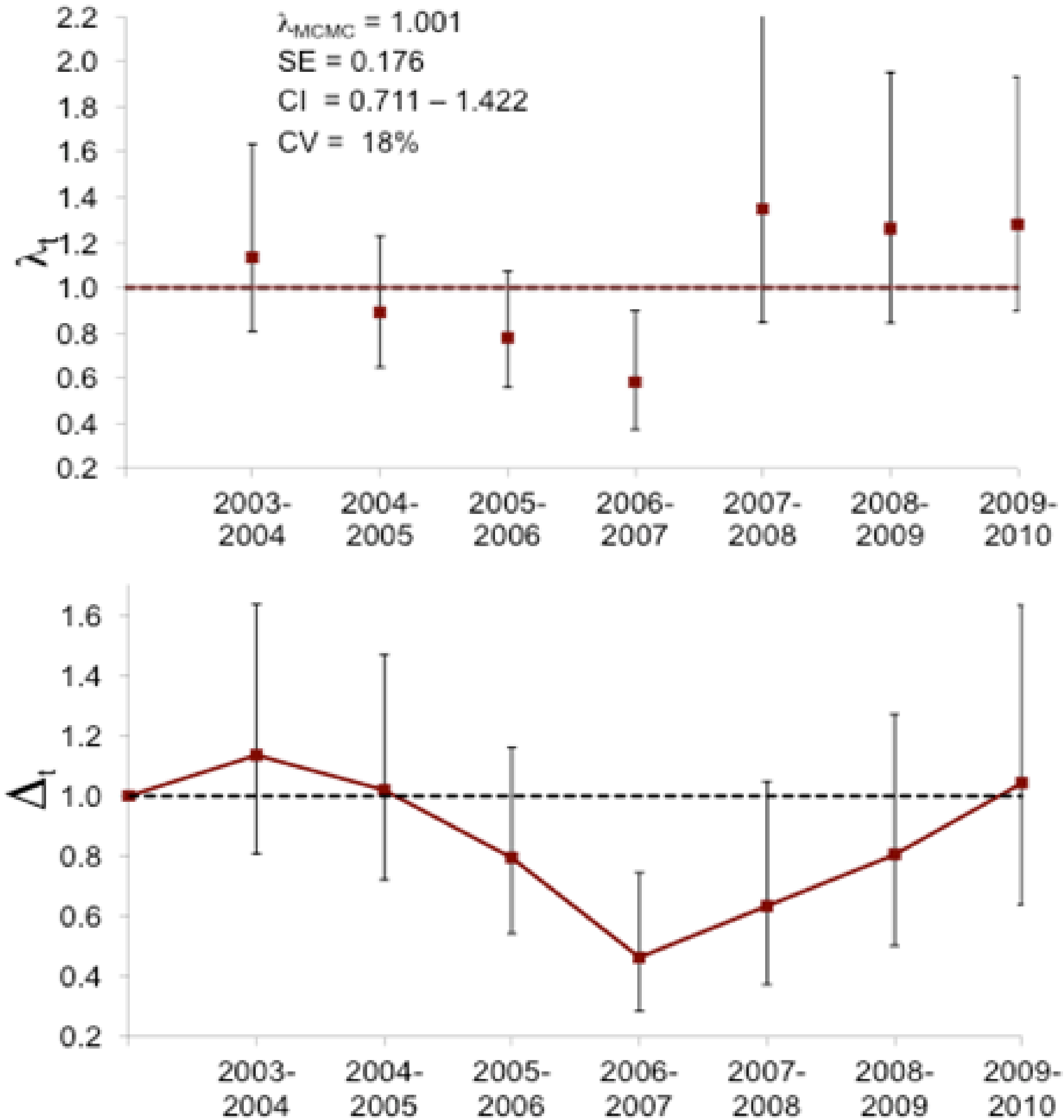

Figure 2.4. Population growth rates (λt; top panel) and realized population change (Δt; bottom panel) from the top model for adults (≥ 300 mm), migratory, non-migratory, and unknown combined.

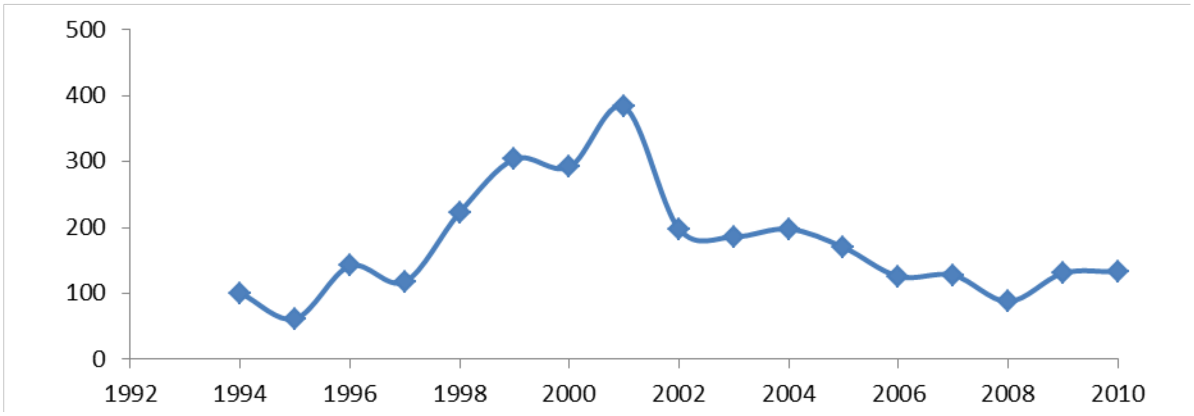

Figure 2.5. Bull trout index reach redd counts for the SFWWR populations from 1994-2011.

The number of bull trout redds varied considerably during the last 2 decades in the SFWWR (Figure 2.5), consistent with patterns from proximate populations of bull trout in the Blue Mountains. The trend in bull trout redds during the period of our mark-recapture study (2002 to 2011), was $\lambda = 0.97$ (95% CI = 0.84-1.13). Previous studies suggested redd counts were most similar to abundance trends observed in large, adult bull trout (Al-Chokhachy and Budy 2005); this is consistent with our Pradel findings.

Survival (S) varied over time and among age/size classes but with no clear time trend for small fish (< 300 mm) (Figure 2.6). Specifically, in the top Barker model, survival rate (S) differed among the three age/size groups of small fish, and was the lowest for the smallest size class of juveniles (< 150 mm) and less than 30% in most years. Survival rates were similar on average for size/ages of large, adult fish (> 300 mm), but with very different patterns across years relative to small fish (Figure 2.6). For example, survival rates for the largest fish (> 300 mm) were lowest in 2005, 2006 and 2009 (when other groups showed higher survival) and generally remained above 50% in other years. In contrast survival rates for the small adults (150-300 mm) varied little across time but were greatest in 2006 and 2010. The pattern of survival across time and age/size groups strongly suggests that different factors determine survival in the upper river, where small adults stay and migrate, versus the lower river, where most large fish attempt to migrate

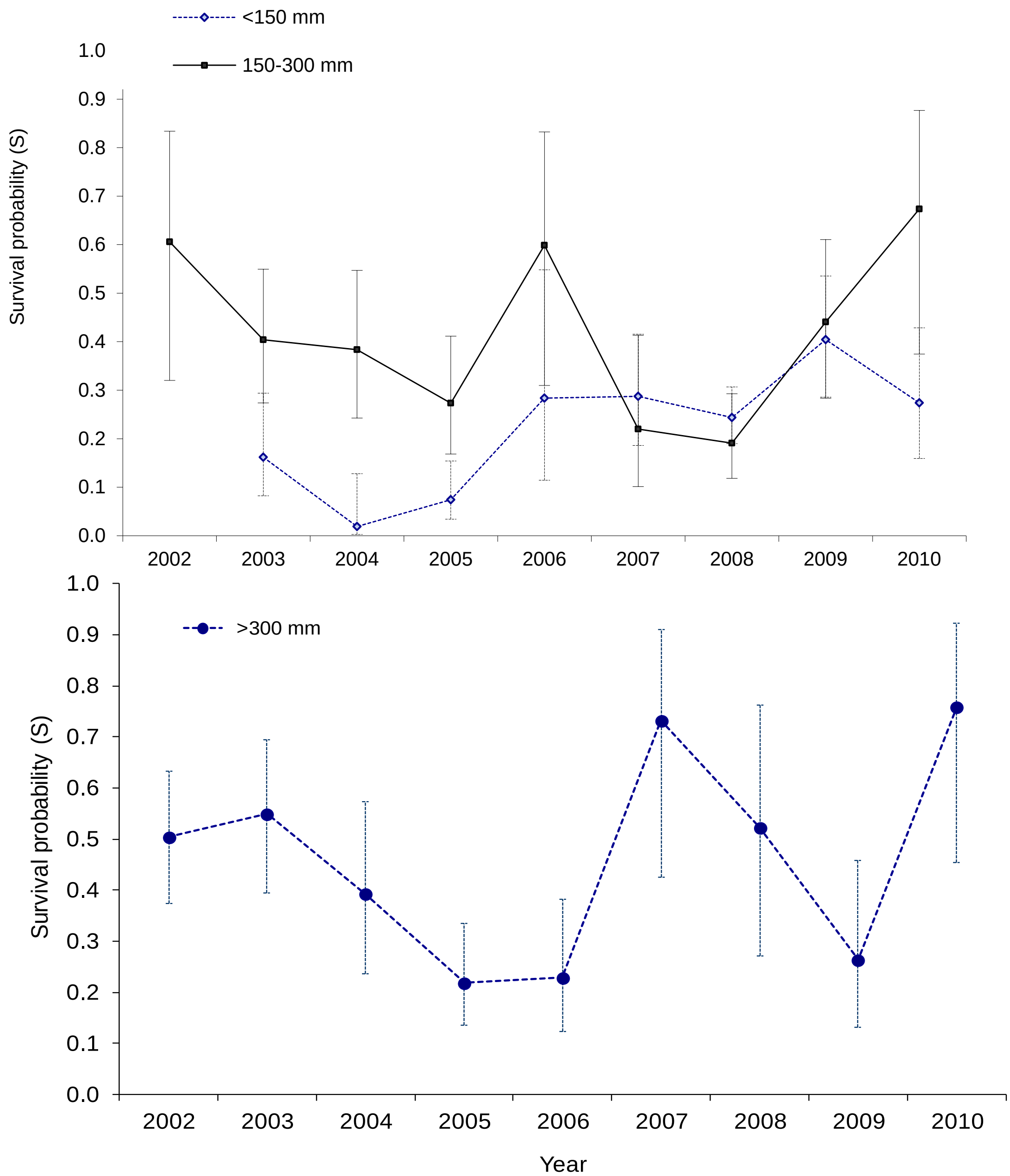

Figure 2.6. Survival probability from the top Barker model, by year and size class.

Populations of many fish species are sensitive to changes in vital rates during early life stages, but our understanding of the factors affecting growth, survival, and movement is often extremely limited for juvenile fish. In previous analyses, we estimated age-class-specific annual survival from the Barker model as 22% for age-1 bull trout and 23% for age-2 bull trout (Bowerman and Budy 2012). The majority of small fish emigrated from the tributaries, important spawning and rearing habitat. In addition, these fish, which are very small in some cases, migrate out of the tributaries across the year and some disperse long distances.

The population of bull trout in the SFWWR appears to be stable however there is some indication that portions of the population may be in decline. Redd counts are stable over the complete time series available but appear to have declined over the more recent study period. In addition, the migratory portion of the population does not appear to be stable and may be declining (low proportion of total fish in the largest size categories, low survival of large fish). Further, the time series is actually quite short and if we were comparing these observations to historical conditions, our conclusions of status may be quite different and likely more dire.

Chapter 8: Estimates of Survival Rates for the South Fork and Lower Walla Walla River Bull Trout

Chapter 8 addresses this objective in the draft Recovery Plan**:**

- Restore and maintain suitable habitat conditions for all bull trout life-history stages and strategies (element of connectivity).

Estimation of survival rates is a key element towards the development of effective conservation and recovery strategies. Evaluation of survival rates and associated variability within a population can provide critical information on how habitat conditions and phenotypic characteristics influence individual and population viability. Flows in the lower WWR are heavily impacted by irrigation withdrawals during late spring and summer, resulting in elevated water temperatures and migratory barriers. In addition, channel and riparian development have dramatically altered river habitat conditions in several areas. Estimation of survival rates provides baseline monitoring data on current demographic parameters for comparisons within the SFWWR and lower WWR over time as well as across other bull trout populations. In addition, these baseline data provide a reference point for evaluation of the effects of restoration and management actions.

The goal of this research is to quantify patterns of survival across individuals, release locations, seasons, and years for bull trout captured and released in the SFWWR and lower WWR.

- We use capture-mark-recapture data to evaluate potential differences in bull trout survival rates between headwater (SFWWR) and mainstem locations (WWR). The results of these analyses provide a framework to understand how differences in riverscape integrity influence bull trout survival.

- Results from these analyses can be used to direct potential management and restoration actions and parameterize models to evaluate the potential benefits of such actions within the Walla Walla Basin. The results can also be applied to other basins, where such data are limited, but critical in directing recovery actions.

During 2002-2010 in the SFWWR and during 2008-2010 in the lower WWR, we used a variety of techniques to capture, measure, PIT-tag, and release individual bull trout. We used these data within a logistic regression modeling framework to estimate the relative recovery rate, an index of survival while accounting for potential effects of release year and fish length for releases at both locations. We also evaluated whether there were seasonal differences in survival for fish released in the lower WWR.

Results for both release locations showed that survival varied by release year and by fish length, with higher survival for larger fish compared to smaller fish (Figure 2.7). However, the strength of the survival advantage for larger fish also varied by year, with some years showing a high survival advantage and some years showing only a moderate survival advantage. Average survival of sub-adult fish from the SFWWR was low, with a mean of 12% across years (range: 3-23%; Figure 2.8). Survival of small adult fish from the SFWWR was higher, with a mean of 25% across years (range: 9-43%). Over the 2008-2010 years when fish were released in both locations, annual length-specific survival patterns were similar between the SFWWR and the lower WWR releases, suggesting that shared factors influenced survival of fish released at both locations.

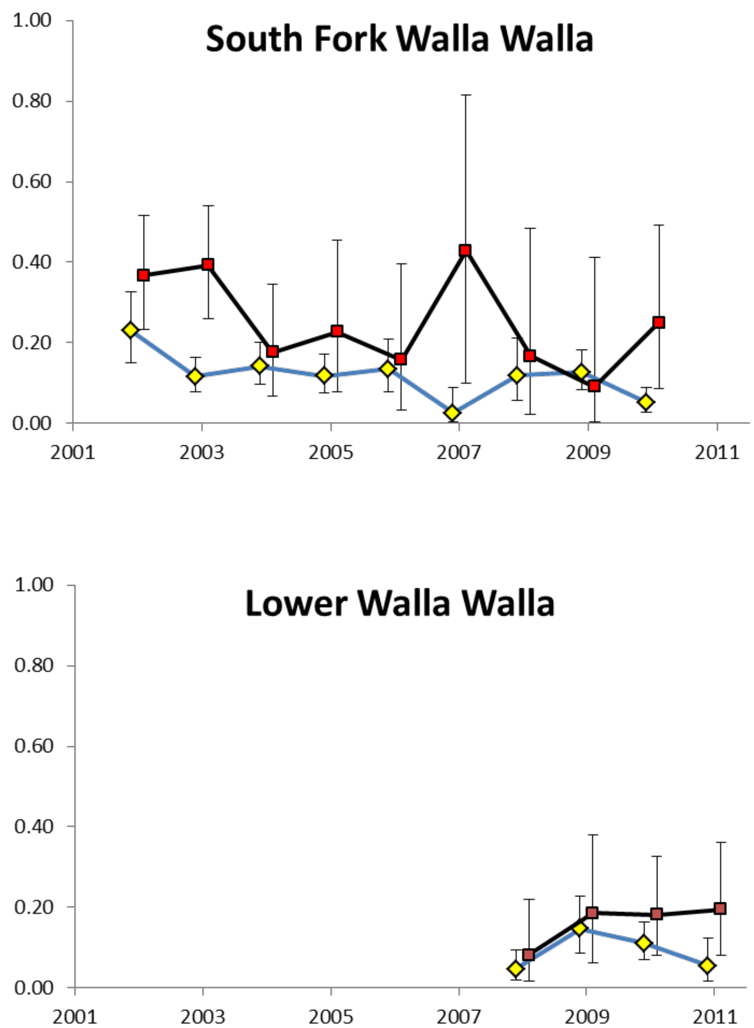

Figure 2.7. Relative recovery rate for bull trout in the WWR and SFWWR by size category with sub-adults marked using yellow symbols and small adults marked using red symbols.

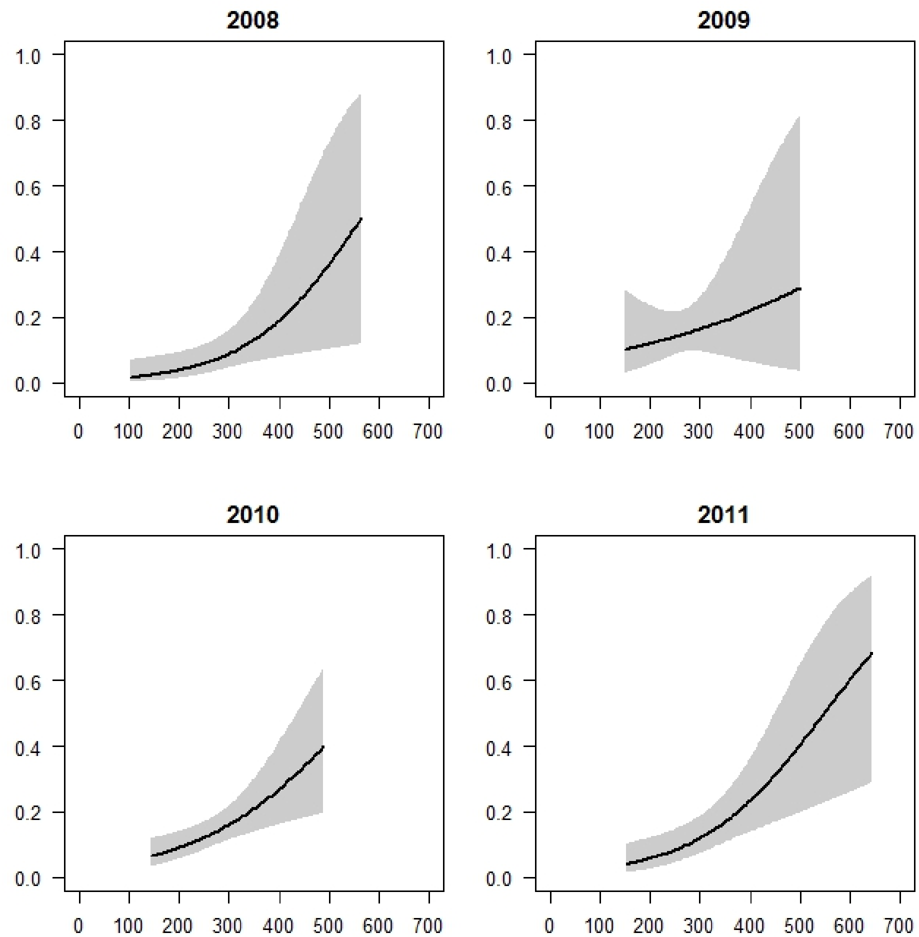

Figure 2.8. Lower WWR marked survival versus fish length at tagging.

The survival rate indices estimated in this research provide baseline monitoring information for comparison to other bull trout populations as well as for comparison over time within the lower WWR. Through such comparisons, it may be possible to determine which environmental factors influence survival across years and across populations. These results highlight the importance of length and growth on survival.

Chapter 9: Conservation Implications of Multiple Life-history Strategies and Metapopulation Structure in a Stream Dwelling Char, Bull Trout

Chapter 9 addresses these objectives in the draft Recovery Plan:

- Maintain current distribution of bull trout within core areas as described in recovery unit chapters.
- Maintain stable or increasing trend in abundance of bull trout.
- Conserve genetic diversity and provide opportunity for genetic exchange (element of connectivity).

Effective management of threatened species requires information about demographic rates, and the environmental factors that affect these rates and subsequently cause populations to grow or decline. WWR bull trout exhibit variation in life-history strategies that leads to considerable variation in vital rates, including growth, survival, and fecundity. Estimates of demographic rates and an understanding of how they vary among life stages and life-history strategies will help inform management decisions specific to habitats used during different parts of the bull trout life cycle. To effectively manage multiple bull trout populations at the spatial scale of core areas, it is also important to understand how vital rates differ among populations, and how connectivity among local populations affects overall metapopulation (e.g., core area) trends in abundance.

Our first goal was to assess the relative sensitivity of bull trout populations composed of different life-history strategies to changes in specific demographic parameters. Our second goal was to estimate dispersal rates and evaluate how changes in dispersal opportunity (i.e., stream connectivity) influenced long-term trends in abundance of local populations and an overall core area population.

- We developed a life-stage model to evaluate how changes in vital rates related to management actions and stochastic events will affect overall long-term population viability. The model provides a framework to evaluate how population redundancy (e.g., the number of individual local populations within a core area) might affect long-term trends for entire metapopulations. Furthermore, the model can also be used to assess potential genetic exchange among local populations, as well as variability in responses among life-history strategies to changes in vital rates.

We integrated life-stage specific vital rate estimates for both resident and migratory life-history strategies into a life-cycle model to assess how populations might respond to changes in survival, growth, reproduction, or migration rates. We evaluated the relative effect of changes to individual demographic rates on long-term population growth rates of resident and migratory life-history types, as well as a population composed of both resident and migratory individuals (termed mixed life-history type). We then estimated empirical dispersal rates among individual populations in a spatially realistic metapopulation model consisting of three bull trout populations. We used this framework to evaluate how changes in dispersal rates (e.g., connectivity) affected overall long-term population trends in each of the three local populations, and the core area population as a whole.

Based on perturbations to the life-cycle model, changes in juvenile survival rates and maturity schedule had the largest influence on overall population trend for all three life-history types. However, the relative effect of changes in fertility and adult survival components varied among life-history types (Figure 2.9). Bull trout populations that were composed of individuals that spawned earlier in their life cycle and grew more slowly were more vulnerable to changes in reproductive success (e.g., egg survival). In contrast, populations composed of late-maturing individuals that grew to larger sizes were more vulnerable to changes in adult survival rates (e.g., via harvest or predation).

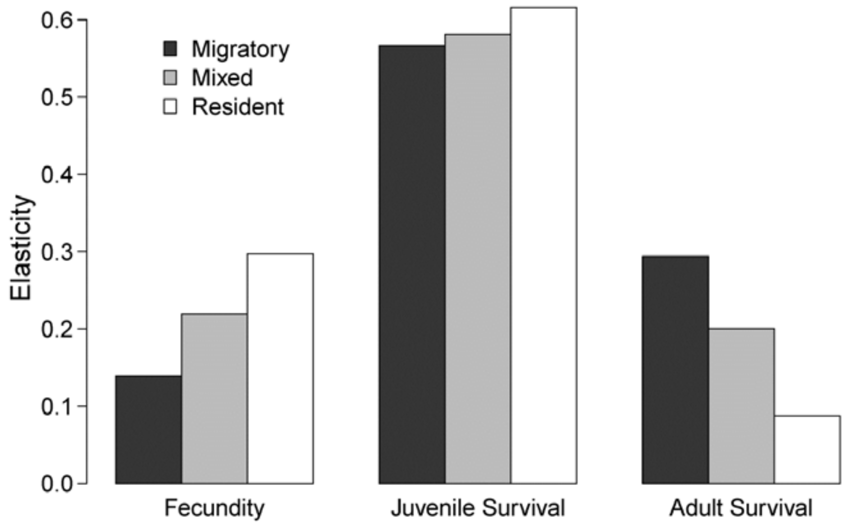

Figure 2.9. Relative sensitivity (e.g., elasticity values) of overall population trend to small changes in life-stage specific vital rates. Vital rates are combined across life stages (fertility, juvenile survival, and adult survival) for three different bull trout life-history types.

We observed infrequent dispersal of individual bull trout among distant patches (>70 km apart), from which we estimated current rates of dispersal (<0.003; Table 2.7). When all populations were declining, dispersal rates across a range of values had little effect on overall metapopulation persistence, or the persistence of individual populations. However, when population trends varied (e.g., some were stable while others decreased), dispersal helped buffer small or declining populations from extinction via a rescue effect (Figure 2.10). Hence, the potential for individuals to disperse, or move from one population into another to reproduce, was important to provide resiliency for declining populations when neighboring populations were stable.

Table 2.7. Metrics used to assess population connectivity between individuals in the SFWWR, Mill Creek (MC), and Touchet River (TR): (a) dispersal rates between populations based on the proportion of marked fish observed moving from one population to another (dispersers moved from each population in a column into the populations in rows), (b) dispersal rates estimated from a movement function developed from combined capture-mark-recapture movement data (assumed equal in either direction), and (c) migrants per generation based on genetic divergence between populations (pairwise F_{st} values).

	(a) Observed dispersal (over 7 yrs)			**(b) Dispersal function rate (applied annually)**			**(c) Migrants per generation**		
	SFWWR	MC	TR	SFWWR	MC	TR	SFWWR	MC	TR
SFWWR		0.0052	0.0000						
MC	0.000		0.0098	0.002			3.580		
TR	0.000	0.000		0.0014	0.0015		3.440	2.380	

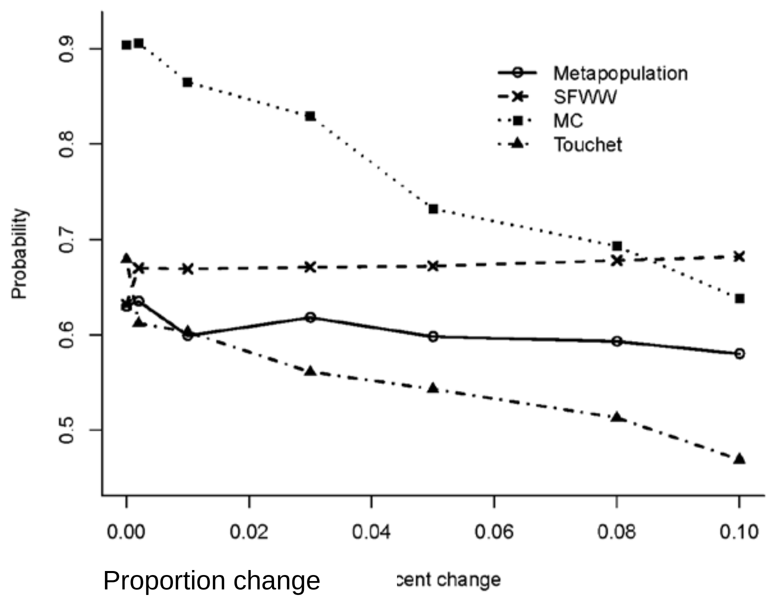

Figure 2.10. Effects of varying dispersal rates (proportion change in annual dispersal rate) on the probability that a population will fall below 75% of its current population size in 25 years based on a scenario in which long term population trend was more stable for SFWWR and TR populations (λ = 0.983), and declining more rapidly for the MC population (λ = 0.928).

This analysis suggests that diversity in life-history strategies can help stabilize demographic responses to environmental perturbations, which may help decrease the risk of extinction to bull trout for both individual local populations and between core areas. To provide as much demographic stability as possible, diversity within and among populations should be maintained along a continuum that emphasizes conservation of the full range of life-history traits expressed by bull trout.

Appendix I: Walla Walla River Passive Instream Antenna Site Descriptions and Operations

This chapter includes a map showing the extensive Passive Instream Antenna (PIA) network throughout the WWR, along with a detailed description for each site. For each site, the individual site operations (i.e., general downtime) times and monthly antenna efficiencies are reported.

Appendix II: Sampling and Tagging Methodologies

The same tagging populations (i.e., SFWWR and WWR) were used for different analyses throughout this report, therefore a condensed version of sampling, marking and detection methods were summarized in Chapter 7.

Appendix III: Low Flow Passage Barrier Assessment of the Walla Walla River

Appendix III addresses this objective in the draft Recovery Plan:

- Restore and maintain suitable habitat conditions for all bull trout life-history stages and strategies (element of connectivity).
- Conserve genetic diversity and provide opportunity for genetic exchange (element of connectivity)

Bull trout populations can be negatively impacted by seasonal periods of low flow that cause dewatering, passage barriers, and high water temperatures. As a result of the 1998 ESA listing and a Civil Penalty Settlement Agreement, discharge from the Nursery River Bridge Dam (rkm 74) on the WWR must currently remain at or above 25 cfs to maintain migratory pathways for bull trout in the system. However, little information existed as to the number of barriers to fish movement under such minimum flows, and how bull trout movement relates to streamflow.

Using established criterion on water depth for passage as a guide, the goal of this field study was to evaluate potential passage barriers on the WWR between Cemetery Bridge (rkm 76) and Burlingame Dam (rkm 61) as related to streamflow. Specific objectives were to 1) evaluate the potential number of barriers in this river reach, 2) examine how changes in discharge rates (cfs) would impact the number of barriers and to estimate the cfs required to eliminate all barriers, 3) examine temporal and seasonal periodicity in barriers, and 4) evaluate bull trout movements as related to streamflow.

- We integrated snorkel survey data with PIT tag and capture-mark-recapture data to quantify relationships between bull trout movement and ambient streamflow patterns. Identifying fish movement patterns in relation to streamflows is an essential part in assessing the importance of minimum flow requirements and in directing future management and restoration strategies. The results from this assessment can be applied to other basins where flow management may be influencing bull trout movement patterns.

During initial sampling, a total of 92 barriers were identified throughout the study reach: 84 between Tumalum Bridge and Burlingame Dam, seven between Nursery Bridge Dam and Tumalum Bridge, and one between Cemetery Bridge and Nursery Bridge Dam. Discharge generally declined in a downstream direction between rkm 74.3 and 66.3. At Pepper Bridge (rkm 66.3), the minimum required streamflow predicted to result in no barriers was 40.6 cfs, which is above the current discharge requirement at Nursery Bridge Dam. Examination of streamflow between 2002 and 2011 along with criteria for passage suggests that passage barriers are most prevalent during the seasonal period of low flow from July through October in all years. Low water years, like 2005, often have more months impacted by barriers, than other years. Only sub-adult (i.e., no adult) bull trout were observed during summer snorkel surveys and they were more prevalent at upstream sites, as compared to downstream sites, within the reach. Bull trout were more often detected migrating at PIT tag antennas during periods before or after summer low flow events, sometimes during flow pulses.

Low stream flows can negatively impact bull trout by reducing or eliminating migratory pathways, which causes fewer juveniles to reach high productivity areas and fewer highly fecund migratory adults from reaching spawning sites. Low flows can also result in higher mortality by trapping fish or requiring fish to traverse shallow areas where they are potentially more susceptible to bird and mammalian predation, competition, and unsuitable temperatures. Inadequate streamflows and the resulting passage barriers also have the potential to negatively impact connectivity between local populations within the WW core area, as well as connectivity between the WW core area and adjacent core areas (e.g., Touchet, Umatilla). And finally, suitable habitat conditions are not available when these seasonally low flows are present.

Results from this study suggest that the required discharge at Nursery Bridge Dam may not be adequate to allow unrestricted passage in downstream reaches during seasonal periods of low flow. This issue may be exacerbated by the apparent decline in discharge moving downstream as water is lost through the streambed to the shallow aquifer, and as water is removed from the system by consumptive users. Increasing baseline streamflow or initiating pulses during migratory periods could improve passage and as a result, have a positive effect on the WWR bull trout population.

Appendix IV – VIII: These publications were completed during the study.

Chapter 3 : Walla Walla Basin Bull Trout Habitat Quality Assessment

authored by

Marshall Barrows
Ryan Koch
Joe Skalicky

U.S. Fish and Wildlife Service

Introduction

For over 100 years, anthropogenic modifications to the landscape and the over-allocation of water resources have resulted in severe declines in fish populations and the alteration or loss of riverine habitat throughout much of the Walla Walla Basin. In general, instream habitat in the headwaters of the South Fork Walla Walla River (SFWWR) and Mill Creek (MC) remain relatively pristine, but habitat becomes increasingly degraded downstream from the Umatilla National Forest Boundaries in both subbasins. At lower elevations, the steepness of canyon slopes decreases, valley bottoms widen and accordingly the stream gradient lessens. This geomorphic transition marks a shift in land-use from forested, sparsely disturbed reaches to that of agricultural pasture land, evidenced by cleared vegetation and altered riparian zones. As canyons give way to rolling foothills, orchards and vineyards predominate the near-river landscape and considerable modifications to the stream channel have been made to accommodate urban development and for flood control. Flood control measures required the construction of levees and grade control structures to contain flood waters and dissipate energy from high water events. Unfortunately, this channelization involves the reshaping of the waterway and can include shortening, straightening, widening, realigning, removing obstructions to flow, and increasing the gradient (Woods and Griswold, 1981). Such modifications often seriously damage or reduce the available riparian habitat and in turn impact the associated biota (Woods and Griswold 1981; Chapman and Knudsen 1980; Geier and Best 1980). The lowlands consist of a massive accumulation of unconsolidated sediments (coarse sands, gravels and clay) deposited as alluvial fans that create the valley floor. Although dry-land farming is common in mid-lower elevation areas (Walla Walla Agricultural Water Quality Management Area Plan 2007), irrigated row crops dominate the valley floor. From the late 1800's through 2000, the majority of surface flow in the Walla Walla River (WWR) was seasonally diverted for irrigation. A section of the mainstem WWR from Milton-Freewater, OR north to the Washington state line was often completely dewatered during the irrigation season. Beginning in 2000, three irrigation districts pledged to keep a minimum water flow in the river and signed an agreement to this effect with the U.S. Fish and Wildlife Service (FWS). Two of the irrigation districts that signed the agreement divert water in Oregon (Hudson Bay District Improvement Company and Walla Walla River Irrigation District) and the third district (Gardena Farms Irrigation District #13) is located in Washington, west of Walla Walla, WA. From 2002 – present, flows ensuring a minimum of 25 cfs at Nursery Bridge Dam in Milton-Freewater, OR and 18 cfs past the Burlingame Diversion in Washington are left in-river. The instream water intends to provide a continuous flow to help enhance passage upriver by bull trout and improve rearing habitat for sub-adult fish.

Bull trout in the Walla Walla Basin have been impacted by alteration and loss of aquatic habitat resulting from basin-wide modifications to the riverscape and over-allocation of water resources for agriculture. Dams, irrigation diversions and channel modifications have influenced fluvial processes, altering riverine biological diversity at multiple temporal and spatial scales (Stanford and Hauer 1992; Stanford et al. 1996). The riverine environment within the Walla Walla Basin is in a constant state of flux, driven primarily by perpetually changing abiotic conditions (e.g. temperature and streamflow). The full expression of life-history stages and strategies exhibited by bull trout depends on the presence of suitable habitat within the riverine environment (Al-Chokhachy and Budy 2007; Rieman and McIntyre 1993). In addition, specific habitat requirements vary both spatially and temporally for differing life stages and strategies (Al-Chokhachy and Budy 2007; Dunham et al. 2003; Rieman and McIntyre 1993; Rieman and Chandler 1999). Following ESA listing, there has been substantial effort directed toward identifying factors limiting the distribution and abundance of bull trout at multiple spatial scales

(Al-Chokhachy et al. 2010; Rieman et al. 2006; Saffel and Scarnecchia 1996; Dunham et al. 2003). Studies commonly use metrics, or a combination of metrics, believed to notably influence the distribution and abundance of bull trout to identify, quantify and determine the distribution of suitable habitats. Research often focusses on habitat suitability for a specific bull trout life stage and strategy.

Walla Walla Basin bull trout exhibit a veritable continuum of life histories involving movements, migrations, spawning, rearing and foraging on time scales ranging from daily to annually or longer, and over different spatial scales. Commonly, multiple life stages concurrently occupy a given stream reach, utilizing its attributes for different purposes. Focused management actions (e.g. habitat restoration) aimed at benefiting a particular life stage or strategy will likely influence others. The diversity of habitats required by bull trout to complete their varying life-cycle stages and strategies requires that habitat protection and recovery strategies address a large number of factors. Resource managers often employ extremely complex, multifaceted models aimed at characterizing aquatic habitat or predicting population performance or response to proposed management actions. These models often incorporate a very large number of input parameters, most of which are estimated with a high degree of uncertainty. These models often lack transparency, transferability may be questionable and derivation methodology may even be proprietary. Our goal is to help resource managers by developing tools (i.e., models) that are useful and practical for decision-making. To this end, we developed a simplified, practical and fundamentally straightforward approach to assessing aquatic habitat quality at the reach-scale in the SFWWR, the WWR, and the MC subbasin to help inform recovery actions.

For this assessment, we developed a model to spatially and temporally identify and rate the quality of bull trout habitat at the reach-scale in the SFWWR, WWR, MC and Yellowhawk Creek (YHC) with respect to each bull trout life-history stage and strategy. The output from this model should be used as a “first cut” tool when determining potential sites for habitat restoration or the implementation of future management actions.

Study Area

The WWR headwaters drain from the coniferous forested, western slopes of the Blue Mountains in northeastern Oregon through steep volcanic canyons, rolling foothills, and broad alluvial lowlands before eventually reaching its confluence with the Columbia River at about rkm 509 (Figure 3.1). The Walla Walla Basin has a predominantly dry, continental climate but some marine characteristics are evident (Harrison et al. 1964). Elevation compellingly influences climate in the Walla Walla Basin, and locally varies from warm and semiarid (< 10 in. annual precipitation) in the western lowlands that lie in the rain shadow of the Cascade Mountains, to cool and relatively wet (40-60 in. annual precipitation) at higher elevations in the Blue Mountains (Walla Walla Watershed Plan 2005). Winter precipitation often falls as snow in higher elevations and is stored as snowpack until warmer spring and summer temperatures initialize melting and subsequent runoff. The magnitude and timing of melting mountain snowpack varies and influences both streamflow and water temperatures throughout the Walla Walla Basin. Generally, water temperatures warm and streamflows increase incrementally downstream. Higher elevations are dominated by Douglas fir, grand fir, western larch and western red cedar, with Ponderosa Pine occupying the mid-elevation uplands. Prior to euro-American settlement and subsequent agricultural practices, much of the lowlands were bunchgrass prairie and shrub-steppe vegetation with cottonwoods, alder and willow along the riverbanks.

Methods

Walla Walla Basin bull trout exhibit a true continuum of life histories involving movements, migrations, spawning, rearing and foraging on time scales ranging from daily to annually or longer, and over different spatial scales. Commonly, multiple life stages concurrently occupy a given stream reach, utilizing its attributes for different purposes. For this assessment, we developed a simplified, straightforward approach to spatially and temporally identify and characterize the quality of bull trout habitat at the reach-scale in the SFWWR and WWR and the Mill Creek subbasin.

Modeling approach

We elected to assess habitat quality, both spatially and temporally, as it relates to multiple varying, and often concurrent, bull trout uses. To accomplish this, we first delineated the SFWWR and the WWR as well as MC and YHC into definable, largely homogenous reaches that differ from neighboring segments. We then identified and defined specific strategies and actions exhibited by Walla Walla Basin bull trout during the differing life stages of resident and migratory life forms. We developed a model to calculate a monthly habitat quality score (HQS) for each reach and for each life stage, strategy or action, based on a suite of habitat variables commonly believed to influence aquatic habitat structure, suitability or function. Each variable was assigned a “rating factor” (RF) to reflect the quality of each habitat variable within each reach during each month as related to each of the identified bull trout life stages, strategies and actions. Each variable was then assigned a "weighting factor" (WF) to reflect the variables' importance relative to one another with respect to their contribution to habitat quality for each life stage, strategy or action. Once calculated, the resulting monthly HQSs for each reach were compared with known spatial and temporal, life stage/strategy-specific bull trout occurrence data. In addition, HQSs were compared with reaches and months where bull trout of a given life stage may conceivably exhibit a certain strategy or conduct a particular action, but have not been (or very rarely) observed doing so within the study area. The following methods for habitat reach delineation and characterizing, rating and evaluating data for model development and calculating HQS are hereafter provided.

<u>Reach delineation</u>

Although describing reaches in terms of a constant spatial distance offers consistency and potential transferability, operational reach delineation lacks flexibility and may not capture distinct habitat variability over smaller scales. By using specific attributes and relatively distinct breaks in channel morphology, hydrological channel junctions and habitat structure we can functionally delineate stream reaches into definable, homogenous segments that differ from neighboring segments. Stream reaches that are relatively homogeneous regarding stream size, temperature, hydrologic regimes and other attributes are known as macrohabitats (The Nature Conservancy 2006). Each macrohabitat type represents a different physical setting that may correlate with bull trout spawning, occupancy, foraging, migratory patterns and survival. To coarsely delineate macrohabitat reaches in the WWR and MC, we selected attributes that we believe to notably influence aquatic habitat structure, suitability and function. Only attributes that could be represented across the entire study area and readily determined or measured from available data, topographic maps and aerial photographs were used. Attributes were further partitioned into categories to characterize the extent of influence that the attribute has on habitat and the associated biota. Reaches were delineated by having the same suite of physical classification attributes and being distinct from other groups. Using only attributes that can be represented across the study area disallows the application of strictly biological data, which are sometimes sparse and inconsistent throughout the Walla Walla Basin. Reaches were delineated manually because similarities and differences were usually distinct and apparent enough to classify reaches without statistical evaluation. The attributes that were used to coarsely delineate stream reaches and that notably influence aquatic habitat, suitability and function include surface flow, channel modification, land use, stream gradient and elevation. Reach delineation matrices that we used to functionally delineate habitat reaches are provided in Appendix A.

Habitat attributes

Streamflow ─ Streamflow cannot be directly linked to fish biology like water temperature or other water chemistry metrics. For example a given flow does not provide the same amount or quality of fish habitat in one stream versus another, or even within differing reaches in the same stream. Instream flow habitat studies can do this by relating the associated depths and velocities from specific flows to specific life stages and species of fish but these studies are expensive and improbable for an entire river basin. Therefore, to help coarsely delineate habitat reaches for this assessment, we have chosen to employ a simplified approach that assumes that major tributaries and diversions markedly influence spatial and temporal habitat conditions. The major tributaries and diversions within the study area are hereafter identified.

Tributaries ─ Habitat within many reaches in the Walla Walla Basin is influenced by major tributaries. In addition to the obvious contribution to mainstem streamflow, water temperature downstream from the tributary input is likely influenced. Also, investigations in geomorphology and riverine ecology have emphasized the important physical and biotic interactions resulting from stream confluences (Rice et al. 2001; Benda et al. 2004). Large woody debris and sediment input and subsequent deposition from the tributaries may influence downstream habitat characteristics. Opportunistic predators (e.g., bull trout) and other feeding salmonids may exploit fish, invertebrates and other prey species delivered to the mainstem from the tributaries as well. Although many tributaries throughout the Basin contribute to the overall, seasonably variable water volume of the WWR (Bower 2007), the spatial and temporal disposition of certain tributaries likely exert a more profound influence on seasonal aquatic habitat. Major tributaries to the WWR that may meaningfully impact instream habitat include: Reser Creek, the North Fork Walla Walla River (NFWWR), YHC, MC and the Touchet River. Blue Creek may considerably influence aquatic habitat in MC.

Diversions ─ The character and persistence of river ecosystems are dependent on flow management and other human activities in river corridors (Bowen et al. 2003). The spatial and temporal aspects in addition to the magnitude and extent of alterations to the river corridor and natural hydrograph may strongly influence aquatic habitat characteristics, thus interrupting critical ecosystem processes. These alterations and the resulting impacts may severely influence migration and survival of bull trout during various life stages. With the exception of headwater areas, there are numerous diversions and irrigation withdrawals along most of the WWR (Bower 2007) and MC. Several major irrigation diversions in the Walla Walla Basin alter the natural hydrograph, thus influencing seasonal habitat suitability for the associated biota, including bull trout. Major diversions on the mainstem WWR are the Little Walla Walla, East Side and Burlingame Diversions. The City of Walla Walla diverts water for municipal purposes from the headwaters of MC at approximately rkm 44.2 and the majority of MC surface flows are diverted through YHC to the WWR during summer and fall months to primarily augment lower river flows for irrigation withdrawals.

Channel modification – Flood control measures often require straightening of the channel, creation of levees to contain flood waters, and construction of grade control structures to dissipate energy from high water events. Major portions of the WWR and MC have been channelized for agricultural purposes, erosion control, flood abatement, urban development and the construction of roadways. Many of these alterations disconnect the river from its floodplain or severely constrain floodplain functions. Channel straightening and bank armoring constrain the channel, increase water velocity and the resulting habitat is often reduced or simplified due to wood removal, reduced vegetative cover and scouring (Chapman and Knudsen 1980; Carline and Klosiewski 1985). Grade control structures impede fish movement (USFWS 2002). Levees, dikes and concrete flumes homogenize stream reaches by restricting natural hydrological functions, decreasing sinuosity, reducing habitat complexity, and restricting the growth of streamside vegetation (USFWS 2002; ODEQ 2001). To help coarsely delineate aquatic habitat reaches, we classified river segments in the SFWWR, WWR, MC and YHC into five general channel modification classes:

Not modified – Natural, principally unmodified channel conditions lacking any significant or notably consequential channel restrictions, confinement, straightening or armored banks.

Minimal modification – Nearly natural, groundwater and hyporheic conditions, subjected to only minimal anthropogenic alterations.

Moderate modification – The river channel has commonly been modified, restricted, confined, straightened or armored.

Highly modified – The river channel has been restricted, significantly straightened and confined by levees or dikes.

Severely modified – The river channel is severely restricted, straightened and confined within a concrete flume or canal.

Stream gradient – Stream gradient can be an important determinant in the distribution of fish (Maret et al. 1997; Rich et al. 2003). Seasonally, bull trout are found in a wide range of stream types, but their presence may be limited in small, high gradient headwater streams (Rich et al. 2003). The channel gradient determines the potential energy of a stream channel, affecting water velocity and the water's ability to move bed and bank material in a stream channel. The interaction of channel gradient and other geomorphic and hydraulic variables drives the movement and subsequent deposition of materials, influencing habitat characteristics within a stream channel. Although channel gradient is generally determined by the geomorphologic disposition of a stream, anthropogenic activities that alter bedload or straighten a stream channel may directly impact channel gradient in a given reach. To help coarsely delineate habitat reaches, we calculated the stream gradient every 10 km in the WWR and MC subbasins. We simply divided the range of stream gradients into five categories and classified the 10 km segments accordingly:

High Gradient – Gradients > 4.2%
Fairly High Gradient – Gradients > 3.2 – 4.2%
Moderate Gradient – Gradients > 2.1 – 3.2%.
Fairly Low Gradient – Gradients > 1.1 - 2.1%
Low Gradient – Gradients ≤ 1.1%

Land use ─ Human activities on the landscape that affect water or sediment supply or that stabilize or destabilize the existing channel shape often eventually lead to changes that ultimately result in altered and degraded stream habitat (Allan 2004). Land use practices may influence instream habitat in differing ways. The impacts of forested and minimally developed areas may be minimal, but more invasive agriculture practices often considerably influence the quality of instream habitat. These impacts often include altered riparian vegetation, bank stabilization and increased sedimentation in streams. Agriculture practices can contribute sediment to streams in several ways. The bare soil left between rows and during cultivation exhibited in row-crop agriculture including wheat, onions and corn, is easily eroded and may be transported to streams and rivers during runoff (Waters 1995). Orchards and vineyards may contribute less sediment during runoff than row-crop agriculture, but chemical treatments may adversely affect water quality. Pasture land and the associated livestock may contribute to soil erosion and changes to the riparian areas depending upon the type of livestock raised, density and management practices. In addition, urban development results in impermeable surfaces and altered landscapes that may contribute pollutants and increased surface runoff to stream channels. To help coarsely delineate habitat reaches, we classified land use adjacent to riparian areas in the WWR and MC subbasins into the following five categories:

Forested, wildlife refuge or wilderness ─ Forested, wildlife refuge or wilderness areas generally have the least detrimental impact on the quality of riverine habitat.

Agriculture – orchards/vineyards ─ Land converted to agricultural uses such as orchards and vineyards likely negatively impact riverine habitat, but the impacts are likely minor relative to other anthropogenic land uses.

Agriculture – pasture land ─ Pasture land and the associated livestock are often detrimental to riparian and riverine habitat if not managed appropriately, but the impacts are likely minor relative to other anthropogenic land uses.

Agriculture – row crops ─ Erosion, fertilizer, insecticides and sedimentation from cultivation all contribute to row crop agriculture being detrimental to neighboring riverine and riparian areas.

Urban development ─ Impermeable surfaces, increased surface runoff, altered landscapes, and pollutants associated with urban development all severely impact riparian and riverine habitat.

Elevation ─ Elevation as an individual metric, cannot be directly linked to various aspects of bull trout biology like temperature or other variables. However, an elevation or range of elevations can be utilized to represent and characterize a multitude of potential influences that may impact the growth, movement or survival of bull trout during various life stages and strategies. In the Walla Walla Basin, stream elevation is generally indicative of water temperatures, riparian composition and often influences precipitation type and magnitude. In addition, elevation can be used as a proxy to generally represent and characterize the occurrence of other influences and attributes including; road density, angling pressure/poaching, predation, pollutants and to grossly approximate the direct impacts of climate change. In the Walla Walla Basin, as elevation increases, road density and public access to streams and rivers generally decreases, likely reducing anthropogenic influences (e.g., angling pressure, harassment). Similarly, as elevation increases, the presence of non-native predators (e.g., smallmouth bass) and artificially elevated avian predation levels decrease. The collective characteristics of higher elevation areas may also lessen the direct effects of changing climatic trends than at lower, more impacted areas within the Walla Walla Basin. To help delineate habitat reaches within the WWR and MC subbasins, we categorized stream elevations by dividing the elevation range within the study area into five classes: low (≤ 433 m), fairly low (> 433 – 762 m), medium (> 762 m – 1091 m), fairly high (> 1091 – 1421 m) and high elevation (> 1421 m).

Geology – Geologic variation has important influences on habitat quality and potential (Long et al. 2006). Reaches of differing topographic disposition represent a suite of formative processes that may include but not be limited to soil formation, erosion, infiltration, precipitation and runoff. These processes are often difficult or labor-intensive to observe, sample and quantify but may significantly influence the structure and quality of instream habitat. To help coarsely delineate habitat reaches, we used aerial photographs and topographic information to coarsely categorize geologic reaches as uplands, foothills, and lowlands. We identified uplands as high elevation areas characterized by steep slopes and volcanic canyons that encompass the headwaters of the major tributaries to the WWR. Foothills are relatively gradual increases in elevation (hills) at the base of a mountain range with less dramatic slopes. The lowlands consist of a massive accumulation of deposited, unconsolidated sediments (coarse sands, gravels and clay) resulting in broad expanses of low elevation land lacking significant changes in topography.

Bull trout life stages, strategies and actions

We elected to assess habitat quality, both spatially and temporally, as it relates to bull trout use. Through a retrospective review of data resulting from PIT array detections, snorkeling, trapping, angling and active monitoring studies (e.g., radio and acoustic telemetry) in the Walla Walla Basin, we identified specific strategies, behaviors and actions exhibited by bull trout during the differing life stages of resident and migratory life forms.

Modeling process

Identification of habitat variables

Aquatic habitat within the study area was coarsely delineated into 22 definable, largely homogenous segments with a unique suite of habitat characteristics that differ from neighboring stream reaches. The model calculates a monthly habitat quality score (HQS) for each reach in relation to each bull trout life stage, strategy or action based on the following eleven habitat variables (HV): surface flow (HV1), groundwater (HV2), water temperature (HV3), passage impediments (HV4), channel modification (HV5), riparian zone (HV6), stream gradient (HV7), elevation (HV8), land use (HV9), geology (HV10) and sinuosity HV11). Only variables that were biologically relevant were included and were chosen based on the authors' knowledge of the species and the availability of relevant datasets. Input data for the model were based on available datasets, attributes measureable from topographic maps and aerial photographs, results from bull trout habitat studies and professional opinion.

Rating of habitat variables

Each variable was assigned a numeric "rating factor" (RF) to reflect the quality of each habitat variable within each reach during each month as related to each of the eight identified bull trout life stages, strategies and actions (Table 3.4). We elected to use the results from recent studies, empirical data and professional opinion to make well-reasoned judgments toward crafting criteria to characterize the quality of each habitat variable over a spectrum of five categories ranging from poor to high quality. Poor, low, fair, good and high quality habitat were assigned an RF of one, two, three, four and five, respectively, for each reach and month in relation to each stage, strategy and action exhibited by resident and migratory bull trout in the

Walla Walla Basin. The following criteria for assigning numeric rating factors are hereafter provided.

Surface flow – Streamflow in and of itself cannot be directly linked to fish biology like temperature or other water chemistry metrics. For example a flow of 100 cfs does not provide the same amount or quality of fish habitat in steam A vs. steam B, or even in a different section of the same stream. Obviously, the relationships between specific geomorphic features within a stream channel, and the quantity of surface flow profoundly influence the quality and quantity of available aquatic habitat within a given stream reach. In the absence of intensive instream flow habitat assessments throughout the Walla Walla Basin, we have chosen to employ a simplified and straightforward approach to rating monthly streamflow conditions within specific stream reaches. This approach makes the reasonable assumption that more high quality bull trout habitat is available in reaches with less depleted and near normative the streamflow. By comparing the monthly average mean daily discharge (MAMDD) with an estimate of a near normative, non-diverted monthly average mean daily discharge (NDMAMDD) for each reach, we can grossly characterize habitat quality in terms of flow. To calculate a monthly streamflow value for each reach, we averaged the available mean daily discharge for each month from stream gauge data collected from 2002 – 2011. For reaches lacking a stream gauge, we used the nearest established stream gauge data that would reasonably represent surface flow within the given reach. For reaches where major diversions or tributaries affect streamflows, we made deductions and additions using available diversion and tributary gauge data as necessary. For the furthest upstream reach in the SFWWR (SFWW1), no representative gauge data exists. To estimate MAMDD for this reach, we used seepage run data (Bower 2007) to approximate Reser Creek's contribution to SFWWR streamflow and subtracted that percentage from the MAMDD for SFWW2. To coarsely estimate a NDMAMDD value for each reach, we cumulatively added MAMDD diversion discharge values from the major upstream diversions to the MAMDD values calculated for each reach as appropriate. We divided the MAMDD for each reach by the estimated NDMAMDD and multiplied by 100 to calculate a monthly percentage of "normal" discharge for each reach. These percentages, representing surface flow quality, were rated using a scale from 1 – 5 based on criteria provided in Table 3.1.

Groundwater – Gaining and losing reaches exist within the Walla Walla Basin and are often influenced by groundwater inputs and hyporheic exchange (Bower 2007). Hyporheic exchange occurs when surface water enters the riverbed and flows along subsurface paths before returning to the main channel. Baxter and Hauer (2000) found that bull trout redds were primarily found in alluvial valley segments which possessed complex patterns of hyporheic exchange and extensive upwelling zones. They further discussed the importance of spatial scale, citing the example that most bull trout redds were actually found at localized downwelling areas within zones of extensive upwelling. Downstream from the spawning grounds, this exchange removes heat/water from the channel when temperature/discharge is high and releases heat/water to the channel when temperature/discharge is low (Grant et al. 2006). This mechanism can afford potential thermal refuge in cold water pockets within stream reaches during periods of heat stress in addition to discrete warm water refugia during extremely cold periods, thus positively influencing survival (Ebersole et al. 2003). Seasonal irrigation withdrawals have altered the natural hydrograph and portions of the WWR and MC are nearly dewatered seasonally. In losing reaches, during severely depressed streamflows, the change from surface to hyporheic flow likely contributes to instream passage impediments and hinders the movements of migratory fish.

For this assessment, we employed a simplified approach by assigning a numeric rating of 1 – 5 based on the criteria provided in Table 3.2. We chose to rate groundwater influence at the reach scale for this assessment by primarily using data in Bower (2007), Baker (2011), Scherberg (2012) and low flow barrier assessments (Appendix III) and by professional judgment. Reaches determined to be of high quality in terms of groundwater influence for bull trout received higher ratings. Reaches where groundwater and hyporheic flows have been altered or do not positively influence bull trout habitat quality received lower ratings.

Water temperature – The spatial distribution of temperatures within streams has long been recognized as a factor influencing fish distribution (Ebersole et al. 2003). The longitudinal heating of instream water along the river continuum can limit fish distribution or impact the ability of a fish to compete or avoid predation. Bull trout spawning, movement patterns, foraging and survival are all closely tied to water temperatures. In addition, the interaction of surface water with the influx of groundwater or hyporheic exchange can result in pockets of thermal refugia within streams that may allow fish to avoid thermally stressful temperatures and tolerate otherwise limiting temperature regimes. The EPA has recommended water temperature standards to protect bull trout during various life stages and strategies that include upper optimum thresholds of 9°C (7DADM) for spawning, 12°C (7DADM) for juvenile rearing and 16°C (7DADM) for foraging and migration. A simple optimal versus non-optimal designation lacks the level of detail appropriate to more accurately assess existing aquatic habitat conditions. We used these general EPA recommendations as a baseline for developing criteria for rating bull trout habitat quality in terms of temperature for each of the identified stages, strategies and actions exhibited by resident and migratory life forms. To this end, we elected to use the results from recent studies, empirical data and professional opinion to make well-reasoned judgments toward crafting criteria to characterize temperature conditions over a spectrum of five categories ranging from poor to high quality (Table 3.3) for each stage, strategy and action exhibited by resident and migratory bull trout in the Walla Walla Basin.

Bull trout spawn in headwater stream reaches that are characterized by consistently cold water temperatures, high water quality, and clean gravel. The threshold spawning temperature for bull trout has been reported at approximately 9°C (McPhail and Baxter 1996). Although spawning generally occurs from 5 – 9°C (Walla Walla Subbasin Plan 2004), bull trout have been known to spawn in temperatures exceeding the threshold. Moore et al. (2006) determined that bull trout likely spawned while experiencing seven day average daily maximum (7DADM) temperatures ranging from 7°C to as high as 16°C.

Following spawning, both adult and non-spawning adult migratory bull trout (≥ 300 mm) move from smaller tributaries and upper stream reaches into larger streams and downriver reaches to overwinter in areas of upwelling groundwater and in deep pools (Craig and Bruce 1982; Stuart and Chislett 1979; McPhail and Baxter 1996; Stewart et al. 1982). Adults and larger sub-adults in the Walla Walla Basin generally migrate rapidly downstream during fall months to overwinter and forage in the SFWWR, WWR, MC, YHC and the mainstem Columbia River (Starcevich et al. 2012; Anglin et al. 2008a, 2008b; Barrows 2012; Mahoney 2003) where there is presumably greater potential for growth, caloric recuperation and gonad development (Gray 2005). Brenkman (1998) observed a surge in fall bull trout migration once water temperature declined to 10°C. Jakober et al. (1998) observed migratory adult downstream movement when daily average temperatures reached 6°C. Jakober et al. (1998) also observed winter downstream movement when temperatures were 1°C or lower and extensive subsurface ice formed.

Unlike migratory forms, resident bull trout typically remain in tributary streams near spawning grounds throughout life (Rieman and McIntyre 1993). By not migrating, resident individuals are unable to take advantage of the more abundant resources in lower basin areas and as a result often experience temperatures that limit foraging, growth and fecundity. A bioenergetics model

(Mesa et al. 2013) estimated temperatures for maximum consumption for bull trout at 15.8-17.5°C and found that consumption and metabolic rates generally declined as temperatures decreased. The EPA recommends temperatures < 12°C for juvenile rearing and Selong et al. (2001) found that feed consumption of age-0 bull trout declined at temperatures greater than 16°C and that small bull trout will stop feeding when temperatures exceed 22°C. Migrant individuals take advantage of more abundant resources in lower basin areas (Starcevich et al. 2012; Anglin et al. 2008a, 2008b; Barrows et al. 2012b; Mahoney 2003) where there is presumably greater potential for growth, caloric recuperation and gonad development (Gray 2005) and as a result, reach sizes in excess of 400 mm (Rieman and McIntyre 1993). If temperatures and oxygen consumption are within an adequate range and nutrition is sufficient, energy can be shunted toward growth and reproduction.

There are two types of upstream adult bull trout migrations and a largely concurrent sub-adult downstream migration in the Walla Walla Basin. The predominant upstream migratory pattern is a prespawning migration that begins following overwintering and ends when the approximate spawning location is reached within a natal stream. The second migratory pattern is similar to the prespawning migration only the adult sized bull trout oversummer short of entering the spawning grounds and do not spawn. Howell et al. (2010) found that migratory adult bull trout began migrating when 7DADM increased from 11°C to 12°C and others initially moved upstream from lower river areas when temperature increased from 12°C to 14°C. Swanberg (1997) found that migration occurred once water temperatures increased to 17.7°C in the Blackfoot River, Montana. Jones et al. (2013) predicted that peak thermal preferences (mean daily) during the month of August for bull trout foraging and migration were predicted at >10°C and <14°C, decreased significantly below 10°C, and ceased to exist above 16°C. EPA guidelines recommend 7DADM temperatures of 16°C as an upper optimal temperature threshold for bull trout migration (EPA 2003) but migratory adults and sub-adults often endure temperatures exceeding this value. Howell et al. (2010) determined that migratory bull trout in the Lostine River were exposed to 7DADM temperatures peaking at 18-25°C. Dunham et al. (2003) predicted that bull trout may be present at potentially lethal temperatures, but the probability of occurrence is relatively low at maximum daily temperatures above approximately 14-16°C and becomes high at approximately 11-12°C. Mortality (at least for age-0) has been shown to occur in less than 24 h when bull trout are exposed to temperatures at or above 26°C (Selong et al. 2001). Often, as temperatures become less tolerable and streamflows drop to summer base flows, sub-adult bull trout that had recently migrated to middle and lower river reaches often retreat back upstream to escape intolerable conditions and find suitable habitat to oversummer.

We used EPA recommendations as a baseline and the abovementioned information to develop criteria for rating bull trout habitat quality in terms of temperature for each of the identified stages, strategies and actions exhibited by resident and migratory life forms (Table 3.4).

7DADM temperatures (°C) from available thermograph data representing each aquatic habitat reach from 2002 to 2011 were compiled. For each reach, the average of the 7DADM temperatures for each month was averaged across years. The resulting temperature value for each reach was then rated using the abovementioned habitat quality criteria for each bull trout life stage, strategy or action. When representative data was not available for a given reach, temperature data from the closest thermograph was used to supplement absent data.

Passage impediments – Development of tributaries and river systems within the Walla Walla Basin for flood control, irrigation withdrawals and municipal purposes has significantly altered aquatic conditions for migratory salmonids, potentially limiting the ability of a fish to migrate freely throughout the Basin. Impediments to movement may limit bull trout access to habitat that allows for the full expression of various bull trout life stages and strategies and may inhibit connectivity with other populations. Although dams and diversion structures are the most obvious and visible potential impediments to fish movement, gravel push-up irrigation dams and recreation dams (i.e., swimming) may adversely affect seasonal bull trout movement as well.

Surface flows in the WWR and many of its tributaries have historically been over-appropriated for irrigation and municipal purposes (Siemann and Martin 2007) resulting in seasonally depressed streamflows and dewatering in middle and lower basin reaches. The 1998 ESA listing of bull trout as threatened led to a Civil Penalty Settlement Agreement between the FWS and two major irrigation districts in the Walla Walla Basin. Goals of this agreement were to maintain surface water connectivity, provide enough seasonal surface water to maintain ecological functions such as invertebrate production, and to provide enough streamflow for bull trout migration and rearing (Anglin et al. 2003). Despite efforts to increase in-river surface flows during the irrigation season, low flow barriers persist in portions of the WWR (Appendix III).

Management concerns for adult migrants include delays and increased exposure to predation and increased incidental angling pressure or poaching exacerbated by passage impediments. Similarly, downstream passage by both sub-adults and adults may be seasonally delayed or inhibited by dams and diversions. In addition to anthropogenic impediments, there are also naturally occurring obstructions such as waterfalls, beaver dams or log jams. Extensive log and debris jams, though often naturally occurring, can profoundly affect bull trout movement, spawning and survival. Further, past logging practices and other land uses may exacerbate debris accumulations. Nelson and Nelle (2008) not only documented evidence that migratory bull trout movement was impeded by extensive log jams, but also directly linked numerous instances of entrapment and subsequent mortality to log and debris jams as well. For this aquatic habitat assessment, reaches were rated monthly based on the presence or absence, as well as severity of passage impediments according to the criteria provided in Table 3.5.

<u>Channel modification</u> – Flood control measures often require straightening of the channel, creation of levees to contain flood waters, and construction of grade control structures to dissipate energy from high water events. Major portions of the WWR and MC have been channelized for agricultural purposes, erosion control, flood abatement, urban development and the construction of roadways. Many of these alterations disconnect the river from its floodplain or severely constrain floodplain functions. Channel straightening and bank armoring constrain the channel, increase water velocity and the resulting habitat is often reduced or simplified due to wood removal, reduced vegetative cover and scouring (Chapman and Knudsen 1980; Carline and Klosiewski 1985). Grade control structures impede fish movement (USFWS 2002). Levees, dikes and concrete flumes homogenize stream reaches by restricting natural hydrological functions, decreasing sinuosity, reducing habitat complexity, and restricting the growth of streamside vegetation (USFWS 2002; ODEQ 2001). For this aquatic habitat assessment, reaches were assigned a monthly numeric rating based on the presence or absence, as well as severity of channel modification according to the criteria provided in Table 3.6.

<u>Riparian zone</u> – For this assessment, we define a riparian zone as the interface between land and the river or stream. These zones function as natural biofilters that protect the riverine environment from excessive sedimentation, polluted surface runoff and erosion. They supply nutrients to the stream, shelter for aquatic organisms and shade that is essential for stream temperature regulation (Lewis and Kovacic 1993). Riparian habitat plays a prominent role in supporting the biodiversity of a stream, and when altered, the functionality of the riverine

environment may be impaired. For this assessment, we have chosen to employ a simplified approach to rating the riparian conditions within specific stream reaches. The quality of the riparian habitat within each reach was rated on a scale of 1-5 based upon two main factors. The first is riparian area: the combined area of the riparian zone measured from each river bank to the adjacent anthropogenic land uses (e.g., pasture, farmland, and urban development) relative to the length of the reach. This measurement represents the general ability of the riparian zone to "buffer" potentially detrimental influxes to the river from the surrounding land uses. The larger the buffer zone area, the greater the ability of the riparian zone to mitigate pollutants. The correlation between buffer zone width and effectiveness diminishes beyond approximately 30 meters (Wenger 1999; Castelle et al. 1994). We limited buffer zone measurements to a maximum of 30 m along each bank of the river. The riparian buffer zone area within each reach was derived from aerial photographs using GIS software. The total riparian buffer zone area within each reach was divided by the length of each reach. The resulting value was assigned a rating from 1-5 based on the criteria provided in Table 3.7. The second factor used to rate the quality of the riparian zone is the relative density of mature canopy trees within the riparian zone within each reach. As riparian canopy cover increases, the quality of aquatic habitat increases, indicating the importance of woody riparian vegetation (Ward et al. 2003). This measurement was approximated from aerial photographs and rated on a scale of 1-5 based on criteria described in Table 3.8. The assigned ratings from both of the abovementioned factors for each reach was averaged and rounded to the nearest whole numeric value to obtain a total riparian zone HQS for the reach.

Stream gradient – Stream gradient can be an important determinant in the distribution of fish (Maret et al. 1997; Rich et al. 2003). Seasonally, bull trout are found in a wide range of stream types, but their presence may be limited in small, high gradient headwater streams (Rich et al. 2003). Relatively low channel gradients within reaches of higher order streams have been listed as an important component for bull trout spawning (Shepard et al. 1984; Graham et al. 1981). The channel gradient determines the potential energy of a stream channel, affecting water velocity and the water's ability to move bed and bank material in a stream channel. The interaction of channel gradient and other geomorphic and hydraulic variables drives the movement and subsequent deposition of materials, influencing habitat characteristics within a stream channel. High flow events (e.g., rain on snow) may scour or bury bull trout redds, especially in relatively higher gradient reaches. Further, the presence of slower velocity habitat, suggested to be important for rearing bull trout (Baxter 1995; Baxter and McPhail 1996; Environmental Management Associates 1993), may be limited in higher gradient reaches. Although channel gradient is generally determined by the geomorphologic disposition of a stream, anthropogenic activities that alter bedload or straighten a stream channel may directly impact channel gradient within a given reach. This may limit overwintering and foraging habitat in lower reaches in the Walla Walla Basin. In addition, lower gradient portions of middle and lower reaches result in areas of extensive gravel deposition. As surface flows are depleted during the irrigation season, low flow barriers to bull trout movement arise in these depositional areas, likely limiting both migratory adult and sub-adult bull trout movements. For this assessment, we have chosen to employ a simplified approach by assigning a numeric rating of 1 – 5 to elevation ranges that generally represent poor, low, fair, good and high quality habitat, respectively in terms of the abovementioned impacts and influences. Stream gradients for each reach were derived via GIS software. We divided the range of stream gradients into 5 categories and rated each reach according to the criteria provided in Table 3.9.

Elevation – Elevation as an individual metric, cannot be directly linked to various aspects of bull trout biology like temperature. However, a particular elevation or range elevations can be used to represent a multitude of influences that potentially impact the growth, movement and survival of bull trout during various life stages and strategies. In the Walla Walla Basin, stream elevation is generally indicative of water temperatures, riparian composition and influences precipitation type and magnitude. In addition, elevation can be used as a proxy to generally represent and characterize the occurrence of other influences and attributes including; road density, angling pressure/poaching, predation and pollutants. Elevation can also be used to grossly approximate the direct impacts of climate change. In the Walla Walla Basin, as elevation increases, road density and public access to streams generally decreases, thus reducing anthropogenic influences (e.g., angling pressure, harassment). Similarly, as elevation increases, predation by non-native, piscivorous predators (e.g., smallmouth bass) and artificially elevated avian predation (e.g., cormorants, pelicans and terns) decreases. The collective characteristics of higher elevation areas may also lessen direct effects of changing climatic trends than at lower, more impacted areas within the Walla Walla Basin. Although aquatic habitat in lower elevation reaches may be critical to growth, movement and survival of bull trout at varying life stages, numerous conditions improve with increase elevation. For this assessment, we have chosen to employ a simplified approach by assigning a numeric rating of 1 – 5 to elevation ranges that represent poor, low, fair, good and high quality habitat, respectively in terms of the abovementioned impacts and influences (Table 3.10). With this approach, headwater areas will generally be influenced less by detrimental impacts associated with lower elevations.

Land use ─ Human activities on the landscape that affect water or sediment supply or that stabilize or destabilize the existing channel shape are likely to set off a complex cascade of changes that ultimately manifest in altered and degraded stream habitat (Allan 2004). Land use practices may influence instream habitat in differing ways. While forested and less developed areas may result in only minimally detrimental impacts, agriculture practices often considerably influence instream habitat by altering riparian vegetation, promoting bank destabilization and contributing sediment to streams. Agriculture practices can contribute sediment and pollutants to streams in several ways. The bare soil left between rows and during cultivation exhibited in conventional row-crop agriculture (e.g., wheat, onions, corn) is easily eroded and can be transported to streams and rivers during runoff (Waters 1995). Orchards and vineyards may contribute less sediment during runoff than row-crop agriculture, but chemical treatments (pesticides, fungicides and herbicides) may adversely affect water quality. Pasture land and the associated livestock may contribute to soil erosion and changes to the riparian areas depending upon the type of livestock raised, density and management practices. In addition, urban development results in impermeable surfaces and altered landscapes that may contribute pollutants and increased surface runoff to stream channels.

For this assessment, we used aerial photographs (Google Earth –TerraMetrix imagery dates 8/10/2011 and 9/6/2012) to identify and measure the longitudinal length of bordering land use types adjacent to or within riparian zones along both banks of the SFWWR, WWR, MC and YHC. Land use types were identified as forested/wildlife refuge (LU1), agriculture-pasture (LU2), agriculture-orchard/vineyard (LU3), agriculture-row crops (LU4), and urban development (LU5). The proportion (*p*) of each land use type longitudinally bordering aquatic habitat within each reach was calculated by dividing the total longitudinal length of each bordering habitat type by the total available length of the stream bank within the reach. Land use types were assigned a numeric rating from 1 – 5 (Table 3.11). The total numeric rating (TNR) for each habitat reach was calculated as follows and rounded to the nearest whole number:

$$TNR = (LU_1 \times p_1 + LU_2 \times p_2 + \ldots + LU_5 \times p_5)$$

Geology ─ Geologic variation has important influences on habitat quality and potential (Long et al. 2006). Reaches of differing topographic disposition represent a suite of formative processes that may include but not be limited to soil formation, erosion, infiltration, precipitation and runoff. These processes are often difficult or labor-intensive to observe, sample and quantify but may significantly influence the structure and quality of instream habitat. We used aerial photographs and topographic information (Google Earth –TerraMetrix imagery dates 8/10/2011 and 9/6/2012) to coarsely categorize geologic reaches as uplands, foothills, and lowlands. We identified uplands as high elevation areas characterized by steep slopes and volcanic canyons that encompass the headwaters of the major tributaries to the WWR. The abundance of bull trout redds has been found to increase within alluvial valley segments confined by geomorphic knickpoints (Baxter and Hauer 2000) commonly found within upland portions of drainages. Juvenile bull trout have been found to be associated with stable channels, relatively stable streamflows and low bed load movements commonly found in upland areas (Goetz 1989; Rieman and McIntyre 1993). Generally, upland tributaries and stream reaches are smaller in magnitude than downstream reaches. Larger fluvial adult bull trout (≥ 300 mm fork length) require overwintering and foraging habitat with deeper water and more abundant prey species that are more commonly found in reaches associated with lowland areas. Similarly, migratory sub-adult bull trout (< 300 mm fork length) move from upland reaches to foothill and lowland reaches in search of rearing, foraging and overwintering habitat that is more conducive to growth and connectivity with other populations. Foothills are relatively gradual increases in elevation (hills) at the base of a mountain range with less dramatic slopes. The riverine environment in foothill areas is transitional between the more polarized habitat conditions associated with upland and lowland areas. In the Walla Walla Basin, lowlands consist of a massive accumulation of deposited, unconsolidated sediments (coarse sands, gravels and clay) resulting in broad expanses of low elevation land lacking significant changes in topography. Low land, alleviated valley bottoms generally provide a diverse geomorphology comprised of deep pools, slow water velocities, adequate cover and provide relatively high prey availability when compared with upland reaches (Watson and Hillman 1997). These attributes generally contribute positively to the quality of habitat for fluvial sub-adult and adult bull trout foraging, rearing and migration. When surface flows in lowland reaches are severely depleted by irrigation withdrawals, the lower river channel geomorphology, fashioned by channel-forming discharge, no longer pairs with the instream flow to contribute positively to habitat conditions conducive to bull trout rearing or migration. For example, in a relatively natural riverine system, fluvial features such as gravel bars, riffles, and pools formed during channel-forming flows are subsequently redistributed by lesser flow events (Gendaszek et al. 2012). If the lesser flow events and associated channel dynamics are artificially reduced in magnitude or largely absent due to irrigation withdrawals, gravel bars can become instream barriers to bull trout movement (Appendix III). Using the abovementioned information for guidance, we coarsely assigned a numeric rating of one, three or five to habit reaches of poor, fair and high quality, respectively, in terms of geology as related to the eight bull trout life stages, strategies and actions (Table 3.12).

Sinuosity ─ River complexity is an important aspect of fluvial geomorphology, especially considering the anthropogenic regulation and channel modifications which have simplified many river systems. Complex rivers have a variety of microhabitats and refuges which can play a vital role in ecological processes, maintaining species richness and balancing aquatic communities (O'Neill and Thorp 2011). Flood control measures often require straightening of the channel, creation of levees to contain flood waters, and construction of grade control structures to dissipate energy from high water events. Major portions of the WWR and MC have been channelized for agricultural purposes, erosion control, flood abatement, urban development and the construction of roadways. Many of these alterations disconnect the river from its floodplain or severely constrain floodplain functions. Channel straightening and bank armoring constrain the channel, increase water velocity and the resulting habitat is often reduced or simplified due to wood removal, reduced vegetative cover and scouring (Chapman and Knudsen 1980; Carline and Klosiewski 1985). A high degree of sinuosity provides for diverse habitat and fauna, and the stream is better able to handle streamflow fluctuations. The absorption of energy by bends helps protect the stream from excessive erosion and provides for refugia for benthic invertebrates and fish during flow events. Intensive, aquatic habitat studies can explicitly evaluate the complexity of river reaches, but these studies are often expensive and improbable for an entire river basin. Therefore, for this assessment, we have chosen to employ a simplified approach that uses the sinuosity of a given reach to infer a coarse level of complexity for the given reach. We make the assumption that habitat within a reach becomes more complex as sinuosity increases. Further, we assume that higher complexity is generally indicative of higher quality habitat for bull trout at a given life stage to exhibit a certain strategy or conduct a particular action. For this assessment, we measured sinuosity within a given reach in 1000 m segments to best represent the complexity of the river channel. The resulting sinuosity values were divided into five categories. Each sinuosity category was assigned a numeric value using a scale of 1-5 ranging from poor to high quality, respectively (Table 3.13).

Weighting habitat variables

The suitability of aquatic habitat for a given action, process or function exhibited by bull trout during varying life stages, while exhibiting various strategies, is often influenced by many variables. The habitat variables (HV) that we believe to notably influence aquatic habitat suitability and function include surface flow (HV1), groundwater (HV2), temperature (HV3), passage impediments (HV4), channel modification (HV5), riparian zone (HV6), stream gradient (HV7), elevation (HV8), land use (HV9), geology (HV10) and sinuosity HV11). Some variables are more influential than others in affecting the quality of habitat for a given bull trout activity, process or function. To account for this, we assigned a "weighting factor" (WF) to each variable that reflects its importance relative to one another with respect to the particular activity process or function that bull trout engage in. An Analytic Hierarchy Process (AHP) method, adapted from Saaty (2008), was used to obtain the weights of the factors for habitat variables for each bull trout life stage, strategy or action. An AHP is a way to generate the approximate importance of the factors by using pair-wise comparisons and relies on the judgments of experts to derive priority scales (Saaty 2008). To make comparisons, we used a scale of numbers that indicates how much more important or influential one variable is over another variable with respect to the particular life-history stage, strategy or action (Table 3.14). To calculate weighting factors, experienced bull trout biologists used professional judgment to complete primary questionnaires to approximate the importance of each habitat variable relative to one another with respect to each of the 8 identified life-history stages, strategies and actions. An example of this questionnaire is provided in Appendix B. A consensus (mean) of the resulting answers to survey questions was used to populate a comparison matrix. Numbers from the comparison matrix were then normalized and weighting factors were derived.

Habitat quality scores

The suitability of aquatic habitat for a given activity, process or function exhibited by bull trout during various life stages and strategies, is often influenced by many variables. The habitat variables (HV) that we believe to notably influence aquatic habitat suitability and function include surface flow (HV1), groundwater (HV2), temperature (HV3), passage impediments (HV4), channel modification (HV5), riparian zone (HV6), stream gradient (HV7), elevation (HV8), land use (HV9), geology (HV10) and sinuosity HV11). Using the aforementioned rating criteria, we rated the quality of each habitat variable in each reach for each life stage, strategy or action for each month. We assessed habitat quality for all reaches and all months, regardless of known occurrence. Some variables are more influential than others in affecting the quality of habitat for a given bull trout activity, process or function, therefore the "weighting factor" that was determined by using the AHP method adapted from Saaty (2008) to each variable to reflect its importance relative to one another with respect to the particular life stage, strategy or action must be applied. The habitat quality score (HQS) for each reach for each month in terms of each life stage, strategy or action was calculated as follows:

$$HQS = (HV_1 \times WF_1 + HV_2 \times WF_2 + \cdots + HV_{11} \times WF_{11})$$

Model evaluation

To help evaluate model performance, one can compare model results with empirical data. Unfortunately, reach-scale temporal and spatial habitat assessments, in relation to the eight identified life stages, strategies and actions that Walla Walla Basin bull trout exhibit, are incomplete or do not exist. However, robust movement and distribution datasets exist for portions of the WWR and MC. To grossly evaluate model performance, we compared coarse spatial and temporal occurrence levels with modeled HQSs. Bull trout at certain life stages, exhibiting strategies and engaging in certain actions, are not always found in the highest quality habitat conditions. Similarly, bull trout can (and do) exist in habitat that is less than suitable. To this end, when comparing occurrence levels to HQSs, we would expect to see relationships indicating that reaches with higher monthly HQSs (i.e., higher quality habitat) are generally associated with higher levels of occurrence and that reaches with lower monthly HQSs are generally associated with lower occurrence levels. We would expect low and poor quality habitat to be generally associated with low or no bull trout occurrence when occurrence could be conceivable.

<u>Bull trout occurrence</u>

The riverine environment within the Walla Walla Basin is in a constant state of flux, driven primarily by perpetually changing abiotic conditions. Bull trout are ecologically connected and in constant interaction with their environment. The full expression of the many diverse life-history stages and strategies exhibited by bull trout depends upon the presence of suitable riverine environment and specific habitat requirements vary both spatially and temporally for differing life stages and strategies (Al-Chokhachy and Budy 2007; Rieman and McIntyre 1993; Saffel and Scarnecchia 1996). The temporal and spatial continuum of bull trout movement observed within the Walla Walla Basin further confounds the ability of resource managers to address specific management needs or threats. To accurately describe and assess habitat conditions with respect to specific bull trout life stages, strategies and actions, it is imperative to identify the temporal and spatial disposition and occupancy of habitat types and migration corridors within the SFWWR, WWR, MC, and YHC throughout the year.

For this assessment, we used datasets resulting from our extensive network of PIT detection arrays in addition to data from radio telemetry, snorkeling, acoustic telemetry, electrofishing, trapping and angling studies to coarsely summarize spatial and temporal occurrence with respect to the identified strategies and actions exhibited by the various life stages of bull trout within the SFWWR, WWR, MC and YHC. Occurrence within each reach for each month was classified into the following four categories and assigned scores with respect to each life-history stage, strategy or action:

High occurrence – A relatively high number of bull trout of a given life stage, exhibiting a certain strategy or conducting a specific action are known to occur within the reach during this given time period. Reaches with high occurrence were assigned a numeric score of 2.

Low occurrence – Bull trout of a given life stage, exhibiting a certain strategy or conducting a specific action are known to occur within the reach during this given time period, but only in relatively low numbers. Reaches with low occurrence were assigned a numeric score of 1.

Conceivable occurrence – Bull trout of a given life stage, exhibiting a certain strategy or conducting a specific action have either not been observed, or very rarely occur within the reach during this given time period. Occurrence within this reach may be possible albeit unlikely under current conditions. Reaches where occurrence is conceivable but not observed were assigned a numeric score of 0.

No occurrence – Bull trout of a given life stage, exhibiting a certain strategy or conducting a specific action are not known (and very unlikely) to occur within the reach during this given time period. Reaches with no occurrence received no numeric score.

Bull trout occurrence and model results comparison

For many reasons, bull trout at certain life stages, exhibiting strategies and engaging in certain actions, are not always associated with the alleged, highest quality habitat (Al-Chokhachy and Budy 2007). Similarly, bull trout can (and do) exist in habitat that is substantially less than optimal (Jakober et al. 1998; Moore et al. 2005; Swanberg 1997; Anglin et al. 2008a; Barrows et al. 2012b). For these reasons, expecting statistically defensible correlations between bull trout occurrence and the quality of habitat may be problematic due largely to naturally low abundances, especially in lower basin areas. Despite validation limitations, insight can be gained by overlaying occurrence information and HQSs to identify patterns and reaches where and when bull trout of varying life stages and strategies may be exposed to detrimental habitat conditions within the Walla Walla Basin and determine reaches where further investigation or management actions may be warranted.

Results

Modeling approach

Reach delineation

Aquatic habitat in the WWR and MC subbasins was delineated functionally by using specific attributes and relatively distinct breaks in channel morphology, hydrological channel junctions and other attributes. Stream habitat was delineated into 22 definable, largely homogenous segments representing a different physical setting that differ from neighboring segments (Table 3.15). Brief, summarized descriptions of each habitat reach are provided in Table 3.16, and reach specific narratives are provided in Appendix C. Figure 3.2 identifies and depicts the geographical location of study reaches.

Bull trout life stages, strategies and actions

Habitat quality was assessed, both spatially and temporally, as it relates to a multitude of varying, and often concurrent, bull trout uses. Through a retrospective review of data resulting from PIT array detections, snorkeling, trapping, angling and active monitoring studies (e.g., radio and acoustic telemetry) in the Walla Walla Basin, we identified 8 specific strategies and actions exhibited by bull trout during the differing life stages of resident and migratory forms. General descriptions and definitions of these specific lifecycle strategies and actions are hereafter provided.

Adult spawning

Resident bull trout complete their entire life cycle in the headwater streams in which they spawn and rear (Rieman and McIntyre 1995; Fraley and Shepard 1989). Migratory bull trout return from downstream reaches to spawn in headwater streams along with resident bull trout (Fraley and Shepard 1989). The size and age of bull trout at maturity depends upon life-history strategy, but both non-migratory (i.e., resident) and fluvial bull trout reach sexual maturity in four to 7 years (USFWS 2002). Both resident and migratory bull trout occupy reaches near their intended spawning grounds prior to spawning and either form may give rise to offspring exhibiting either resident or migratory behavior (Rieman and McIntyre 1993). Generally, spawning takes place between late August and early November. In the Walla Walla Basin, most spawning has been observed from August through October upstream of Harris County Park (rkm 95.5). Occasionally, migratory bull trout have been observed engaging in spawning behavior in downstream reaches, but this occurrence is decidedly rare. In MC, most spawning occurs upstream from the City of Walla Walla Intake Dam (rkm 44.2), but limited spawning has been observed downstream of the dam. A strictly non-migratory population resides in Low Creek, a headwater tributary to MC.

Juvenile rearing, foraging and growth

Optimal egg incubation temperatures are generally less than 8 °C and survival is optimal from 2 to 4°C (Goetz 1989; McPhail and Murray 1979). Depending on water temperature, the in-gravel incubation and yolk-sac absorption period may span from 6 to 8 months (Parametrix 2005). Juvenile bull trout are bottom dwellers and newly emerged bull trout fry may use shallow, complex backwater areas of streams and occupy interstitial spaces in the streambed (Baxter 1995; Brown 1992). For approximately the first 1 to 3 years following hatching, juvenile bull trout rear in or near their natal tributary (Bjornn 1991; Goetz 1989; Fraley and Shepard 1989). Juvenile bull trout primarily feed on terrestrial and aquatic insects, macro-zooplankton, amphipods, mysids and other zoobenthos (Parametrix 2005). There is likely a shift in prey species composition as well as the quantity consumed that corresponds to the spatial and temporal disposition and metabolic needs of a juvenile bull trout.

Fluvial adult upstream migration

Migratory adult bull trout return to ascend the WWR from overwintering in the lower WWR and Columbia rivers beginning in March and continuing into July (Barrows et al. 2012b; Barrows et al. 2014). Adult sized bull trout (fork lengths ≥ 300 mm) evacuate lower basin areas and begin to occupy upper basin reaches on the descending limb of the hydrograph (Mahoney 2003; Mahoney et al. 2006; Barrows et al. 2012a, 2012b, 2014; Anglin 2008b; Koch *in review*) as temperatures in lower and middle basin areas become less tolerable. Similar movement patterns have been documented in other basins (Starcevich et al. 2012; Dupont et al. 2007; Swanberg 1997; Schoby and Keeley 2011). Recently, multiple adult-sized bull trout have been observed migrating upstream from middle and lower basin reaches in the WWR and entering the NFWWR. After staying in the NFWWR (presumably foraging on abundant prey species) from two to four weeks, they resumed migrating upstream to the headwater reaches of the

SFWWR (Barrows et al. *in review*). Most of the fluvial adults reach near-spawning areas by July and hold until triggered to spawn. In addition to migratory adult bull trout, there are also adult-sized, nonspawning migratory bull trout in the Walla Walla Basin. These include fish that are ≥ 300 mm that migrate upstream from lower reaches, but oversummer short of the spawning reaches. Bull trout exhibiting a similar migration and life-history pattern were observed in the Blackfoot River Basin in Montana (Swanberg 1997).

Adult foraging and maintenance

Resident and migratory adult bull trout are primarily piscivorous, actively foraging predators (Fraley and Shepard 1989; Schoby and Keeley 2011; Rieman and McIntyre 1993). Although foraging on fish where available, there is likely a shift in prey species composition as well as the quantity consumed that corresponds to the spatial and temporal disposition and metabolic needs of migratory adult bull trout as well as prey availability. For example, an analysis of bull trout stomach samples by Schoby and Keeley (2011) revealed that samples from adult fish in the mainstem Salmon River (Idaho) contained 74% fish prey items. In contrast, stomach samples from adult bull trout in tributaries within the drainage were dominated by aquatic invertebrates (87% of prey items). Both postspawning and nonspawning migratory adult bull trout move from smaller tributaries and upper stream reaches into larger streams and downriver reaches to overwinter and forage. Adult fish arrive at overwintering locations from September through February. Adult bull trout overwinter in suitable habitat throughout the Walla Walla Basin and were recently documented in the mainstem Columbia River (Barrows et al. 2012b, 2014). Fish are known to show a high degree of winter location fidelity, often returning to previously occupied reaches in consecutive years (Mahoney 2003; Mahoney et al. 2006; Starcevich et al. 2012). Bull trout overwinter in areas of upwelling groundwater and in deep pools (Craig and Bruce 1982; Stuart and Chislett 1979; McPhail and Baxter 1996; Stewart et al. 1982) within a wintering range prior to the upstream spawning migration (Starcevich et al. 2012) and generally remain within the reaches until water temperatures and flows begin to increase in March.

Fluvial adult downstream migration

Following spawning, adult migratory bull trout move from smaller tributaries and upper stream reaches into larger streams and downriver reaches to overwinter in areas of upwelling groundwater and in deep pools (Craig and Bruce 1982; Stuart and Chislett 1979; McPhail and Baxter 1996; Stewart et al. 1982). Although the timing varies among basins, most bull trout begin their postspawning migration from September to November (Starcevich et al. 2012). Postspawning adults in the Walla Walla Basin generally migrate rapidly downstream to overwintering and foraging habitats (Starcevich et al. 2012; Anglin et al. 2008a, 2008b; Barrows 2012, 2014; Mahoney 2003) where there is presumably greater potential for growth, caloric recuperation and gonad development (Gray 2005). An atypical movement pattern involving an initial downstream migration and subsequent upstream migration into an adjacent tributary or river to overwinter has been documented in other basins (Starcevich et al. 2012; Dupont et al. 2007). A similar pattern has been recently observed in the Walla Walla Basin, where postspawning adults migrate from spawning reaches in the SFWWR to overwinter in the NFWWR (Barrows et al. *in review*; Mahoney et al. 2006). Most downstream movement of adult-sized migratory bull trout declines through the winter months and ceases in February (Anglin et al. 2009a, 2009b, 2010; Barrows et al. 2012a, 2012b, 2014). In addition to postspawning bull trout, there are also adult-sized, nonspawning migratory bull trout in the Walla Walla Basin. These include fish that previously migrated upstream, but did not enter the spawning reaches. Having not recently spawned, fish exhibiting this migration strategy may be utilizing downstream resources to maximize growth potential and to further mature as opposed to recuperating following spawning.

Fluvial sub-adult downstream migration

After 2 to 3 years, fluvial sub-adult bull trout migrate downstream to mainstem river reaches (Goetz 1989). In the Walla Walla Basin, migratory sub-adult bull trout (fork length < 300 mm) initially begin migrating downstream from headwater spawning and juvenile rearing areas in the spring (March) during high flows and as water temperatures begin to rise. Migratory sub-adult bull trout tend to use deeper areas (runs and pools) containing unembedded boulder and cobble substrate and large woody debris as they make incremental downriver movements to lower basin areas (Muhlfeld and Marotz 2005). This downstream migration continues to occur on the declining portions of the hydrograph throughout middle basin areas through July. Spring migrant sub-adult bull trout have been detected moving into areas downstream of Burlingame Dam (rkm 60.3). As irrigation diversions draw surface water to summer base flows and water temperatures elevate, there is a short cessation of movement during peak summer months before downstream migration resumes during fall and winter months to middle and lower basin reaches of the WWR and into the mainstem Columbia River (Anglin et al. 2009a, 2009b, 2010; Barrows et al. 2012b, 2014) where they occasionally disperse downstream far enough to connect with other basins including the Umatilla River (Small et al. 2012; Barrows et al. 2014). Most downstream movement of adult-sized migratory bull trout declines throughout late winter and ceases in February (Anglin et al. 2009a, 2009b, 2010, 2010a; Barrows et al. 2012b, 2014).

Fluvial sub-adult upstream movement

The spatial distribution of temperatures within streams has long been recognized as a factor influencing fish distribution (Ebersole et al. 2003). The longitudinal heating of instream water along the river continuum can limit fish distribution or impact the ability of a fish to compete or avoid predation. In the Walla Walla Basin, as water temperatures become less tolerable and irrigation diversions draw surface water to summer base flows, sub-adult bull trout that had recently migrated to middle and lower river reaches must seek refuge in deeper areas (e.g., pools) with adequate cover and groundwater influence or retreat back upstream to find more tolerable habitat conditions upstream to oversummer. In MC, sub-adult bull trout that migrate to reaches downstream of the Mill Creek Diversion Dam (rkm 20.1) and into YHC, have been observed subsequently returning to upstream reaches. A similar downstream, then subsequent upstream movement pattern has been documented in the WWR as well.

Fluvial sub-adult rearing, foraging and growth

After 2 to 3 years, fluvial sub-adult bull trout migrate downstream to mainstem river reaches (Goetz 1989) to forage and grow to adulthood. This downstream movement allows access to denser forage and alleviates potential intraspecific competition in rearing areas (Schlosser 1991). Sub-adult bull trout are opportunistic feeders, and shift their diet as they grow and primarily prey upon terrestrial and aquatic invertebrates and small fish. As bull trout mature, they tend to rely less on invertebrates and may prey more exclusively on fish (Parametrix 2005; Pratt 1992). There is likely a shift in prey species composition as well as the quantity consumed that corresponds to the spatial and temporal disposition and metabolic needs of sub-adult bull trout.

Modeling process

Identification of habitat variables

For this assessment, we chose the following eleven habitat variables: surface flow, groundwater, water temperature, passage impediments, channel modification, riparian zone, stream gradient, elevation, land use, geology and sinuosity.

Rating habitat variables

Each variable was assigned a numeric "rating factor" to reflect the quality of each habitat variable within each reach during each month as related to each of the eight identified bull trout life stages, strategies and actions.

Weighting habitat variables

We requested survey participation from 18 bull trout experts and received from six to eight completed surveys per topic with which to create comparison matrices. Respondents included primarily fish biologists, a hydrologist and one graduate student studying bull trout movements. Experience ranged from approximately seven years to more than two decades. Derived weighting factors for each habitat variable in relation to each of the eight bull trout life stages, strategies or actions identified within the Walla Walla Basin are summarized in Table 3.17. Hierarchal results from completed surveys are hereafter provided.

Adult spawning – Among the eight bull trout experts that responded to the survey, water temperature was identified as the most influential variable in determining the quality of bull trout spawning habitat. Surface flow was also highly weighted, as were ground water and passage impediments. Riparian zone, stream gradient and elevation were identified as being moderately influential and sinuosity, geology and land use were rated as only slightly influential. Channel modification was weighted by bull trout experts as the least influential variable in determining the quality of bull trout spawning habitat.

Juvenile rearing, foraging and growth – The eight bull trout experts that responded to the survey identified water temperature as the most influential variable in determining the quality of juvenile bull trout rearing, foraging and growth. Surface flow was also highly weighted, as was riparian zone and groundwater. Sinuosity, passage impediments and elevation were identified as being moderately influential and stream gradient, channel modification and land use were rated as only slightly influential. Geology was weighted by bull trout experts as the least influential variable in determining the quality of habitat for juvenile rearing, foraging and growth.

Fluvial adult upstream migration – Results from seven respondents heavily weighted surface flow as the most influential variable in determining the quality of habitat for fluvial adult upstream migration. Passage impediments, water temperature and channel modification were determined to be highly influential as well. Ground water, land use, stream gradient and riparian zone were believed to be less influential. Sinuosity, elevation and geology were rated as the least important variables influencing the quality of aquatic habitat for fluvial adult upstream migration.

Adult foraging and maintenance – Survey results from six respondents weighted water temperature as the most influential variable in determining the quality of adult bull trout foraging and maintenance habitat. Surface flow was also weighted as highly influential. Riparian zone, channel modification, passage impediments and ground water were only moderately influential, followed by land use, sinuosity, elevation and stream gradient. Geology was identified as the least important variable influencing the quality of adult bull trout foraging and maintenance habitat.

Fluvial adult downstream migration – Seven bull trout experts that responded identified surface flow as the most influential variable in determining the quality of habitat for fluvial adult bull trout downstream migration. In addition to surface flow, water temperature and passage impediments were identified as very influential variables as well. Less influential variables included: channel modification, riparian zone, groundwater, land use, elevation and stream gradient. Sinuosity and geology were identified by bull trout experts as the variables that are least important for fluvial bull trout downstream migration habitat.

Fluvial sub-adult downstream migration – Six bull trout experts that responded identified water temperature as the most influential variable in determining the quality of habitat for fluvial sub-adult bull trout downstream migration. In addition to water temperature, surface flow, passage impediments and channel modification were identified as notably influential as well. Less influential variables included: riparian zone, ground water, land use, stream gradient, and elevation. Sinuosity and geology were identified by bull trout experts as the variables that are least important for influencing the quality of habitat for fluvial sub-adult bull trout downstream migration.

Fluvial sub-adult upstream migration – Results from seven respondents weighted surface flow, water temperature and passage impediments as the most influential variables in determining the quality of habitat for fluvial sub-adult upstream migration. Channel modification, ground water, land use and riparian zone were believed to be less influential. Stream gradient, sinuosity, elevation and geology were believed to be the least important variables influencing the quality of aquatic habitat for fluvial sub-adult upstream migration.

Fluvial sub-adult rearing, foraging and growth – Among the seven survey respondents, water temperature was identified as the most influential variable in determining the quality of fluvial sub-adult bull trout rearing, foraging and growth. Surface flow was also highly weighted, as were riparian zone and channel modification. Ground water, passage impediments and land use were identified as being moderately influential and sinuosity, elevation and stream gradient were believed to be less influential. Geology was weighted by bull trout experts as the least influential variable in determining the quality of habitat for fluvial sub-adult rearing, foraging and growth.

Habitat quality scores

Monthly habitat quality scores were calculated for each reach in relation to each bull trout life-history stage, strategy or action. To achieve a more comprehensive assessment, monthly habitat quality scores were calculated for each reach in relation to each life stage or strategy regardless of known or estimated temporal or spatial occurrence or occupancy.

Spawning – Modeled scores indicate that good and high quality spawning habitat exists in the upper basin portions of the SFWWR and MC during all months (Table 3.18). Bull trout, being fall spawners, are known to spawn primarily from August through as late as November range-wide. Despite this narrow timeframe, we characterized the quality of habitat throughout the study area and during all months. Reaches SFWW1 and SFWW2 scored high during September through November, reaches SFWW1 – SFWW3 had good quality scores during August and SFWW3 and WW4 received good scores for September and October (Figures 3.3, 3.4, 3.5 and 3.6). Reach MC14 in MC scored as good during August through October and high scores were calculated for both MC14 and MC15 during November. Reaches downstream of WW5 scored as low and poor quality for spawning (average HQS of 1.96) primarily from June through October in the SFWW and WWR (Appendix D, Table D1). In MC, most reaches downstream of MC15 scored as low and poor quality conditions (average HQS of 1.78) from approximately May through November (Appendix D, Table D2).

<u>Juvenile rearing, foraging and growth</u> – Following hatching, juveniles rear in or near the spawning grounds, therefore we expect juvenile bull trout to occur in reaches SFWW1 through WW4 in the Walla Walla subbasin and reaches MC14 and MC15 in MC. Despite knowing the likely distribution of juvenile bull trout in the SFWWR and MC, we characterized rearing habitat for juvenile bull trout throughout the entire study area. Modeled scores indicate that high and good quality habitat for pre-migratory, juvenile bull trout rearing, foraging and growth exists within the aforementioned reaches during all months (Table 3.19). Reaches downstream of WW7 scored as low and poor quality conditions for juvenile rearing (average HQS of 2.18) from approximately June through September in the SFWWR and WWR (Appendix D, Table D4). In MC, most reaches downstream of MC16 scored as low and poor habitat quality conditions (average HQS of 1.85) from approximately June through December (Appendix D, Table D5). Figures 3.7, 3.8, 3.9 and 3.10 show the spatial distribution of habitat quality throughout the study area during February, May, August and November respectively.

<u>Fluvial adult upstream migration</u> – Migratory adult bull trout (fork lengths ≥ 300 mm) begin moving upstream from overwintering in the mainstem Columbia River and lower reaches of the WWR beginning in March. Upstream migration continues throughout the study area until most adult fish reach headwater spawning areas by July. Localized movement may occur within or near the spawning grounds prior to spawning from August through October as well. Modeled scores indicate that good habitat quality for upstream migrating adult bull trout exists from March through May in most reaches of the WWR and the SFWWR (Table 3.20). Habitat conditions worsen to fair or low quality during June from reach WW7 to reach WW12 and generally become low and poor quality through the summer months with average HQS of 2.27 (Appendix D, Table D7). In MC, modeled scores indicate that good habitat conditions exist for adult upstream movement in reaches MC14, MC15 and MC16 during most months. With the exception of May, most reaches from MC17 to MC21 received low and poor quality scores during most months. Yellowhawk Creek (YH22) received good habitat quality scores for upstream migrating adult bull trout during all months. Figures 3.11, 3.12, 3.13 and 3.14 show the spatial distribution of habitat quality throughout the study area during March, May, July and September respectively. Habitat quality conditions within the study area for fluvial adult bull trout upstream migration are further summarized in Appendix D.

<u>Adult foraging and maintenance</u> – For this assessment, adult bull trout are believed to be foraging, growing and recuperating (following spawning) during all months. Modeled scores indicate that habitat conditions are generally good throughout most reaches in the SFWWR and the WWR from December through May (Table 3.21). Habitat quality scores are highest from June through October in reaches SFWW1 through SFWW3. Scores indicate that fair, low and poor quality habitat exists from reach WW7 through WW13 from June to approximately November. In MC, the highest HQSs for adult foraging and maintenance occur from April through October in reach MC14. Reaches MC15 and MC16 received good HQSs during most months. Primarily fair habitat quality conditions exist in reaches MC17 through MC21 from January through April before deteriorating to low and poor quality from May through December. Reaches downstream of WW6 scored as low and poor for adult foraging (average HQS of 2.22) from approximately June through September in most SFWWR and WWR reaches (Appendix D,

Table D10). In MC, many reaches downstream of MC16 scored as low and poor habitat quality conditions (average HQS of 2.05) from approximately June through December (Appendix D, Table D11). Adult bull trout foraging and maintenance HQSs are further summarized in Appendix D. Figures 3.15, 3.16, 3.17 and 3.18 show the spatial distribution of habitat quality throughout the study area during February, May, August and November respectively.

<u>Fluvial adult downstream migration</u> – Following spawning, adult migratory bull trout move from smaller tributaries and upper stream reaches into larger streams and downriver reaches to overwinter. This generally occurs from September through as late as February. During this time period, scores for reaches SFWW1 through WW5 indicate either high or good quality habitat for adult downstream migration during all relevant months (Table 3.22). In addition, reaches WW6 through WW13 received high and good HQSs from December through February, but conditions were of fair and low quality for adult downstream migration from September through November. In MC, habitat in reaches MC14, MC15 and MC16 primarily scored as high or good quality from September through February. Habitat quality for reaches MC17 through MC20 was mostly fair from December through February, but low during October and November. Reach MC21 was of either fair or good quality during the relevant months. Yellowhawk Creek (YHC22) scored as good quality habitat for adult downstream migration during all months. Reaches downstream of WW6 scored as low and poor quality conditions for fluvial adult downstream migration (average HQS of 2.26) from approximately July through September in the SFWWR and WWR and averaged 3.85 when conditions in reaches were fair to high quality (Appendix D, Table D13). In MC, many reaches downstream from MC16 that scored as low and poor habitat quality averaged 1.94 from primarily June through December (Appendix D, Table D14). Figures 3.19, 3.20, 3.21 and 3.22 show the spatial distribution of habitat quality throughout the study area during September, October, November and December respectively.

<u>Fluvial sub-adult downstream migration</u> – Fluvial sub-adult bull trout (fork length < 300 mm) in the Walla Walla Basin generally migrate downstream during all months. Migratory sub-adults begin moving downstream from spawning areas in the spring (March) during high flows and as water temperatures begin to rise and make incremental downriver movements to lower basin areas until approximately August. Downstream migration resumes during fall months through February. The highest quality habitat for fluvial sub-adult bull trout migration exists primarily within reaches SFWW1 through WW4 during all months (Table 3.23). Reach WW5 scores indicate good quality habitat during all months. Primarily good and high quality habitat exists in reaches WW6 through WW13 from December through April but decrease to mainly fair and low quality habitat from June through October. In MC, scores indicate that high quality habitat exists within reach MC14 during all months and reach MC15 contains good quality habitat year-round. Reach MC16 through MC21 scored as primarily good or fair quality habitat from December through May but habitat quality declined to mainly low and poor from June through November. Scores indicate that good quality habitat for downstream migrating sub-adult bull trout exists during most months in reach YHC22. Figures 3.23, 3.24, 3.25 and 3.26 show the spatial distribution of habitat quality throughout the study area during March, June, September and December respectively. Habitat quality scores for sub-adult downstream migration are further summarized in Appendix D.

<u>Fluvial sub-adult upstream movement</u> – As temperatures become less tolerable and streamflows drop to summer base flows, sub-adult bull trout that had recently migrated to middle and lower river reaches often retreat back upstream to escape intolerable conditions and find suitable habitat to oversummer. Habitat quality for upstream sub-adult movement is primarily good from reach WW6 to WW13 during May, but declines to fair scores in June and to low and poor quality in July and August (Table 3.24). Model scores in reaches MC17 through

MC21 indicate fair and good quality habitat in May, but decline to primarily low quality in June and poor quality in July and August. Habitat quality for sub-adult upstream movement is good in May and June and fair during July and August in reach YHC22. Figures 3.27, 3.28, 3.29 and 3.30 show the spatial distribution of habitat quality throughout the study area during May, June, July and August respectively. Reaches in the SFWWR and the WWR that scored as low and poor habitat quality conditions (average HQS of 2.22) for sub-adult upstream movement were generally downstream of WW6 and from July to September and into October. Reaches in MC that scored as low and poor habitat quality conditions (average HQS of 1.96) were downstream of MC16 and conditions persist from approximately June through November in most of the reaches (Appendix D, Table D20).

<u>Fluvial sub-adult rearing, foraging and growth</u> – After 2-3 years of rearing in headwater reaches, fluvial sub-adult bull trout migrate to downstream reaches to access denser forage and utilize habitat that is more metabolically favorable for growth. In the SFWWR and the WWR, model scores indicate primarily good and high quality habitat for sub-adult rearing, foraging and growth in reaches SFWW1 through WW4 during all months. Reaches WW5 and WW6 received scores ranging from fair to good during most months (Table 3.25). Habitat quality scores were either good or fair in reaches WW7 through WW13 from December through June and declined to mostly low and fair quality during July, August and September. In MC, reaches MC14 through MC16 primarily scored as good quality habitat during most months. Reaches MC17 through MC21 scored as low, poor or fair quality habitat from June through February. Reach YHC22 was either fair or good quality habitat during all months. Reaches in the SFWWR and the WWR that scored as low and poor habitat quality conditions (average HQS of 2.24) for sub-adult upstream movement were generally downstream of WW6 and persisted in some reaches from July to November (Appendix D, Table D22).from July to September and into October. Reaches in MC that scored as low and poor habitat quality conditions (average HQS of 2.03) were downstream of MC16 from approximately June through February in some reaches. Figures 3.31, 3.32, 3.33 and 3.34 show the spatial distribution of habitat quality throughout the study area during February, May, August and November, respectively.

Model evaluation

<u>Bull trout occurrence</u>

We summarized the spatial and temporal occurrence of the eight identified strategies and actions exhibited by the various life stages of bull trout within the SFWWR and the WWR, as well as MC and YHC. Occurrence periodicity within the study area is hereafter described. Summary tables are provided in Appendix E.

Spawning

Bull trout commonly spawn in headwater reaches (SFWW1 and SFWW2) of the SFWWR and in reach MC14 in MC from August through October. Spawning occurs during 25% of the year and occurrence is high in just 6% of the linear habitat available in both the SFWWR and MC (Appendix E, Table E1). Bull trout also spawn less commonly within an additional 6% (reach MC15) in MC, downstream of the City of Walla Walla Intake Dam. Although bull trout spawning may be conceivable in additional downstream reaches throughout the study area from August through October and into November, only on rare occasion has such spawning activity been observed. Bull trout spawning does not occur from December through July. Table 3.26 is a summary of bull trout spawning occurrence periodicity within the study area.

Juvenile rearing, foraging and growth

Juvenile bull trout rear at or near natal spawning areas during all months prior to downstream migration as sub-adults. Juvenile bull trout commonly rear and forage in reaches SFWW1 and SFWW2, occurrence is low within reach SFWW3 and their occurrence is conceivable but rarely observed in downstream reaches (66% of the subbasin). In MC, juvenile fish commonly occur in the upper 25% of the subbasin (reach MC14) and less commonly occur in reach MC15 (Appendix E, Table E2). Juvenile bull trout could conceivably occupy downstream reaches in the lower 50% of the MC subbasin but have not been observed. Table 3.27 is a summary of juvenile bull trout rearing, foraging and growth occurrence periodicity within the study area.

Fluvial adult upstream migration

Fluvial adult upstream migration could conceivably occur throughout the Walla Walla Basin from March through October (60% of the year) without considering limiting factors and other influences (Appendix E, Table E3). Fluvial adults are known to begin moving upstream in March within lower basin reaches, becoming common in May before becoming less common into June. Upstream movement within middle basin areas is common in May and June, and is less common into July. Fluvial adults continue moving incrementally upstream into the headwater areas from approximately June through September. Adult migratory bull trout are rarely observed moving upstream from November through February. Upstream adult bull trout movement is low in YHC and has only been observed from April through July. No MC bull trout known to have moved into the WWR has returned to the MC subbasin via the YHC migration corridor. A few adult bull trout have likely overwintered within YHC and have been subsequently detected while moving back upstream to MC. Table 3.28 is a summary of monthly occurrence periodicity within the study area for fluvial adult bull trout upstream migration.

Adult foraging and maintenance

Adult foraging and maintenance could conceivably occur throughout the Walla Walla Basin and at all times of the year if no limiting factors were present. Under current habitat conditions, adult-sized bull trout commonly forage within all study area reaches from November through May (Appendix E, Table E4). Beginning in June and into July, fluvial adult occurrence becomes increasingly less common within lower basin reaches. From July through September (30% of the year), almost no bull trout occupy lower basin reaches downstream of reach WW9 (approximately 60 rkms) in the WWR and reach MC16 (approximately 20 rkms) in MC. Adult bull trout are not known to occur in YHC during August and September. In the fall, adult-sized, fluvial bull trout begin to occupy middle and lower basin reaches to overwinter, becoming more common following October. Table 3.29 is a summary of monthly occurrence periodicity within the study area for adult bull trout foraging and maintenance.

Fluvial adult downstream migration

Fluvial adult downstream migration could conceivably occur following spawning as early as August, but is observed initiating in September and becomes increasingly common through December in middle basin reaches and is commonly observed in lower basin reaches through February. This pattern holds true in MC, but the occurrence of adult downstream migration is relatively low during January and February. There is no notable occurrence of adult bull trout downstream movement from March through July (Appendix E, Table E5). Table 3.30 is a summary of monthly occurrence periodicity within the study area for fluvial adult bull trout downstream migration.

Fluvial sub-adult downstream migration

Fluvial sub-adult downstream migration could conceivably occur during all months and within all reaches if there were no limiting factors. Spring downstream migrants disperse from headwater areas beginning in March and this movement pattern is common throughout the spring and early summer months within most reaches. Spring outmigrant occurrence is low within reaches WW10 and WW11, and there have been no observations of spring outmigrant bull trout in the lower 31.3 linear km (reaches WW12 and WW13) of the WWR (Appendix E, Table E6). Sub-adult downstream migration within middle and lower basin reaches recommences in the fall months and continues to commonly occur through January and February in lower basin reaches. Many sub-adults that initially migrated to middle basin reaches during the spring and early summer resume their downstream trajectory to overwintering habitat once conditions allow in the fall and winter months. Spring downstream migration does not occur downstream of reach MC18 in August and September in the MC subbasin. Table 3.31 is a summary of monthly occurrence periodicity within the study area for fluvial sub-adult bull trout downstream migration.

Fluvial sub-adult upstream migration

Larger, sub-adult bull trout, that had previously migrated to middle and lower basin reaches to overwinter, migrate upstream during the spring and early summer months. This movement pattern is similar to adult sized bull trout (≥ 300 mm fork length) but they generally do not continue upstream to spawning reaches, indicating they are likely not yet mature. In addition to the aforementioned movement pattern, smaller sub-adult bull trout that previously dispersed downstream during spring and early summer months to middle and lower basin reaches often move back upstream to more tolerable habitat as conditions progressively deteriorate downstream of reach WW5 in the WWR and downstream of reach MC16 in MC. In the WWR, fluvial sub-adult upstream movement occurs during up to 6 months and in as much as 62% (linear distance) of the subbasin (Appendix E, Table E7). In MC and YHC, sub-adults are known to migrate upstream from May to August. There is no notable upstream sub-adult bull trout migration from approximately September through February in the Walla Walla Basin. Table 3.32 is a summary of monthly occurrence periodicity within the study area for fluvial sub-adult bull trout upstream migration.

Fluvial sub-adult rearing, foraging and growth

Fluvial sub-adult rearing and foraging could conceivably occur throughout the Walla Walla Basin and at all times of the year if no limiting factors were present. Under current habitat conditions, fluvial sub-adult bull trout commonly forage within all study reaches from November through June and July in many reaches. Sub-adult bull trout become less common within reaches starting in July and become scarce from August through September in reaches downstream of WW9 in the WWR and MC17 in MC. Table 3.33 is a summary of monthly occurrence periodicity within the study area for fluvial sub-adult rearing, foraging and growth.

<u>Bull trout occurrence and model results comparison</u>

We compared monthly habitat quality scores and bull trout occurrence within study reaches with respect to each of the eight identified life stages, strategies and actions exhibited by Walla Walla Basin bull trout during time periods when occurrence is conceivable. We found that mean HQSs are usually higher when bull trout occurrence is high and lower when occurrence is low for most life stages and strategies (Table 3.34). One exception was the inverse relationship between mean HQSs and the level of bull trout occurrence for fluvial sub-adult upstream migration.

Low and poor habitat conditions may reduce bull trout survival and compromise migration and connectivity between local populations. By characterizing instream habitat by reach and identifying when and where low and poor quality habitat conditions interface with bull trout occurrence within the Walla Walla Basin, we can provide managers with useful information to inform future conservation actions or initiate additional studies that target the particular bull trout life stage or strategy of concern. Habitat quality and occurrence for each bull trout life stage, strategy or action are hereafter compared.

Spawning

Bull trout commonly spawn in headwater reaches (SFWW1 and SFWW2) of the WWR during August, September and October. Our model scored the quality of habitat within these reaches as good quality in August, improving to high quality in September and October. Conditions within these two reaches remained of high quality into November, but despite being conceivable, bull trout in the Walla Walla Basin are not known to regularly spawn in November. Only limited spawning activity has been observed downstream of SFWW2 despite HQSs that indicate there may be good quality habitat conditions during the months when bull trout generally spawn. Conditions within reaches SFWW3 and WW4 improve to high quality HQSs in November, overlapping with conceivable spawning occurrence. Bull trout commonly spawn during August, September and October in reach MC14 in MC, and during this period, HQSs were good. Conditions improve to high quality in November, but spawning is considered rare or only conceivable. Bull trout are known to spawn occasionally, and in low numbers just downstream from the City of Walla Walla Intake Dam in reach MC15. Conditions within this reach scored only as fair quality, but improved to high quality in November during a time period when bull trout spawning is considered only conceivable. Monthly spawning occurrence within the study area overlays HQSs in Table 3.35. Mean HQSs were higher for reaches and months when bull trout spawning occurrence was high, lower when occurrence was low and lowest when occurrence was conceivable but not observed in the SFWWR, the WWR and in MC (Table 3.34 and Figure 3.35).

Juvenile rearing, foraging and growth

Juvenile bull trout commonly occur in reaches SFWW1 and SFWW2 to rear, forage and grow. The model scored these reaches as good and high quality during all months of the year. Juveniles likely utilize reach SFWW3 and conceivably reach WW4 for foraging and rearing as well. These two reaches scored as high quality for almost all months. The model scored reach MC14 as high quality for the majority of the year, and scores indicate that habitat within reach MC15, where juvenile occurrence is generally low, is of good quality during all months. Conditions downstream of the aforementioned reaches deteriorate incrementally downstream, especially during summer months. Table 3.36 compares monthly juvenile rearing, foraging and growth habitat quality scores with juvenile bull trout occurrence for reaches within the study area. Monthly juvenile rearing, foraging and growth occurrence within the study area overlays HQSs in Table 3.35. Mean HQSs were slightly higher for reaches and months when juvenile rearing, foraging and growth occurrence was high when compared to reaches where occurrence was low. Scores were lowest when occurrence was conceivable but not observed in the SFWWR, WWR and in MC (Table 3.34 and Figure 3.36).

Fluvial adult upstream migration

Fluvial adult upstream migration could conceivably occur throughout the Walla Walla Basin from March through October. Upstream adult migration commonly occurs from May to June in lower basin reaches, May to July in middle basin areas and primarily July through September in upper basin reaches. There is a low occurrence of upstream migration within lower basin reaches in March and April. In both the WWR and in MC, our model scores lower and middle basin reaches as primarily fair and good quality in May. This coincides with peak adult upstream migration through these areas. The HQSs for many middle and lower basin reaches decline to fair and low quality in June, indicating that many adult upstream migrating bull trout are likely exposed to unfavorable habitat conditions within these reaches. In July, HQSs indicate that conditions further deteriorate to low and poor quality within these reaches, likely limiting or otherwise negatively influencing bull trout migration. These conditions coincide with a low level of adult upstream movement. Model scores indicate that habitat conditions remain of primarily high and good quality for upstream movement throughout the year upstream from reach WW6 in the WWR and upstream from reach MC17 in MC. Conditions for migration within YHC remain of good quality throughout the year, but very few (if any) adult bull trout migrate upstream through the YHC migration corridor to return to MC following overwintering in the WWR. Monthly occurrence for fluvial adult upstream migration within the study area overlays HQSs in Table 3.35. Mean HQSs were highest for reaches and months when occurrence for fluvial adult bull trout upstream migration was high, lower when occurrence was low and lowest when occurrence was conceivable but not observed in the SFWWR, the WWR and in MC (Table 3.34 and Figure 3.37). There was no notable difference in mean HQSs between occurrence levels in YHC.

Adult foraging and maintenance

Adult foraging and maintenance could conceivably occur, during all months and in all reaches within the study area. Adult bull trout forage concurrently with other life stages and actions (e.g., overwintering, migration). Habitat conditions, according to HQSs, are generally conducive to adult foraging within most reaches of the WWR from December through June. Scores indicate primarily low and fair quality conditions from WW7 downstream from July through approximately October and into November in some reaches. With the onset of low quality habitat conditions, adult bull trout occurrence within the particular reaches declines to low and non-existent, especially in July, August and September. Scores indicate that primarily good and high quality instream habitat conditions for adult foraging and maintenance exist in MC during all months upstream from reach MC17. Model scores for reaches within the Mill Creek Flood Control Project (MC17 - MC20) indicate primarily fair and low quality habitat during most months and poor quality during July, August and September. Adult fluvial bull trout are largely void from this reach during these months. During the months and in reaches at the interface between bull trout occurrence and the onset or of low and poor quality conditions, adult bull trout may experience detrimental foraging habitat conditions. Monthly occurrence for adult foraging and maintenance within the study area overlays HQSs in Table 3.35. Mean HQSs were highest for reaches and months when occurrence for adult bull trout foraging and maintenance was high, lower when occurrence was low and lowest when occurrence was conceivable but not observed in the SFWWR, WWR and in MC (Table 3.34 and Figure 3.38). The same pattern occurred in YHC except that mean HQSs were slightly higher in months with no occurrence than in low occurrence months.

Fluvial adult downstream migration

Fluvial adult downstream migration could conceivably occur following spawning as early as August, but is observed initiating in September and becomes increasingly common through December in middle basin reaches and is commonly observed in lower basin reaches through February. This pattern holds true in MC, but adult downstream migration occurrence is relatively low during January and February. Model scores indicate that habitat conditions for adult downstream migration are primarily high and good quality upstream from the Little Walla Walla Diversion in reach WW6 during the migration season. During September and October, bull trout that are migrating downstream encounter low quality conditions downstream of reach WW7 until HQSs indicate habitat conditions improve throughout the WWR from November through February. In MC, HQSs indicate that downstream migrating adult bull trout likely encounter low habitat quality conditions in reach MC17 in September. Although conceivable, no adult migration is observed downstream in reaches MC18, MC19 and MC20 during September largely due to a lack of instream flow due to the Yellowhawk Creek Diversion (rkm 20). In most years, bull trout likely occur downstream of MC17 during October and November when conditions are of low quality. At no point during the migration season do HQSs within the Mill Creek Flood Control Project indicate better than fair quality habitat. Monthly occurrence for fluvial adult downstream migration within the study area overlays HQSs in Table 3.35. In the SFWWR, the WWR and in MC, mean HQSs were slightly higher for reaches and months when occurrence for fluvial adult bull trout downstream migration was low than when occurrence was high. Mean HQSs were notably higher when adult downstream migration occurs compared to when occurrence was conceivable but not observed (Table 3.34 and Figure 3.39). In YHC, mean HQSs were slightly higher during months when occurrence was high than when occurrence was low and was the lowest when there was no occurrence.

Fluvial sub-adult downstream migration

Fluvial sub-adult downstream migration could conceivably occur during all months and within all reaches if there were no limiting factors. Spring outmigrant bull trout disperse from headwater areas beginning in March. This movement pattern is common throughout the spring and early summer months within most reaches. Spring outmigrant occurrence is lower within reaches WW10 and WW11, and there have been no observations of spring outmigrant bull trout in reaches WW12 and WW13. Low quality habitat conditions develop in reach WW7 during June and in all reaches downstream in July. Concurrent to the onset of unfavorable habitat conditions in the lower river, the occurrence of downstream sub-adult migration trends toward low and nonexistent in the lower river reaches from July through September. As habitat conditions improve in the middle and lower basin reaches in October, occurrence becomes more common. Downstream sub-adult migration remains common from November through February. Our model scores habitat quality for downstream migration as primarily good throughout this timeframe. The same pattern generally holds true for downstream sub-adult migration through reaches in MC (Table 3.40). In the SFWWR, the WWR and in MC, mean HQSs were higher for reaches and months when occurrence for fluvial sub-adult bull trout downstream migration was high, lower when occurrence was low and was the lowest when occurrence was conceivable but not observed (Table 3.34 and Figure 3.40). In YHC, mean HQSs were slightly higher during months when occurrence was high than when occurrence was low and was the lowest when there was no occurrence.

Fluvial sub-adult upstream migration

Larger, sub-adult bull trout, that had previously migrated to middle and lower basin reaches to overwinter, migrate upstream during the spring and early summer months along with adult-sized bull trout (≥ 300 mm fork length) but they generally do not continue upstream to spawning reaches, indicating they are likely not yet mature. This movement pattern begins in March and April and commonly occurs in May and June before conditions in the middle and lower basin reaches deteriorate to low and poor quality in July. In addition to the aforementioned movement pattern, smaller sub-adult bull trout that previously dispersed downstream during spring and early summer months to middle and lower basin reaches often move back upstream to more tolerable habitat as conditions progressively deteriorate downstream of reach WW5 in the WWR and downstream of reach MC16 in MC. At the onset of low and poor quality habitat conditions in middle and lower basin reaches, upstream movement of spring migrant bull trout begins. Occurrence of this movement pattern becomes common in July and August as the habitat quality declines (Table 3.41). Upstream movement becomes less common in lower river reaches during August and is largely nonexistent in September. A similar downstream, then subsequent upstream movement pattern of sub-adult bull trout is apparent in MC at the onset of low and poor quality habitat conditions (Table 3.41). Unlike the other seven bull trout life stages and strategies, the relationship between mean HQSs and level of occurrence is distinctly inverse. Mean HQSs were highest when sub-adult upstream migration is conceivable but does not regularly occur (Table 3.34). Mean HQSs were lowest in reaches and months when the occurrence of sub-adult upstream migration was high in the SFWWR and WWR as well as MC and YHC (Figure 3.41).

Fluvial sub-adult rearing, foraging and growth

Fluvial sub-adult rearing and foraging could conceivably occur throughout the Basin and at all times of the year if no limiting factors were present. Our model indicates that habitat throughout the SFWWR and the WWR is primarily good or high quality for fluvial sub-adult bull trout rearing and foraging upstream of reach WW6 during all months, and fair or good quality from November through June. Fluvial sub-adult bull trout are uncommon or are absent from reaches downstream of WW8 during July, August and September when HQSs indicate primarily low quality habitat for foraging and rearing. In MC, sub-adult bull trout are uncommon or are absent from reaches downstream of MC17 from August through October when HQSs indicate primarily low quality habitat for foraging and rearing. Sub-adults that are rearing in MC downstream from reach MC17 are exposed to low and poor quality habitat conditions during most months of the year, with the exception of March through May when HQSs indicate fair habitat quality. In YHC (reach YHC22) our model scores sub-adult rearing and foraging habitat conditions as fair and good during all months. Table 3.42 compares monthly HQSs for fluvial sub-adult rearing, foraging and growth with occurrence for reaches throughout the study area. Mean HQSs were highest for reaches and months when occurrence for sub-adult bull trout foraging and maintenance was high, lower when occurrence was low and lowest when occurrence was conceivable but not observed in the SFWWR, the WWR and in MC. This same pattern was not apparent in YHC (Table 3.34 and Figure 3.42).

Discussion

Our goal was to develop a relatively simple, adaptable, fundamentally straightforward and transferrable approach to assessing aquatic habitat quality at the reach scale. To accomplish this goal, we chose to incorporate habitat variables that are largely temporally and spatially static (e.g., channel modification) in addition to dynamic variables (e.g., surface flow) to more effectively characterize habitat quality as it changes throughout the year. Proxy variables (e.g., elevation, land use) were also incorporated to generally represent numerous, but not well quantified, factors that are commonly considered to influence the quality of habitat for bull trout (e.g., angling pressure, predation, pollution). Approaches to model development often vary and may or may not use existing presence/absence data. Because we intended to temporally and spatially characterize the quality and summarize the quantity of available bull trout habitat for each life stage and strategy, we elected not to allow known occurrence data to influence model results. Instead, we used the bull trout occurrence data to help evaluate, discuss and inform model results. Although specific bull trout habitat suitability data exists for portions of the Walla Walla Basin, we chose to rate the quality of habitat variables within each reach using criteria developed from a range of findings and observations from past bull trout studies and recent field and laboratory investigations along with professional judgment and widely accepted biological benchmarks. We felt this approach could increase the applicability of this model to assess habitat for bull trout in other basins or river systems.

Temperature is widely believed to be the variable that most significantly influences bull trout occurrence and the quality of habitat with respect to the multiple life stages, strategies and actions. However, this does not mean that other variables are not important. To try to account for this, many models use occurrence data and metrics most often associated with bull trout presence at the micro-scale to determine importance. In these models, the assumption is made that bull trout occur in the most suitable habitat. In addition, the habitat metrics or combination of metrics most often associated with bull trout occurrence are often assumed to be the most influential. Models at larger spatial and temporal scales or with numerous variables often cannot rely on empirically collected datasets to assign a level of importance to each variable. We employed an analytic hierarchy process, adapted from Saaty (2008) that relies on the professional judgments of experts to make pair-wise comparisons to derive priority scales. Experienced bull trout biologists used professional judgment to complete primary questionnaires to approximate the importance of each habitat variable relative to one another with respect to each of the 8 identified life-history stages, strategies and actions. A consensus (mean) of the resulting answers to survey questions was used to populate a comparison matrix and weighting factors were derived.

There are some obvious limitations to our bull trout habitat quality assessment. First, we only characterize current bull trout habitat conditions by month and at the reach scale. We do not describe habitat conditions in relation to an estimate of historical conditions or try to predict future conditions (e.g., following habitat restoration or changes in climate). Second, dynamic variables (i.e., temperature and surface flow) were averaged monthly and over multiple years to obtain a single representative value to be rated for each reach and during each month. This does not allow for short term variation within months or between years to be expressed. We chose the aforementioned scales based upon available data and the goal of the assessment. The adaptability of this model allows for the spatial and temporal scales to be adjusted as long as input data are available at the desired scale. Third, some of the selected habitat variables are related or influenced by each other (e.g., surface flow and passage impediments). This could conceivably weight certain types of habitat variables higher than others that are less related. It should be noted that very few variables in a riverine environment are truly independent of one another. Another limitation to our bull trout habitat quality assessment is that extremely limiting factors such as impassable obstructions (e.g., waterfalls or dams without fish passage) and their profound effect on upstream migration may not be correspondingly realized in the HQS for a given reach. For example, this assessment weights passage impediments as approximately 19% of the total HQS for adult upstream migration. If an impassable barrier exists within the reach, the low score for passage impediment variable will undoubtedly reduce the total HQS, but it may not be apparent from the score alone that the reach is completely impassable.

Habitat variation exists at a variety of spatial and temporal scales, requiring habitat quality to be assessed at multiple scales as well. Therefore, the output from this model should be used as a "first cut" tool when determining potential sites for habitat restoration or the implementation of future management actions to work toward bull trout recovery. A narrative discussion of model results and bull trout occurrence in relation to each bull trout life-history stage, strategy and action for the SFWWR, WWR, MC and YHC is hereafter provided.

Bull trout spawning habitat

Both the MC and SFWWR local populations include migratory and resident individuals. Despite dissimilarities in physical stature and likely divergent habitat requirements at the micro-scale, reach-scale habitat requirements are similar. Suitable bull trout spawning habitat within the Walla Walla Basin predominantly occurs in headwater river reaches and tributaries. Migratory fish utilize more productive waters downstream where growth rates are greater, and as a result, they become larger and more fecund (e.g., more and larger eggs) than residents. Bull trout generally reach maturity between four and seven years (Fraley and Shepard 1989). Spawning initiates during falling temperatures in the fall and has primarily been observed in the Walla Walla Basin from August through October. Approximately 22% of the linear distance within study area (3 of the 22 reaches) is commonly utilized by bull trout for spawning during only 25% of the year (Appedix D, Table D2). Spawning occurrence is low in an additional 7% (14.4 rkm) of the study area (reach MC15). Almost all documented bull trout spawning activity within the SFWWR subbasin has been observed within the mainstem SFWWR or tributaries (e.g., Reser and Skiphorton creeks) upstream from the Harris County Park Bridge (rkm 95.5). Spawning in the MC subbasin predominately occurs in the mainstem and select tributaries (e.g., Low Creek) upstream of the City of Walla Walla Intake Dam (rkm 44.2).

Water temperature and surface flow heavily influenced the spawning HQSs derived by our model. Water temperature was the most influential (WF 0.26) and the quality of surface flow within each reach had a WF of 0.22. Variables that also notably influenced spawning HQSs, albeit to a lesser extent, were groundwater, passage impediments and riparian zone, and had WF's of 0.11, 0.11 and 0.08 respectively. The other six variables each influenced HQSs considerably less (WF's of less than 0.05). Habitat quality scores predicted by the model indicate that reaches with primarily high and good quality spawning habitat coincide with reaches where and when bull trout spawning commonly occurs (SFWW1, SFWW2 and MC14) within the study area. In reaches where spawning is less commonly observed (MC15), HQSs indicate only fair habitat quality conditions. Model scores indicate that spawning habitat conditions conducive to spawning may occur in downstream reaches (SFWW3, WW4) or develop during November (SFWW1 – WW5 and MC14 – MC15), but spawning activity is likely limited due to biological timing and a suite of micro-scale habitat requirements (e.g., substrate composition), among other factors. Redd counts tend to be much higher in the headwaters of the SFWWR than in MC. This is likely due to many factors, but HQSs were generally higher in known SFWWR spawning reaches than in MC when most bull trout spawn (August – October). This may indicate a more favorable synergy between higher quality habitat conditions and biological timing in the SFWWR when compared to MC. Very limited bull trout spawning activity has been observed in lower reaches (e.g., WW5), and is believed to be rare. In addition, suspected, but unverified bull trout redds have been observed in the NFWWR, tributary to the WWR.

The near-pristine, largely undisturbed disposition of riparian habitat within the abovementioned spawning reaches, combined with adequate surface flows and groundwater influence, contribute to the apparent resilience of the bull trout populations within this core area against downstream impacts including, but not limited to: channel modifications, over-appropriation of surface flows and elevated predation and land use. Despite the lack of anthropogenic influences, spawning grounds within MC and the SFWWR subbasins are not free from limiting factors. The relatively low channel complexity and frequent high flow events may combine to scour redds and otherwise adversely impact egg to fry survival and displace juvenile bull trout to less favorable downstream habitats (Figure 3.43). Although the presence of sizeable log jams within reaches SFWW1 and SFWW2 (Figure 3.44) likely has little direct effect on bull trout spawning, they may inhibit migratory adults from accessing suitable upstream habitat. Similarly, the City of Walla Walla Intake Dam at the downstream end of reach MC14 may delay, or otherwise influence bull trout access to upstream spawning areas (Figure 3.45).

Temporal and spatial assessments and descriptions of bull trout spawning habitat at the reach-scale are important tools for informing and crafting management actions and strategies critical for the recovery of the species, especially in areas lacking robust, empirical datasets. Results from reach-scale assessment models could be used in conjunction or “stepped down” by using predictive, micro-scale spawning habitat models to assess specific details or quantify spawning habitat within reaches. Gallion et al. (*in review*) describes the development of such models for both resident and migratory bull trout redd sizes. Although these models have been developed in the Walla Walla Basin, if transferrable, both the reach-scale and micro-scale models could be used to identify in-basin areas or habitat in other basins to focus restoration efforts or assess production potential.

Juvenile rearing, foraging and growth

Following spawning, bull trout egg incubation generally occurs in temperatures less than 8°C and survival is optimal from 2 to 4°C (Goetz 1989; McPhail and Murray 1979). Depending on water temperature, the in-gravel incubation and yolk-sac absorption period may span from 6 to 8 months (Parametrix 2005). Juvenile bull trout are bottom dwellers and newly emerged bull trout fry may use shallow, complex backwater areas of streams (Figure 3.46) and occupy interstitial spaces in the streambed (Baxter 1995; Brown 1992). For approximately the first 1 to 3 years following hatching, bull trout juveniles rear in or near their natal tributary (Bjornn 1991; Goetz 1989; Fraley and Shepard 1989) until the migratory component of the population migrates downstream to forage and grow to adulthood. Within the study area, juvenile bull trout are known to commonly rear and forage within reaches SFWW1 and SFWW2 in the SFWWR and occurrence is likely low within reach SFWW3. In MC, juveniles commonly rear and forage within reach MC14 and occurrence is likely low in reach MC15. Juvenile bull trout could conceivably occupy habitat near wherever successful spawning may occur or where high flow events have displaced them downstream.

As with spawning, water temperature was the variable believed to most influence the quality of juvenile bull trout rearing and foraging habitat (WF 0.29). Groundwater inputs generally moderate water temperatures in the winter and contribute to keeping water cooler during the summer months. Most headwater reaches received only fair temperature ratings during winter months because colder water is less conducive to the growth and metabolic needs of juvenile bull trout. Higher quality ratings for most other notably influential habitat variables including surface flow, riparian zone and groundwater (WF’s of 0.21, 0.14 and 0.08 respectively) contributed to good and high quality HQSs for all months and reaches where juvenile bull trout rearing occurrence is high and low in both MC and the WWR subbasin. Low and poor quality habitat conditions for juvenile bull trout rearing develop from approximately June through September in approximately 55% of the SFWWR/WWR subbasin downstream of reach WW7. In MC, low and poor quality conditions are prevalent following June downstream of reach MC16 (34% of the subbasin). Model scores indicate that riverine habitat conditions may seasonally become conducive to juvenile bull trout rearing, foraging and growth in downstream reaches (e.g., December to May). Because we define juvenile bull trout as small, non-adult and pre-migratory fish that occur in or immediately downstream of natal areas, most juvenile bull trout are not exposed to low or poor rearing and foraging conditions within the study area.

Fluvial adult upstream migration

Migratory adult bull trout (FL ≥ 300) overwinter in portions of the SFWWR, the WWR (Anglin et al. 2010, 2009a, 2008b) and use of the mainstem Columbia River during winter months has also been confirmed (Barrows et al. 2012b, 2014). In addition, fluvial adult bull trout use habitat in the NFWWR to overwinter (Barrows et al. *in review*; Mahoney et al. 2006). After overwintering throughout the study area, adult bull trout in lower basin reaches begin migrating upstream in March, peaking in May before ceasing in June. Upstream migration occurs in middle basin reaches from May through July and in upper basin reaches primarily from June through September. Habitat quality scores for fluvial adult upstream migration are heavily influenced by the quality of surface flow (WF 0.28) as well as passage impediments (WF 0.19), water temperature (WF 0.18) and channel modification (WF 0.11). The other seven habitat variables influence HQSs to a lesser extent (WF < 0.05). Although conceivable during 8 months of the year, fluvial adult upstream migration is spatially successional, occurring in most reaches between four and seven months, 33 – 58% of the year respectively.

Adult bull trout return to the lower WWR from overwintering in the mainstem Columbia River beginning in March. Despite backwater influence from the Columbia River (Figure 3.47), close proximity to avian predators (cormorant and pelican colonies), low channel complexity, and a lack of canopy trees within the riparian zone (Figure 3.48), HQSs in reaches WW13 and WW12 indicate good quality habitat for adult upstream migration from March through May. Scores decline from fair quality in June to low quality during July coinciding with a lack of adult upstream migration.

Habitat quality conditions within reaches WW11 and WW10 follow a similar pattern in that good HQSs prevail until May. The Garden City- Old Lowden #2 Diversion (Figure 3.49) within reach WW11 and the Burlingame Diversion Dam (Figure 3.50) in reach WW10 may affect upstream bull trout migration, and seasonally divert surface flows contributing to only fair HQSs in June and poor – low scores for July. Poor and low HQSs persist through August before improving slightly in September, but no adult upstream movement is observed during this time period in these reaches.

Adult bull trout commonly migrate through reaches WW9 and WW8 during May when HQSs indicate good habitat conditions. Increased sinuosity, relatively intact riparian canopy, groundwater inputs and only moderate channel modifications contribute to favorable habitat quality conditions within these reaches. Migration is common into June, but conditions decline to fair quality, due primarily to the onset of the irrigation season where depleted surface flows and associated elevated water temperatures affect HQSs. Habitat quality scores indicate that conditions deteriorate to low and poor quality during July when bull trout migration through these reaches is a less common occurrence. Severely reduced seasonal surface flows within reach WW8 create numerous barriers at hydraulic controls (e.g., riffles) and likely inhibit bull trout upstream movement (Figure 3.51). The HQS for reach WW9 is slightly higher during summer months than WW8 because diverted MC water via YHC and return flow from the Little Walla Walla River increase surface flow in this portion of the WWR, slightly enhancing habitat quality for upstream migration.

The Nursery Bridge Dam (rkm 73.1) is the upstream bound of reach WW7 (Figure 3.46). In combination with downstream levees, it provides flood control for the City of Milton-Freewater, OR and the surrounding agricultural land. This dam consists of two permanent concrete gravity dams with a 70 foot stilling basin between them that dissipates hydrologic energy and has two fish ladders. The habitat within this highly modified reach is similar to the adjacent, upstream segment, but is differentiated by more intensive vegetation management on and along its control structures. In addition, the stream channel between the two levees in this reach is much larger (i.e., wider), and the highly degraded aquatic habitat is almost entirely unshaded (Figure 3.53). Seepage runs indicate that this reach is a losing reach and at times, more than half of the bypassed surface water becomes subsurface prior to reaching the end of the reach (Bower 2007). Due largely to the abovementioned attributes, HQSs indicate no better than fair habitat quality for fluvial adult bull trout upstream migration during any given month. When migration through this reach is common, the May HQS indicates fair habitat conditions, but scores deteriorate to low quality in June due primarily to depleted surface flows associated with upstream irrigation withdrawals for approximately 50% of the year. Despite seasonally depleted surface flows, elevated water temperatures and extensive channel modification, reach WW7 generally lacks the passage impediments (e.g., low flow barriers) that would further reduce HQSs within this reach if present.

The Little Walla Walla Diversion (Figure 3.54) marks the upstream boundary of reach WW6 and is the largest, single irrigation diversion of the WWR. This reach is similar to reach WW7 in that flood control levees line both banks, but it is differentiated by less intensive vegetation management on and along its control structures and the stream channel is narrower. Water temperatures, although elevated during summer months, remain more tolerable to bull trout, and in general, bypassed surface flow during the irrigation season is greater than in the adjacent downstream reach. The abovementioned attributes contribute to good and fair quality HQSs for fluvial adult upstream migration during all months with the exception of July where the HQS indicates low habitat quality.

Upstream movement of fluvial adult bull trout through reaches WW5, WW4 and SFWW3 commonly occurs from approximately May through August. Habitat quality scores for these reaches indicate that good and high quality habitat for migration corresponds with this time period. Cooler water temperatures, less diverted surface flows and a lower level of channel modification profoundly influence the quality of habitat within these reaches. Adult bull trout migrate into and through reaches SFWW2 and SFWW1 primarily from July through September. Habitat quality scores show good quality habitat for upstream migration exists within the reaches during all months. Scores for reaches SFWW2 and SFWW1 are slightly less than SFWW3 scores due primarily to the existence of log jams within both reaches that likely hinder upstream movement (Figure 3.55).

After overwintering in the WWR, some bull trout, destined for the headwaters of MC, enter reach MC21 at its confluence with the WWR (rkm 54.8). In this portion of MC, movement begins in approximately April when the HQS for this reach indicates fair migratory conditions. Habitat quality increases briefly in May when movement through this reach is more common before dropping back to fair conditions during June. With the onset of summer, elevated water temperatures and severely low flow conditions decrease habitat quality and HQSs remain low throughout the summer months. Most surface flow during summer months is shunted to the YHC distributary, effectively depleting lower MC of flows conducive to upstream movement of adult bull trout. The transition from reach MC21 to MC20 (rkm 12.0) is marked by a flume-type fish ladder at the Gose Street Bridge (Figure 3.56). Currently, bull trout passage at this site has not been evaluated. Upstream from the ladder is a series of 145 stabilization sills (91 sheet pile and 54 concrete capped) that are spaced 21.3 m apart and are approximately 21.3 m long (Burns et al. 2009). These sills dissipate energy during high flows (Figure 3.57). Pools have been scoured out downstream from each of the weirs providing limited, unnatural habitat. Despite extensive channel modification, habitat conditions are fair during May when adult bull trout movement through this reach is most likely to occur. As summer streamflow drops to base levels, HQSs drop to low quality in June and poor for the remainder of the summer months, severely restricting movement through this section, and fish may be confined to areas where temperatures may become lethal and exposure to predation will likely be increased.

In reach MC19, upstream migrating bull trout encounter a 3.2 km concrete flume (Figure 3.58), which is an open channel with a low flow trench down the center that varies from 2.7 to 4.6 m wide and is approximately 0.5 m deep (Burns et al. 2009). Some portions of the channel are split while others remain a single flume. Some sections of the flume run underground and remain completely dark. Regardless of flume geometry and channel type, the flume likely impedes bull trout movement since the relative uniformity of the flume results in very low channel complexity and velocities (Burns et al. 2009), holding water is lacking, no substrate or functional floodplain exists, no hyporheic interaction can occur, and there is very limited riparian canopy. As MC reaches base summer flows, almost all surface flow is diverted down YHC, largely dewatering this reach. Habitat quality scores reflect the degraded habitat conditions and are of low and poor quality during months (with the exception of May) when adult upstream migration could conceivably occur (March through October). Habitat within this reach scored as fair quality for May, coinciding with peak bull trout movement through this portion of MC.

The Mill Creek Division Dam (rkm 18.5) marks the upstream boundary of reach MC18 (Figure 3.53). As MC reaches base summer flows, at this location, almost all surface flow is diverted to YHC, largely dewatering the reach. There are 77 concrete capped gabian style sills in this reach that are spaced from 21.3 to 62.5 m apart with lengths that vary from 21.3 to 167.6 m (Burns et al. 2009). The channel widens the wetted width, limits fish movement, affects water temperatures and likely exposes bull trout to increased predation (Figure 3.60). Migrating fluvial adult bull trout occurrence is low beginning in April, but is more common during May and June. Habitat Quality Scores indicate fair migration conditions from March through May before declining to low in June and poor throughout the rest of the summer months. Once habitat conditions for upstream movement drop below fair quality conditions, the ability of adult bull trout to move upstream through this reach to connect with more hospitable habitat is likely compromised and may result in lower survival.

Within reach MC17, there are 80 concrete stabilization sills spaced approximately 18 m apart to dissipate energy during high flows (Figure 3.61). Pools have been scoured out downstream from each of the concrete weirs providing limited holding habitat. The sills are approximately 30 m wide, spreading the water evenly across the sills, likely impeding fish passage during lower streamflows and increasing exposure to mammalian and avian predators. This reach is upstream from where MC flows are shunted to YHC, but the lack of channel complexity, large water surface exposure and functionally absent riparian canopy contribute to seasonally elevated stream temperatures. Relatively good surface flows in this reach (when compared to the adjacent downstream reach) contribute to fair and good quality HQSs from April through June when migratory bull trout commonly move through this reach before declining to low quality during July, August and September. The Mill Creek Diversion Dam (rkm 20.1) is the upstream bound of this reach (Figure 3.62). PIT detection data demonstrates that upstream migrating bull trout (and other salmonids) are often delayed at this facility and unsuccessfully attempt to ascend the low flow outlet until they find the fish ladder (Koch *in review*). The entrance location and general design of the fish ladder may be detrimental to migrating salmonids (Figure 3.63). The drop from high occurrence of adult upstream movement in June to low occurrence in July coincides not only with declining HQSs within this reach, but with very poor quality HQSs in downstream reaches. This represents a circumstance where our model results can be used to spatially and temporally identify a potential habitat concern with regards to a particular bull trout life stage that may warrant further investigation.

Upstream from the Mill Creek Diversion Dam, MC remains in a less modified, more natural state than downstream reaches. Habitat quality scores indicate that primarily good habitat conditions for fluvial upstream migrating bull trout exists during most months for reaches MC16, MC15 and MC14. This can largely be attributed to only moderate channel modification, greater sinuosity and channel complexity, relatively intactness of riparian areas, higher surface flow, cooler water temperatures and fewer passage impediments. Migratory bull trout commonly enter the upper watershed (reach MC14), where most of the spawning in MC occurs, during June through August, but upstream movement is observed less commonly through September. To move upstream into this reach, adult bull trout must pass the City of Walla Walla Intake Dam via fish ladder (Figure 3.64).

Adult foraging and maintenance

Resident and migratory adult bull trout are primarily piscivorous, actively foraging predators (Fraley and Shepard 1989; Schoby and Keeley 2011; Rieman and McIntyre 1993). Although foraging on fish where available, there is likely a shift in prey species composition as well as the quantity consumed that corresponds to the spatial and temporal disposition and metabolic needs of migratory adult bull trout as well as prey availability. Resident adult bull trout are generally smaller in size and therefore require less caloric intake to grow, maintain metabolic processes and recuperate following spawning. In addition, they can utilize smaller, headwater microhabitat that may be less suitable for larger, migratory conspecifics. Microhabitat attributes and the availability of prey species unquestionably influence the specific areas that bull trout use for foraging and maintenance within stream reaches and likely contribute to the seasonal distribution of adult bull trout into downstream reaches. Despite probable differences between microhabitat requirements for each life-history form, reach-scale habitat requirements for resident and migratory adult bull trout are likely similar.

In the Walla Walla Basin, both the MC and SFWWR local populations are comprised of individuals expressing both resident and fluvial life-history forms. While resident bull trout do not actively migrate from natal headwater areas (reaches SFWW1, SFWW2 and MC14), the migratory component of the population moves varying distances downstream to rear to maturity, then return to headwater areas to spawn.

Adult bull trout forage, grow, recuperate and maintain bodily development (e.g., gonadal development) during all months, coinciding with other life stages, strategies and actions. Mesa et al. (2013) estimated temperatures for maximum consumption for bull trout to be at 15.8-17.5°C and that consumption declined as temperatures increased or decreased from this temperature range. Both postspawning and nonspawning adult-sized bull trout move from smaller tributaries and upper stream reaches into larger streams and downriver reaches to overwinter and forage. Migratory bull trout are opportunistic and forage en route to overwintering locations, taking advantage of resources including juvenile Chinook salmon, steelhead and other prey species that are abundant in middle and lower basin reaches. Within the migration corridor, migrating bull trout make incremental downstream movements and arrive at suitable overwintering habitat locations from September through February throughout the Walla Walla Basin and were recently documented in the mainstem Columbia River (Barrows et al. 2012b, 2014). Fish are known to show a high degree of winter location fidelity, often returning to previously occupied reaches in consecutive years (Mahoney 2003; Mahoney et al. 2006; Starcevich et al. 2012). Bull trout overwinter in areas of upwelling groundwater, deep pools, adjacent tributaries with abundant forage and in the mainstem Columbia River prior to the upstream spawning migration (Figure 3.59). Often, adult bull trout utilize pool-type habitat created by water control structures and diversion dams in middle and lower basin areas (Figure 3.66). This is especially true in MC, where most of the overwintering habitat downstream of Bennington Dam (rkm 20.1) is limited to scoured pools immediately downstream of stabilization sills within the flood control project (Figure 3.67).

Of the eleven habitat variables, water temperature and surface flow heavily influenced the habitat quality scores derived by our model for adult bull trout foraging and maintenance. Water temperature was the most influential (WF 0.25) and the quality of surface flow within each reach had a WF of 0.22. Variables that also notably influenced foraging and maintenance HQSs, albeit to a lesser extent, were riparian zone quality, channel modification, passage impediments and groundwater with WF's of 0.11, 0.08, 0.08, and 0.07, respectively. Land use and sinuosity were slightly influential with WF's of 0.05, but the other three variables influenced HQSs considerably less (WF's of less than 0.03).

Habitat quality scores predicted by the model indicate that reaches SFWW1 through WW5, totaling a linear distance of 50.3 rkm contain primarily good and high quality habitat for adult bull trout foraging and maintenance during all months. The river in this portion of the Walla Walla Basin has not been diverted for irrigation, has generally experienced minimal channel modifications and has not been affected by anthropogenic land uses to the extent that lower reaches have. All of which contribute to cooler water temperatures and adult bull trout occurrence is common during most months. Habitat quality scores indicate good quality foraging and maintenance habitat for adult bull trout from December through May in reach WW6, but at the onset of summer base flows, paired with substantial irrigation withdrawals at river kilometer 75.1, HQSs decline to only fair quality from July through November. Due to upstream irrigation withdrawals, a high level of channel modification, a lack of channel complexity and a largely absent riparian zone, reach WW7 contains only fair quality habitat for foraging and maintenance during December through June and HQSs drop to poor and low quality from July through November. The only deep water habitat that is conducive to adult bull trout foraging and occupancy within this reach is at the upstream boundary (rkm 73.1), and is associated with the Nursery Bridge Dam (Figure 3.68).

Non-depleted surface flows accompanied by temperatures that are generally conducive to food consumption and metabolic processes contribute to HQSs that indicate good quality habitat for adult bull trout foraging and maintenance from reach WW8 downstream to the mouth of the WWR (reach WW13) from December through May. Declining instream surface flows during June and warmer water temperatures decrease HQSs to fair quality before habitat conditions deteriorate to low quality during July and August. As water temperatures moderate during September, HQSs for reaches WW8 through WW10 increase to fair, but the quality of habitat remains poor from WW11 to WW13 until October and November. Adult bull trout either do not occur or occur only at low levels in the WWR during months and in reaches with low and poor HQSs. Overall, 79% of the linear distance of the SFWWR and the WWR exhibit fair-high quality adult bull trout foraging habitat for up to 87% of the year (Appendix D, Table D10). Despite only 16% of the linear distance exhibiting poor and low quality habitat for approximately 13% of the year, the months and reaches where these conditions occur may detrimentally affect the fitness and survival of migratory adult bull trout.

In the MC subbasin, reaches MC14 through MC16 have HQSs indicating good or high quality habitat for foraging and maintenance during most months. A multitude of detrimental anthropogenic alterations to the stream channel for flood control in reaches MC17 to MC20 result in HQSs that indicate primarily fair quality foraging and maintenance habitat from January through April, declining to low quality during May and June and further declining to poor conditions when the majority of surface flow is diverted to YHC during the summer and early fall months (Figure 3.69). Foraging and maintenance habitat quality scores for adult bull trout in YHC (reach YHC22) remain fair and good for most months of the year.

The act of migrating can be energetically demanding on an individual bull trout even through reaches where habitat conditions are favorable. In the Walla Walla Basin, adult fluvial bull trout migrate from the Columbia River and lower basin reaches to the headwaters to stage prior to spawning during months that often coincide with worsening habitat conditions. In addition to stress associated with survival at the edge of their physiological capability, food limitation may be exacerbated at the upper end of a fish’s thermal range (Warren et al. 2012). Similarly, if upstream migratory timing is delayed (e.g., low flow barriers) or stress levels are increased due to inclement habitat conditions, a fish’s overall physiological condition and even gonad development may be compromised (Warren et al. 2012).

Fluvial adult downstream migration

Following spawning, resident adult bull trout recuperate in headwater reaches while the migratory component of the population moves from smaller tributaries and upper stream reaches into larger streams and downriver reaches (including the mainstem Columbia River) to alleviate potential intraspecific competition for forage and habitat in the headwaters. This generally occurs from September through February in the Walla Walla Basin. To reach overwintering areas, bull trout make rapid, incremental downstream movements through migratory corridors. For this assessment, surface flow was believed to be the most important factor influencing this movement pattern (WF 0.26), followed by water temperature (WF 0.20) and passage impediments (WF 0.16). Without adequate surface flow, large bull trout seeking downstream habitat to recuperate following spawning may be delayed or exposed to elevated levels of mammalian and avian predation as they attempt to migrate through reaches with inadequate, depressed surface flows due to irrigation withdrawals. Habitat quality scores indicate that good and high quality habitat for adult downstream movement exists within reaches SFWW1 through WW5 during the months when movement occurs. This is primarily due to adequate water temperatures for migration, and a lack of major irrigation diversions. The Little Walla Walla Diversion removes the majority of surface flow at the upstream bound of reach WW6, causing HQSs to decline to only fair from August to October before streamflows increase and irrigation demand decreases in November. Low quality habitat for adult movement in reaches WW7 and WW8 during September and October, due primarily to low surface flows, likely delays timely movement of adult fish through this area. Figure 3.70 shows two examples of the numerous, shallow riffles that bull trout encounter as they attempt to move downstream through middle and lower basin portions of the WWR. Input from YHC, at the upstream boundary of reach WW9 and return flows from the Little Walla Walla River contribute to improved surface flows, but HQSs indicate primarily low and fair habitat quality for adult downstream movement from reaches WW11 to WW13 until flows increase substantially starting in November.

In MC, riverine habitat is relatively conducive to adult downstream bull trout migration during all relative months from reach MC14 through MC16. At the upstream bound of reach MC17, the Mill Creek Diversion Dam (rkm 20.1) marks the beginning of the flood control project where stabilization sills may delay or otherwise affect passage. This highly modified channel lacks habitat complexity and is largely void of riparian vegetation, likely leaving bull trout exposed to higher levels of avian and mammalian predation during migration. Almost all of MC surface flow is diverted to YHC, largely dewatering the lower 18.5 km of MC. Poor and low HQSs persist until streamflows improve by December. Habitat quality for downstream migration through YHC is generally good, evidenced by good HQSs. Although only relatively small portions of the WWR and MC exhibit low and poor habitat conditions when adult downstream migration is conceivable (Appendix D and E), the timing and location of such conditions may reduce post-spawning survival and delay or inhibit connectivity with other bull trout populations and possibly jeopardize bull trout recovery.

Fluvial sub-adult downstream migration

In the Walla Walla Basin, migratory sub-adult bull trout (fork length < 300 mm) initially begin migrating downstream from headwater spawning and juvenile rearing areas in the spring (March) during high flows and as water temperatures begin to rise. Although peak sub-adult migration from the headwaters occurs in the spring, movement occurs during all months. This incremental downriver movement pattern continues to occur on the declining portions of the hydrograph throughout middle basin areas through July and into August. In the WWR, spring migrant sub-adult bull trout have been detected moving into areas as far downstream as Burlingame Dam (rkm 60.3). As irrigation diversions draw surface water to summer base flows and water temperatures elevate, there is a short cessation of movement in middle and lower basin reaches during summer months before downstream migration resumes during fall and winter into lower basin reaches of the WWR and into the mainstem Columbia River. Some Walla Walla Basin bull trout that enter the Columbia River during fall and winter months have been shown to connect with other basins (Small et al. 2012; Barrows et al. 2014). Connectivity with other bull trout populations has been identified as important to the long term persistence and eventual recovery of the species (USFWS 2002). Most downstream movement of sub-adult bull trout declines throughout late winter and ceases in February.

Monthly HQSs for fluvial sub-adult downstream migration were heavily influenced by the quality of water temperature (WF 0.24), surface flow (WF 0.21), passage impediments (WF 0.17) and channel modification (WF 0.11) for each reach. Scores indicate that primarily high and good quality habitat for downstream movement exists within reaches SFWW1 through WW5 during all months. This is primarily due to adequate water temperatures for migration, and a lack of major irrigation diversions. The Little Walla Walla Diversion removes the majority of surface flow at the upstream bound of reach WW6 during the irrigation season, decreasing HQSs to fair quality from June through October before irrigation demands decrease and instream flows increase in November. Sub-adult bull trout intending to move through middle and lower basin reaches downstream from rkm 73.1 will encounter primarily low quality habitat resulting from depleted surface flows, elevated water temperatures, channel modifications, and low flow barriers from approximately June through October. Sub-adult bull trout movement downstream of reach WW9 is not often observed from June through September, likely due to both thermal and physical passage impediments. Low quality habitat conditions in lower basin areas likely increase the exposure of migratory sub-adult bull trout to avian predators including herons, pelicans and cormorants. Evidence of unsuccessful avian predation has been commonly observed during summer sampling activities (Figure 3.71).

In MC, HQSs indicate primarily good and high quality habitat for fluvial sub-adult bull trout migration during most months in reaches MC14, MC15 and MC16. Habitat conditions are of mostly fair quality for sub-adults moving downstream through flood control project reaches from December through May, but deteriorate to mostly low and poor quality from June through November (Figure 3.72). Despite increased water temperatures during summer months, HQSs indicate that habitat for sub-adult downstream movement through YHC (reach YHC22) is generally good during most months and declines to fair quality during July and August.

Similar to adult downstream migration, relatively small portions of middle and lower basin reaches in the WWR and MC exhibit seasonally low and poor quality habitat conditions for sub-adult downstream migration (Appendix D). The temporal and spatial occurrence of such conditions may profoundly affect sub-adult downstream migration timing, compromise the full expression of life-history strategies and delay or inhibit connectivity with other bull trout populations. All of which are important components of eventual bull trout recovery (USFWS 2002).

Fluvial sub-adult upstream movement

In the Walla Walla Basin, as water temperatures become less tolerable and irrigation diversions draw surface water to summer base flows, sub-adult bull trout that had recently migrated to middle and lower river reaches must seek refuge in deeper areas (e.g., pools) with adequate cover and groundwater influence or retreat back upstream to find more tolerable habitat conditions upstream to oversummer. This upstream movement pattern commonly occurs in reaches downstream from WW5 (rkm 78.1), starting when surface flows decrease and water temperatures increase in approximately June and continuing through August. Of the eleven habitat variables, surface flow (WF 0.27), water temperature (WF 0.20) and passage impediments (WF 0.17) influenced HQSs for sub-adult upstream migration the most. Once irrigation diversions severely deplete surface flows in middle and lower basin reaches, a multitude of low flow barriers at riffles develop, the most numerous being within reaches WW8, WW9 and WW11. A portion of the low flow barriers are complete barriers to all movement, in that surface flow reduces to subsurface at riffles. Many other riffles that maintain at least some surface flow are very shallow, making fish passage demanding and energetically taxing. A similar downstream, then subsequent upstream movement pattern has been observed in MC as well (Koch, *in review*). Sub-adults that migrate during the spring and early summer months into habitat within the Mill Creek Flood Control Project (reaches MC17 to MC20) and into YHC, encounter habitat conditions that compel them to escape back upstream to conditions more conducive for foraging and rearing. In addition to the abovementioned movement pattern, some immature sub-adult sized fish (< 300 mm) that previously migrated to middle and lower basin reaches during the fall to overwinter, but are not yet mature and intending to spawn, migrate upstream to oversummer in reaches WW6 – SFWW3, short of the spawning grounds. The cumulative effect of passing multiple shallow water riffles, stabilization sills, or fish ladders en route to better quality habitat conditions likely adversely affects a bull trout's ability to survive and thrive. Efforts to benefit both adult and sub-adult upstream fish passage through the Mill Creek Flood Control Project have been initialized in recent years (Figure 3.73).

Unlike the other seven bull trout life stages, strategies and actions, the occurrence of sub-adult upstream movement has a notably inverse relationship with HQSs from our model. For example, when HQSs are higher, upstream sub-adult movement occurs at a lower level. This relationship was expected because upstream movement often occurs in response to worsening habitat conditions. If habitat conditions were suitable for sub-adult bull trout in middle and lower basin areas, there would likely be little or no sub-adult upstream movement.

Fluvial sub-adult rearing, foraging and growth

Juvenile bull trout eat primarily insects, but as they grow to sub-adults, they become primarily piscivorous (Fraley and Shepard 1989; Schoby and Keeley 2011; Rieman and McIntyre 1993). Microhabitat attributes and availability of prey species likely influence the specific areas that bull trout use for foraging and rearing within stream reaches and likely contribute to the seasonal distribution of fluvial sub-adult bull trout into downstream reaches. Sub-adult bull trout are not sexually mature and therefore caloric intake is shunted toward primarily growth instead of gonadal development. Sub-adults forage during all months, coinciding with other strategies and actions (e.g., overwintering, migration and rearing). Migratory sub-adult bull trout move from smaller tributaries and upper stream reaches into larger streams and downriver reaches (including the mainstem Columbia River) to take advantage of more abundant resources including juvenile Chinook salmon, steelhead and other prey species. Mesa et al. (2013) estimated temperatures for maximum consumption by bull trout at 15.8-17.5°C and noted that consumption declined as temperatures increased or decreased from this range. Of the eleven habitat variables, water temperature and surface flow heavily influenced the HQSs assigned by our model for sub-adult bull trout rearing, foraging and growth with weighting factors of 0.27 and 0.21, respectively. Riparian zone quality, channel modifications, groundwater and passage impediments were also influential for assessing habitat quality for foraging and rearing sub-adults with weighting factors of 0.10, 0.10, 0.09 and 0.07, respectively. Habitat quality scores predicted by the model indicate that reaches SFWW1 through WW5 contain primarily good and seasonally high quality habitat for bull trout foraging and maintenance during all months. The river in this portion of the Walla Walla Basin has not been diverted for irrigation, has undergone minimal channel modifications and has not been affected by anthropogenic land uses to the extent that lower reaches have. Due to upstream irrigation withdrawals, a high level of channel modification, a lack of channel complexity and a largely absent riparian zone, reach WW7 contains only fair quality habitat for sub-adult foraging and rearing from December through June, declines sharply to poor quality in July and HQSs indicate low quality habitat in this reach persists until surface flows substantially increase in December. Habitat quality scores, driven by cool water temperatures and higher streamflows, indicate good and fair quality foraging and rearing habitat for sub-adult bull trout from October through June in all reaches from WW8 to the mouth of the WWR. Habitat quality declines to mainly low quality during July, August and September when temperatures increase and surface flow is depleted for agricultural purposes.

Non-depleted surface flows accompanied by temperatures that are generally conducive to food consumption and metabolic processes contribute to HQSs that indicate primarily good quality foraging and rearing habitat for sub-adult fluvial bull trout within reaches MC14, MC15 and MC16 during most months. Habitat between the Mill Creek Diversion Dam (rkm 20.1) and the Division Dam (rkm 18.5) scored as fair quality habitat during most months, with the exception of July, August and September where scores indicate a low quality of habitat. Due to diverted streamflows, extensive channel modification and other unfavorable attributes, fair quality habitat exists within reaches MC18 through MC20 during only three months of the year (March, April and May). Habitat quality scores indicate low quality habitat for sub-adult foraging and rearing during all other months except for July, August and September when poor quality habitat is prevalent. Scores for the reach downstream from the flood control project on MC (MC21) indicate that fair and good quality habitat exists during most months, but quality declines to low quality during summer months as well. Due largely to a consistently adequate supply of surface flows, YHC (reach YHC22) contains fair and good quality habitat for fluvial sub-adult bull trout rearing, foraging and growth during all months.

Summary and Management Implications

Effective management of threatened species requires a sufficient knowledge of fundamental habitat requirements, particularly for species occurring in intensively managed and modified landscapes. Walla Walla Basin bull trout exhibit a veritable continuum of life histories involving movements, migrations, spawning, rearing and foraging on time scales ranging from daily to annually or longer, and over different spatial scales. In general, instream habitat in the headwaters of the SFWWR and MC remain relatively pristine, but habitat becomes increasingly degraded downstream from the Umatilla National Forest Boundaries in both subbasins. While the resident component of the population only experiences headwater conditions, migratory bull trout may be exposed to a spectrum of anthropogenic channel modifications, riparian habitat degradation and other influences throughout the Basin and in the mainstem Columbia River. Commonly, bull trout of differing life stages concurrently occupy a given stream reach, utilizing its attributes for differing purposes. For example, a given bull trout found within middle basin reach WW7 (rkm 73.1 – 69.3), near Milton-Freewater, OR, in July could be exhibiting any one of the following life-history stages, strategies or actions:

<u>Downstream migrating sub-adult</u> – Sub-adult fluvial bull trout that is actively migrating downstream to oversummering habitat within the WWR.
<u>Oversummering sub-adult</u> – Fluvial sub-adult bull trout that has recently migrated from the headwater areas during the spring and is oversummering within this reach.
<u>Upstream migrating sub-adult</u> – Fluvial sub-adult bull trout that has recently migrated from the headwater areas during the spring, but is currently moving upstream to escape unfavorable downstream conditions.
<u>Upstream migrating adult (spawning)</u> – Fluvial adult bull trout moving upstream en route to headwater reaches to eventually spawn.
<u>Upstream migrating adults (non-spawning)</u> – Adult-sized bull trout en route to upstream oversummering areas but short of the spawning grounds and not intending to spawn.
<u>Oversummering adults (non-spawning)</u> – Adult-sized bull trout, which previously migrated to middle basin reaches and oversummer within this reach, not intending to spawn the subsequent fall.

The abovementioned example demonstrates the multitude of potential bull trout uses within a given reach during a given month. Further, a suite of habitat characteristics important to bull trout at one life stage and exhibiting a certain strategy within a given river reach during a given month may be less important to bull trout at a differing life stage or exhibiting a different strategy or action (e.g., foraging and rearing sub-adults vs. upstream migrating adults). Focused management actions (e.g., habitat restoration) aimed at benefiting a particular life stage or strategy will likely influence others. This inherent complexity exemplifies the challenges resource managers are faced with while crafting effective management strategies and actions to benefit bull trout and work toward species recovery. Management becomes even more complex when coordinating with management actions aimed at benefiting other imperiled and valued species in the Walla Walla Basin (i.e., summer steelhead, Spring Chinook salmon, redband trout). In addition, balancing resource and land use needs for agricultural, flood control and municipal purposes with the intrinsic needs of imperiled species further complicates management decisions.

The FWS in recent years has renewed its long-term commitment to Strategic Habitat Conservation (SHC). This is a landscape approach that emphasizes planning, science, partnerships, monitoring and assumption-based research. This approach begins with biological planning that incorporates results from sound research and outcome-based monitoring to update biological models that suggest what factors may be limiting populations or preventing the full expression of various life stages and strategies. Resource managers often employ extremely complex, multifaceted models aimed at characterizing aquatic habitat or predicting population performance or response to proposed management actions. These models often incorporate a very large number of input parameters, most of which are estimated with a high degree of uncertainty. These models often lack transparency, transferability may be questionable and derivation methodology may even be proprietary. There is value in these types of tools, but many are intended for assessing habitat for anadromous species and not geared toward the differing and complex habitat requirements specific to bull trout. Some models assess habitat by how it compares in its current state to an approximation of the ecosystem and habitat that existed prior to Euro-American settlement. And, although restoring habitat in relation to an estimated "natural" or "normative" state is desirable, realization of such an effort may be both impractical and improbable in most areas and may simply be inaccurate. We believe that resource managers, working toward bull trout recovery and utilizing the SHC approach, could benefit from the tool we developed which is a simplified, adaptable, practical and fundamentally straightforward approach to assessing aquatic habitat quality at the reach-scale to help inform recovery actions explicitly for bull trout in the SFWWR and MC sub-basins.

Model development included delineating the study area into habitat reaches, the selection of habitat variables, rating the quality of habitat variables within each reach, and weighting each variable based on its overall importance to habitat quality with respect to each bull trout life-history stage and strategy. Our habitat assessment model utilized findings and observations from past bull trout studies and recent field and laboratory investigations along with professional judgment and widely accepted benchmarks to develop criteria to rate the quality of habitat monthly by reach for each of eight identified bull trout life-history stages, strategies or actions exhibited by Walla Walla Basin bull trout. We chose to incorporate habitat variables that are largely temporally and spatially static (e.g., channel modification) in addition to dynamic variables (e.g., surface flow) to more effectively characterize habitat quality as it changes throughout the year. Proxy variables (e.g., elevation, land use) were also incorporated to generally represent numerous, but not well quantified, factors that are commonly considered to influence the quality of habitat for bull trout within the Walla Walla Basin (e.g., angling pressure, predation, pollution). We assigned a "weighting factor" to each variable reflecting its relative importance with respect to the particular life stage, strategy or action for Walla Walla Basin bull trout. Weighting factors were derived through an AHP (Saaty 2008), informed through professional consensus, by experienced bull trout biologists who used professional judgment to complete online questionnaires to approximate the importance of each habitat variable relative to one another with respect to each of the 8 identified life-history stages, strategies and actions.

Our model assigned a monthly habitat quality score to each of the 22 reaches for each of the eight identified bull trout life stages, strategies and actions exhibited by Walla Walla Basin bull trout. Not surprisingly, model scores generally suggest that the quality of habitat for most bull trout life stages, strategies and actions is better in headwater reaches and degrades incrementally downstream as the severity and often cumulative, anthropogenic modifications and other influences become more prevalent. Similarly, scores indicate that even in greatly modified and degraded stream reaches, seasonal habitat conditions ranging from fair to high quality exist during many fall, winter and spring months. In middle and lower basin areas, as flows decrease and are largely diverted for agricultural purposes and water temperatures elevate, habitat conditions become progressively less favorable for most bull trout uses. Reaches downstream of WW6 in the WWR often were assigned scores indicating low and poor habitat conditions for most bull trout life stages and strategies from approximately July through October. The same is generally true for reaches downstream of MC17 from approximately June through November in MC. Reach WW11 consistently scored the lowest of all reaches in the WWR during the summer and early fall months. In MC, reaches MC18, MC19 and MC20 contained the worst habitat conditions for all eight bull trout life stages and strategies during the summer months and through December. One notable finding in our study was that habitat within YHC (reach YHC22) scored fair or good during all months and with respect to each of the eight identified bull trout life-history stages, strategies and actions. Unfortunately, reaches in MC and WWR that connect to YHC primarily scored as low and poor from approximately July through September. However, due to its many groundwater inputs and consistent surface flow, YHC could function seasonally as a refuge for bull trout from unfavorable WWR and MC environments and also seasonally function as an important migration corridor connecting the two subbasins until improvements to habitat and passage issues throughout the Mill Creek Project are rectified.

We evaluated the results of our model by comparing monthly HQSs for each reach with estimates of bull trout occurrence derived primarily from existing empirical movement and occupancy datasets with respect to each life-history stage and strategy. Despite the coarse nature of this evaluation, we found that mean habitat quality scores are usually higher when bull trout occurrence is high and lower when occurrence is low for most life stages and strategies. Mean HQSs were usually lowest for each life stage and action when there is no observed occurrence. One expected exception was the inverse relationship between mean HQSs and the level of bull trout occurrence for fluvial sub-adult upstream migration. The mean HQSs for fluvial sub-adult upstream migration were higher when there is no or low occurrence and HQSs were lowest when occurrence was high. This relationship was expected since sub-adults often move back upstream to more favorable habitat in response to deteriorating downstream habitat conditions. By characterizing instream habitat by reach and identifying when and where low and poor quality habitat conditions interface with bull trout occurrence in the Walla Walla Basin, we can provide managers with useful information to inform future conservation actions or initiate additional studies that target the particular bull trout life stage or strategy of concern.

Habitat variation exists at a variety of spatial and temporal scales, requiring habitat quality to be assessed at multiple scales as well. To this end, the output from this model should be used as a “first cut” tool when determining potential sites for habitat restoration or the implementation of future management actions to work toward bull trout recovery. Depending upon the desired output, results from this reach-scale assessment model could be further “stepped down” by adjusting the temporal or spatial scales under the existing model framework, or used in conjunction with predictive, smaller scale (e.g., micro-scale) habitat models and empirical data to assess specific details or quantify habitat within reaches. Further, due to its simplicity, this model may be applicable to assess habitat for bull trout in other basins or river systems.

Literature Cited

Al-Chokhachy, R. and P. Budy. 2007. Summer Microhabitat Use of Fluvial Bull Trout in Eastern Oregon Streams. North American Journal of Fisheries Management 27:1068-1081, 2007.

Al-Chokhachy, R., B. B. Roper, T. Bowerman, and P. Budy. 2010. A Review of Bull Trout Habitat Associations and Exploratory Analyses of Patterns across the Interior Columbia River Basin. North American Journal of Fisheries Management 30:464-480, 2010.

Allan, J. D. 2004. Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. Annual Review of Ecology, Evolution and Systematics: 35:257-84.

Anglin, D. R., D.G. Gallion and T.J. Kisaka. 2003. Evaluation of the Effect of Increased Instream Flows during 2002 and Implications for Bull Trout in the Upper Walla Walla River. U.S. Fish and Wildlife Service, Columbia River Fisheries Program Office, Vancouver, WA.

Anglin, D.R., D.G. Gallion, M. Barrows, C. Newlon, P. Sankovich, T.J. Kisaka, and H. Schaller. 2008a. Bull Trout Distribution, Movements and Habitat Use in the Walla Walla and Umatilla River Basins 2004 Annual Progress Report.

Anglin, D.R., D.G. Gallion, M. Barrows, C. Newlon, R. Koch. 2008b. Current Status of Bull Trout Abundance, Connectivity, and Habitat Conditions in the Walla Walla Basin 2007 Update.

Anglin, D.R., D.G. Gallion, M. Barrows, R. Koch, and C. Newlon. 2009a. Monitoring the Use of the Mainstem Columbia River by Bull Trout from the Walla Walla Basin. Final Report for 2007 prepared for the U.S. Army Corps of Engineers, Walla Walla, WA.

Anglin, D.R., D.G. Gallion, M. Barrows, R. Koch, and C. Newlon. 2009b. Monitoring the Use of the Mainstem Columbia River by Bull Trout from the Walla Walla Basin. Final Report for 2008 prepared for the U.S. Army Corps of Engineers, Walla Walla, WA.

Anglin, D.R., D.G. Gallion, M. Barrows, R. Koch, and C. Newlon. 2010. Monitoring the Use of the Mainstem Columbia River by Bull Trout from the Walla Walla Basin. Final Report for 2009 prepared for the U.S. Army Corps of Engineers, Walla Walla, WA.

Baker, T. W. 2011. 2011 Walla Walla Basin Seasonal Seepage Assessments Report: Walla Walla River, Mill Creek, Touchet River, and Yellowhawk Creek. Walla Walla Basin Watershed Council, Milton-Freewater, OR.

Barrows M.G, R. Koch, C. Newlon, D. Gallion, J.J. Skalicky, and D.R. Anglin. 2012a. Use of the Mainstem Columbia River by Walla Walla Basin Bull Trout. Annual Report for 2010 prepared for the U.S. Army Corps of Engineers, Walla Walla, WA.

Barrows, M.G., D.R. Anglin, R. Koch, and J.J. Skalicky. 2012b. Use of the Mainstem Columbia River by Walla Walla Basin Bull Trout. 2011 Annual Report to the U.S. Army Corps of Engineers, Walla Walla District. Project BT-W-10-2.

Barrows, M.G., R. Koch, and B. Silver. *In review.* North Fork Walla Walla River Bull Trout Patch Occupancy and Habitat Use Assessment. 2012-2013 Annual Report. U.S. Fish and Wildlife Service, Columbia River Fisheries Program Office, Vancouver, WA.

Baxter, J.S. 1995. Chowade River bull trout studies 1995: Habitat and population assessment. Report prepared for British Columbia Ministry of Environment, Lands and Parks, Fisheries Branch, Fort St. John, British Columbia. 108 pp.

Baxter, C.V. and F. R. Hauer. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences: 57(7):1470-1481.

Baxter, J. S., and J. D. McPhail. 1996. Bull trout spawning and rearing habitat requirements: summary of the literature. Fisheries Technical Circular No. 98, 27 p.

Benda, L. N., L. N. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. The network dynamics hypothesis: how channel networks structure riverine habitats. BioScience 54:413-427.

Bjornn, T.C. 1991. Bull trout (*Salvelinus confluentus*). Pages 230-235 *In:* J. Stolz and J. Schnell, eds. Trout. Stackpole Books, Harrisburg, Pennsylvania.

Bowen, Z. H., K. D. Bovee and T. J. Waddle. 2003. Effects of Flow Regulation on Shallow-Water Habitat Dynamics and Floodplain Connectivity. Transactions of the American Fisheries Society 132:809-823.

Bower, B. J. 2007. Walla Walla River Surface Water Budget Assessment. Walla Walla Basin Watershed Council. Walla Walla, WA.

Brown, L. 1992. On the zoogeography and life history of Washington's native char. Washington Department of Fish and Wildlife, Report #94-04, Fisheries Management Division. Olympia. 41 pp.

Burns, B., P. D. Powers, K. K. Bates, and J. Kidder. 2009. Mill Creek Fish Passage Assessment. Final Report. Prepared for the Tri-State Steelheaders, Walla Walla, Washington.

Carline, F. C. and S. P. Klosiewski. 1985. Responses of Fish Populations to Mitigation Structures in Two Small Channelized Streams in Ohio. North American Journal of Fisheries Management 5:1-11.

Castelle, A. J., A. W. Johnson and C. Conolly.1994. Wetland and stream buffer requirements – A review. Journal of Environmental Quality 23: 878-882.

Chapman, D. W., and E. Knudsen. 1980. Channelization and Livestock Impacts on Salmonid Habitat and Biomass in Western Washington, Transactions of the American Fisheries Society 109:357-363.

Craig, P. C., and K. A. Bruce. 1982. Fish resources in the upper Liard River drainage. *In* A. D. Sekerak (ed.) Fish resources and proposed hydroelectric development in the upper Liard drainage. Report to British Columbia Hydro and Power Authority, 184 p.

Dunham, J., B. Rieman and G. Chandler. 2003. Influences of Temperature and Environment Variables on the Distribution of Bull Trout within Streams at the Southern Margin of Its Range. North American Journal of Fisheries Management 23:894-904.

Dupont. J. M., R. S. Brown, and D. R. Geist. 2007. Unique Allacustrine Migration Patterns of a Bull Trout Population in the Pend Oreille River Drainage, Idaho. North American Journal of Fisheries Management 27:1268-1275.

Ebersole, L. E., W. J. Liss, and C. A. Frissell. 2003. Cold Water Patches in Warm Streams: Physicochemical Characteristics and the Influence of Shading. Journal of the American Water Resources Association 39:355-368.

Environmental Management Associates. 1993. Bull trout juvenile and spawning habitat preference criteria, Smith-Dorrien Creek, Alberta. Unpublished report to Fish and Wildlife Division, Alberta Environmental Protection, Edmonton, Alberta, 26p.

Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Science 63:133-143.

Geier, A. R., and L. B. Best. 1980. Habitat Selection by Small Mammals of Riparian Communities: Evaluating Effects of Habitat Alterations. Journal of Wildlife Management 44:16-24.

Gendaszek, A. S., C. S. Magirl, and C. R. Czuba. 2012. Geomorphic response to flow regulation and channel and floodplain alteration in the gravel-bedded Cedar River, Washington, USA. Geomorphology 179:258-268.

Goetz, F. 1989. Biology of the bull trout, *Salvelinus confluentus*, a literature review. Eugene, OR: U.S. Department of Agriculture, Forest Service, Willamette National Forest. 53 p.

Graham, P.J., B. B. Shepard, and J. J. Fraley. 1981. Use of stream habitat classifications to identify bull trout spawning areas in streams. Pp. 186-190 in N. B. Armantrout (ed.) Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society Symposium (Western Division), Portland, OR.

Grant, G., B. Burkholder, A. Jefferson, S. Lewis, and R. Haggerty. 2006. Hyporheic flow, temperature anomalies, and gravel augmentation: Preliminary findings of a field investigation on the Clackamas River, OR. Prepared for Portland General Electric.

Gray, S. 2005. Determine the Origin, Movements, and Relative Abundance of Bull Trout in Bonneville Reservoir, 2004-2005 Annual Report. Project No. 200306500, 26 electronic pages. (BPA Report DOE/BP-00016701-1).

Harrison, E. T., N. C. Donaldson, F. R. McCreary, A. O. Ness, S. Krashevski. 1964. Soil Survey of Walla Walla County, Washington. Prepared for the Soil Conservation Service, U. S. Department of Agriculture.

Howell, P. J., J. B. Dunham, and P. M. Sankovich. 2010. Relationships between water temperatures and upstream migration, cold water refuge use, and spawning of adult bull trout from the Lostine River, Oregon, USA. Ecology of Freshwater Fish 19:96-106.

Jakober, M.J., T.E. McMahon, R.F. Thurow and C.G. Clancy. 1998. Role of Stream Ice on Fall and Winter Movements and Habitat Use by Bull Trout and Cutthroat Trout in Montana Headwater Streams. Transactions of the American Fisheries Society 127:223-235.

Jones, L.A., C.C. Muhlfeld, L.A. Marshall, B. L. McGlynn, and J.L. Kershner. 2013. Estimating Thermal Regimes of Bull Trout and Assessing the Potential Effects of Climate Warming on Critical Habitats. River Research and Applications. DOI: 10.1002/rra.2638.

Koch, R. (*In review*). Movement of bull trout in Mill Creek, Walla Walla County, Washington. 2005-2012 Summary Report. U.S. Fish and Wildlife Service, Columbia River Fisheries Program Office, Vancouver, WA.

Lewis, L.L., D. A. Kovacic. 1993. Riparian vegetated buffer strips in water-quality restoration and stream management. Freshwater Biology 29:243-258.

Long, J. W., A. L. Medina, A. Tecle. 2006. Geologic influences on Apache trout habitat in the White Mountains of Arizona. Journal of the Arizona-Nevada Academy of Sciences 38: 88-101.

Mahoney, B.D. 2003. Summer Steelhead and Bull Trout Radio Telemetry. Chapter Six, in Contor, C. R. and A. D. Sexton, editors. Walla Walla Basin Natural Production Monitoring and Evaluation Project Progress Report, 1999-2002. Confederated Tribes of the Umatilla Indian Reservation. Report submitted to Bonneville Power Administration. Project No. 2000-039-00.

Mahoney B.D., M.B. Lambert, T.J. Olsen, E. Hoverson, P. Kissner, and J.D.M. Schwartz. 2006. Walla Walla Basin Natural Production Monitoring and Evaluation Project Progress Report, 2004 - 2005. Confederated Tribes of the Umatilla Indian Reservation. Report submitted to Bonneville Power Administration. Project No. 2000-039-00.

Maret, T.R., Robinson, C.T., Minshall, G.W. 1997. Fish assemblages and environmental correlations in least disturbed streams of the Upper Snake River Basin. Transactions of the American Fisheries Society 126:200–216.

McPhail, J.D., and J.S. Baxter. 1996. A review of bull trout (*Salvelinus confluentus*) life-history and habitat use in relation to compensation and improvement opportunities. Fisheries Management Report No. 104, 35 p.

McPhail, J.D., and C.B. Murray. 1979. The early life history and ecology of Dolly Varden (*Salvelinus malma*) in the upper Arrow Lakes. Report to BCHydro and Ministry of Environment, Fisheries Branch, Nelson, British Columbia. 113 p.

Mesa, M. G., L. K. Weiland, H. E. Christiansen, S. T. Sauter and D. A. Beauchamp. 2013. Development and Evaluation of a Bioenergetics Model for Bull Trout. Transactions of the American Fisheries Society 142:41-49.

Moore, T.L., S.J. Starcevich, S. Jacobs, and P.J. Howell. 2006. Migratory Patterns, Structure, Abundance, and Status of Bull Trout Populations from Subbasins in the Columbia Plateau and Blue Mountain Provinces. 2005 Annual Report prepared for U.S. Department of Energy, Bonneville Power Administration, Portland, OR. Project Number 199405400, Contract Number 22664.

Muhlfeld, C.C., and B. Marotz. 2005. Seasonal Movement and Habitat Use by Subadult Bull Trout in the Upper Flathead River System, Montana. North American Journal of Fisheries Management 25:795-810.

Nelson, M.C. and R.D. Nelle. 2008. Seasonal movements of adult fluvial bull trout in the Entiat River, WA 2003-2006. U.S. Fish and Wildlife Service, Leavenworth, WA.

O'Neill, B.J. and J. H. Thorp. 2011. A simple channel complexity metric for analyzing river ecosystem responses. River Systems 19/4:327-335.

Oregon Department of Environmental Quality (ODEQ). 2001. Umatilla Total Maximum Daily Limit. Portland, Oregon.

Parametrix. 2005. Montana DNRC Forested Trust Land HCP Species Account. Prepared for Montana Department of Natural Resources and Conservation (DNRC) Forest Management Bureau. Appendix A.

Pratt, K.L. 1992. A Review of Bull Trout Life History. In: Howell, P.J.; Buchanan, D.B., eds. Proceedings of the Gearhart Mountain Bull Trout Workshop; 1992 August; Gearhart Mountain, OR. Corvallis, OR: Oregon Chapter of the American Fisheries Society: 5-9.

Rice, S. P., M. T. Greenwood, and C. B. Joyce. 2001. Tributaries, sediment sources, and the longitudinal organization of macroinvertebrate fauna along river systems. Canadian Journal of Aquatic Sciences 58:824-840.

Rich, C. F. Jr., T. E. McMahon, B. E. Rieman and W. L. Thompson. 2003. Local-Habitat, Watershed, and Biotic Features Associated with Bull Trout Occurrence in Montana Streams. Transactions of the American Fisheries Society 132:1053-1064.

Rieman, B. E. and G. L. Chandler. 1999. Empirical Evaluation of Temperature Effects on Bull Trout Distribution in the Northwest. Boise, Idaho: Final report to U.S. Environmental Protection Agency.

Rieman, B. E. and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service General Technical Report INT-302.

Rieman, B. E. and J. D. McIntyre. 1995. Occurrence of Bull Trout in Naturally Fragmented Habitat Patches of Varied Size. Transactions of the American Fisheries Society 124:285-296.

Rieman, B. E., J. T. Peterson, and D. L. Myers. 2006. Have brook trout (*Salvelinus fontinalis*) displaced bull trout (*Salvelinus confluentus*) along longitudinal gradients in central Idaho streams. Canadian Journal of Fisheries and Aquatic Sciences 63:63–78.

Saaty, T. L. 2008. Decision making with the analytic hierarchy process. International Journal of Services Sciences 1:83-98.

Saffel, P. D., and D. L. Scarnecchia. 1996. Habitat use by juvenile bull trout in belt-series geology watersheds of northern Idaho. Northwest Science 69:304–317.

Scherberg, J.N. 2012. The Development of a Hydrological Model of the Walla Walla Basin Using Integrated Water Flow Model. Master of Science Thesis. Oregon State University.

Schlosser, J.J. 1991. Stream fish ecology: A landscape perspective. BioScience 41:704-712.

Schoby, G. P., and E. R. Keeley. 2011. Home Range Size and Foraging Ecology of Bull Trout and Westslope Cutthroat Trout in the Upper Salmon River Basin, Idaho. Transactions of the American Fisheries Society 140:636-645.

Selong, J. H., T. E. McMahon, A. V. Zale, and F. T. Barrows. 2001. Effect of Temperature on Growth and Survival of Bull Trout, with Application of an Improved Method for Determining Thermal Tolerance in Fishes. Transactions of the American Fisheries Society 130:1026-1037.

Shepard, B. B., K. L. Pratt, and P. J. Graham. 1984. Life histories of westslope cutthroat and bull trout in the upper Flathead River Basin, Montana. Report (Contract R008224-01-5) of Montana Department of Fish, Wildlife, and Parks to U.S. Environmental Protection Agency, Washington, D.C.

Siemann, D., and S. Martin. 2007. Managing Many Waters: An Assessment of Capacities for Implementing Water and Fish Improvements in the Walla Walla Basin. The William D. Ruckelshaus Center. Washington State University and University of Washington.

Small, M.P., M. Barrows, and E. Martinez. 2012. Genetic assignments for migratory bull trout captured in the Walla Walla and Umatilla rivers: assessing connectivity through genetic analyses. WDFW Genetics Laboratory, Olympia, Washington.

Stanford, J.A. and E.R. Hauer. 1992. Mitigating the impacts of stream and lake regulation in the Flathead River catchment, Montana, USA: an ecosystem perspective. Aquatic Conservation: Marine and Freshwater Ecosystems 2:35–63.

Stanford, J.A., J.V. Ward, W.J. Liss, C.A Frissell, R.N. Williams, J.A. Lichatowich, and C.C. Coutant. 1996. A general protocol for restoration of regulated rivers. Regulated Rivers 12:391–414.

Starcevich, S.J., P. J. Howell, S.E. Jacobs, and P.M. Sankovich. 2012. Seasonal Movement and Distribution of Fluvial Adult Bull Trout in Selected Watersheds in the Mid-Columbia River and Snake River Basins. PLoS ONE 7(5): e37257. Doi:10.1371/journal.pone.0037257.

Stewart, R. J., R. E. McLenehan, J. D. Morgan, and W. R. Olmstead. 1982. Ecological studies of arctic grayling, *Thymallus arcticus,* Dolly Varden, *Salvelinus malma,* and mountain whitefish, *Prosopium williamsoni,* in the Liard River drainage, B.C. Report to Westcoast Transmission Company and Foothills Pipe Lines Ltd. by E. V. S. Consulting, North Vancouver, British Columbia.

Stuart, K. M., and G. R. Chislett. 1979. Aspects of the life history of arctic grayling in the Sukunka drainage. British Columbia Fish and Wildlife Branch, Prince George, British Columbia, 111 p.

Swanberg, T. R. 1997. Movements and habitat use by fluvial bull trout in the Blackfoot River, Montana. Transactions of the American Fisheries Society 126:735–746.

The Nature Conservancy. 2006. An Assessment of Freshwater Systems in Washington State.

U.S. Fish and Wildlife Service (USFWS). 2002. Chapter 10, Draft Umatilla-Walla Walla Recovery Unit, Oregon and Washington. 149 p. In: U.S. Fish and Wildlife Service. Bull Trout (Salvelinus confluentus) Recovery Plan. Portland, Oregon.

U.S. Fish and Wildlife Service (USFWS). 2010. Chapter 14. Mid-Columbia Recovery Unit – Walla Walla River Critical Habitat Unit. 409-424. In: U. S. Fish and Wildlife Service. Bull Trout Final Critical Habitat Justification. Portland, Oregon.

Walla Walla Agricultural Water Quality Management Area Plan. 2007. Guidance Document and Administrative Rules. Developed by the Walla Walla Local Agricultural Water Quality Advisory Committee with assistance from the Oregon Department of Agriculture and the Umatilla County Soil and Water Conservation district.

Walla Walla Subbasin Plan. 2004. Walla Walla County (on behalf of the Walla Walla Watershed Planning Unit) and the Walla Walla Basin Watershed Council. Prepared for Northwest Power and Conservation Council.

Walla Walla Watershed Plan. 2005. Planning Unit Final. Prepared by HDR/EES, Inc. and Dr. Michael Barber, WSU and Steward and Associates, Inc.

Ward, T.A., K.W.Tate, E.R. Atwill, D.F. Lile, D.L. Lancaster, N. McDougald, S. Barry, R.S. Ingram, H.A. George, W. Jensen, W. E. Frost, R. Phillips, G.G. Markegard, and S. Larson. 2003. A comparison of three visual assessments for riparian and stream health. Journal of Soil and Water Conservation 58:83-88.

Warren, D.R., J.M. Robinson, D.C. Josephson, D.R. Sheldon, and C.E. Kraft. 2012. Elevated summer temperatures delay spawning and reduce redd construction for resident brook trout (*Salvelinus fontinalis*). Global Change Biology 18:1804-1811.

Watson, G., and T. W. Hillman. 1997. Factors Affecting the Distribution and Abundance of Bull Trout: An Investigation at Hierarchical Scales. North American Journal of Fisheries Management 17:237-252.

Waters, T. F. 1995. Sediments in Streams: Sources, Biological Effects and Control. Bethesda, Maryland, USA: American Fisheries Society. 251pages.

Wenger, S. 1999. A Review of the Scientific Literature on Riparian Buffer Width, Extent and Vegetation. Report for the Office of Public Service and Outreach Institute of Ecology, University of Georgia. Athens, Georgia.

Woods, L. C., and B. L. Griswold. 1981. Channelization and Mitigation: Their Effects on Macroinvertebrate Communities of the Olentangy River, Columbus, Ohio. American Fisheries Society Warm water Streams Symposium, 1981, pp. 113-118.

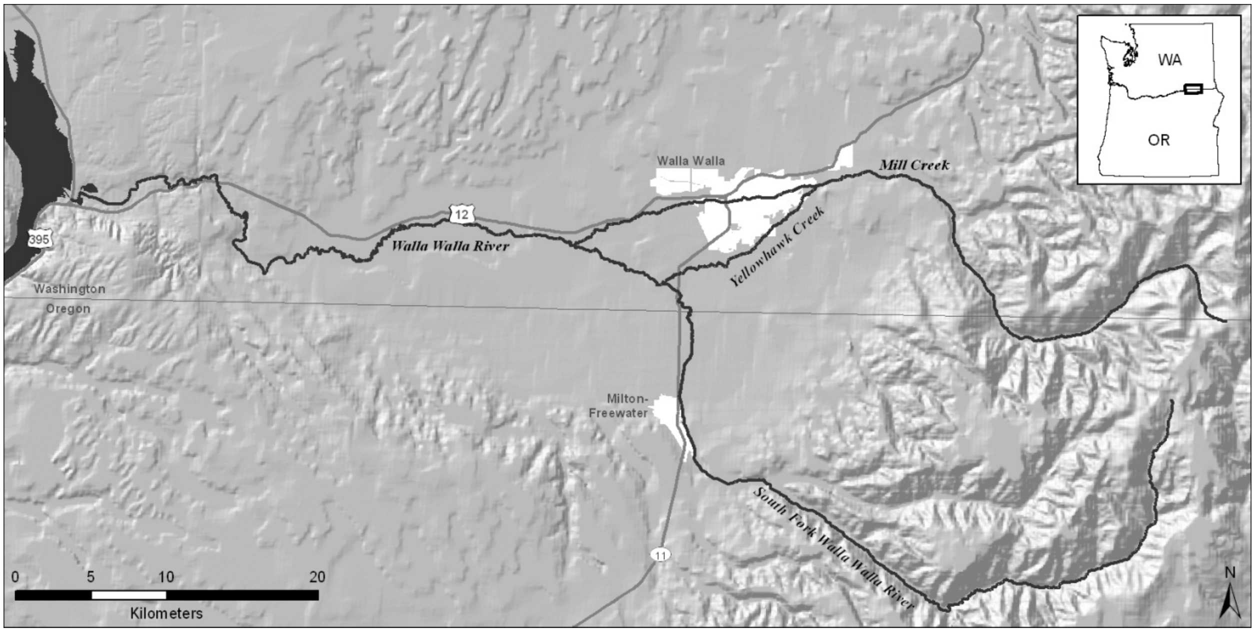

Figure 3.1.Study area map depicting the Walla Walla River and Mill Creek subbasins.

Table 3.1.Description of surface flow categories and criteria for rating the quality of surface flow within reaches of the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks.

Surface Flow Categories	Numeric Rating	Percentage Rating Criteria	Explanation
High Quality	5	> 80.0%	Near normative, less-diverted streamflows inferring high quantity and quality of habitat for bull trout at all life stages.
Good Quality	4	> 60.0 – 80.0%	Partially-diverted streamflows inferring good quantity and quality of habitat for bull trout at all life stages and for all strategies and actions in terms of surface flow.
Fair Quality	3	> 40.0 – 60.0%	Moderately-diverted streamflows inferring a fair quantity and quality of habitat for bull trout at all life stages and for all strategies and actions in terms of surface flow.
Low Quality	2	> 20.0 – 40.0%	Very depleted streamflows inferring low quantity and quality of habitat for bull trout at all life stages and for all strategies and actions in terms of surface flow.
Poor Quality	1	≤ 20.0 %	Severely depleted streamflows inferring a poor quantity and quality of habitat for bull trout at all life stages and for all strategies and actions in terms of surface flow.

Table 3.2. Description of groundwater categories and associated numeric rating.

Groundwater Categories	Numeric Rating	Explanation
High Quality	5	Natural, principally unmodified, optimal groundwater and hyporheic exchange conditions that allow for bull trout at a given life stage to exhibit a certain strategy or conduct a particular action and thrive.
Good Quality	4	Nearly natural, groundwater and hyporheic conditions, subjected to only minimal anthropogenic alterations that likely contribute positively to the quality of aquatic habitat conditions for bull trout at a given life stage to exhibit a certain strategy or conduct a particular action and thrive.
Fair Quality	3	Groundwater and hyporheic conditions that only moderately positively influence habitat conditions for bull trout at a given life stage to exhibit a certain strategy or conduct a particular action and persist.
Low Quality	2	Groundwater and hyporheic conditions which negatively influence or worsen habitat conditions for bull trout at a given life stage to exhibit a certain strategy or conduct a particular action and persist.
Poor Quality	1	Groundwater and hyporheic conditions that severely limit the ability of a bull trout at a given life stage to exhibit a certain strategy or conduct a particular action.

Table 3.3. Description of temperature categories and associated numeric rating.

Temperature Categories	Numeric Rank	Explanation
High Quality	5	Optimal temperature conditions for bull trout at a given life stage to exhibit a certain strategy or conduct a particular action and thrive.
Good Quality	4	Temperature conditions, albeit not optimal, that allow bull trout at a given life stage to exhibit a certain strategy or conduct a particular action and thrive.
Fair Quality	3	Tolerable temperature conditions that likely allow bull trout at a given life stage to exhibit a certain strategy or conduct a particular action and persist.
Low Quality	2	Temperature conditions, albeit tolerable, likely only marginally allow bull trout at a given life stage to exhibit a certain strategy or conduct a particular action and persist.
Poor Quality	1	Temperature conditions that severely limit the ability of a bull trout at a given life stage to exhibit a certain strategy or conduct a particular action and may be lethal or may inhibit the long-term persistence of the population.

Table 3.4. Criteria for rating the quality of temperature within reaches of the South Fork Walla Walla River and Mainstem Walla Walla River as well as Mill and Yellowhawk creeks.

Activity/Process/Action	Poor Quality (1)	Low Quality (2)	Fair Quality (3)	Good Quality (4)	High Quality (5)
Adult Spawning	>16°C*	>10 - 16°C*	>7 - 10°C*	≤5°C*	>5 - 7°C*
Juvenile Rearing, Foraging and Growth	>22°C	>18 -22°C and ≤1°C	1 – 6°C and >16 – 18°C	>6 - 10°C and >12 - 16°C	>10 - 12°C
Fluvial Adult Upstream Migration	>26°C and ≤5°C	>20 - 26°C and >5 - 11°C	>16 to 20°C	>11 to 14°C	>14 - 16°C
Adult Foraging and Maintenance	>26°C	>20 -26°C and ≤1°C	1 – 6°C and >18 – 20°C	>6 - 14°C and >16 - 18°C	>14 - 16°C
Fluvial Adult Downstream Migration	>26°C	>20 -26°C and ≤1°C	>16 -20°C	>1 - 6°C and >10 - 16°C	>6 – 10°C
Fluvial Sub-adult Downstream Migration	>26°C	>20 -26°C and ≤1°C	>16 -20°C	>1 - 6°C and >10 - 16°C	>6 – 10°C
Fluvial Sub-adult Lower River Evacuation	>26°C	>20 -26°	>18 - 20°C	>16 - 18°C	< 16°C
Fluvial Sub-adult Rearing, Foraging and Growth	>26°C	>20 -26°C and ≤6°C	6 - 10°C and >18 - 20°C	>10 -14°C and >16 - 18°C	>14 - 16°C

Table 3.5. Description of passage impediment categories and criteria for rating the quality of impediments to bull trout passage within reaches of the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks.

Impediments Categories	Numeric Rating	Explanation/Rating Criteria
High Quality	5	Reaches containing no apparent passage impediments that would influence the given bull trout life stage, strategy or action negatively.
Good Quality	4	Reaches containing impediments that would likely influence the given bull trout life stage, strategy or action, but would allow for primarily unobstructed fish passage.
Fair Quality	3	Reaches where passage impediments exist and are believed to notably delay or otherwise moderately influence the given bull trout life stage, strategy or action negatively.
Low Quality	2	Reaches containing passage impediments that likely severely delay or inhibit bull trout passage or would otherwise severely influence the given life stage, strategy or action negatively.
Poor Quality	1	Reaches where passage impediments exist that are known to be a barrier to all bull trout passage and would profoundly influence the given life stage, strategy or action negatively.

Table 3.6. Description of channel modification categories and criteria for rating the quality of a reach in terms of channel modification in the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks.

Channel Modification Categories	Numeric Rating	Explanation/Rating Criteria
High Quality	5	Principally natural, unmodified channel conditions lacking any significant or notably consequential channel restrictions, confinement, straightening or armored banks. Channel conditions within the reach are near optimal and allow for bull trout at a given life stage to exhibit a certain strategy or conduct a particular action.
Good Quality	4	Sparsely modified channel conditions where only occasional, largely inconsequential and intermittent channel restrictions, confinement, straightening or armored banks occur. Channel conditions within the reach collectively only minimally affect bull trout at a given life stage to exhibit a certain strategy or conduct a particular action.
Fair Quality	3	The river channel has commonly been modified, restricted, confined, straightened or armored resulting in conditions within the reach that likely moderately affect bull trout at a given life stage to exhibit a certain strategy or conduct a particular action.
Low Quality	2	The river channel has been restricted, significantly straightened and confined by levees or dikes. Channel conditions likely significantly impair the ability of bull trout at a given life stage to exhibit a certain strategy or conduct a particular action.
Poor Quality	1	The river channel is severely restricted, straightened and confined within a concrete flume or canal, and likely severely limits the ability of a bull trout at a given life stage to exhibit a certain strategy or conduct a particular action.

Table 3.7. Description of riparian zone area categories and criteria for rating the quality of the riparian zone within reaches in the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks.

Riparian Zone Area Categories	Numeric Rating	Explanation/Rating Criteria
High Quality	5	Riparian zone area > 48,000 m^2/km. The substantial size of the riparian zone in the given reach likely provides a high potential to buffer the river from the impacts from adjacent anthropogenic land uses.
Good Quality	4	Riparian zone area from > 36,000 – 48,000 m^2/km. The relatively large size of this riparian zone likely provides notable protection from impacts resulting from neighboring, anthropogenic land uses.
Fair Quality	3	Riparian zone area from > 24,000 – 36,000 m^2/km. The relatively moderate size of this riparian zone likely provides a moderate level of protection from impacts resulting from neighboring, anthropogenic land uses.
Low Quality	2	Riparian zone areas from 12,000 – 24, 000 m^2/km. The relatively narrow riparian zone in the given reach is likely largely ineffective at buffering the aquatic habitat from impacts resulting from neighboring, anthropogenic land uses.
Poor Quality	1	Riparian zone areas ≤ 12,000 m^2/km. The very narrow riparian zone in the given reach likely only negligibly buffers the aquatic habitat from impacts resulting from neighboring, anthropogenic land uses.

Table 3.8. Description of riparian canopy categories and criteria for rating the quality of the riparian zone within reaches in the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks.

Riparian Canopy Categories	**Numeric Rating**	**Explanation/Rating Criteria**
High Quality	5	Largely natural, principally unmodified, optimal riparian canopy conditions. Dense stands of mature canopy trees that overhang the river and line both banks throughout most of the given reach.
Good Quality	4	Nearly natural, dense stands of mature canopy trees that commonly overhang the river and largely line both river banks throughout most of the given reach.
Fair Quality	3	Mature canopy trees that commonly, but inconsistently line portions of the river banks throughout most of the given reach.
Low Quality	2	Only sporadic canopy trees along the river margins throughout most of the given reach.
Poor Quality	1	The riparian area is largely void of mature canopy trees along the river banks throughout most of the given reach.

Table 3.9. Description of stream gradient categories and criteria for rating the quality habitat quality in terms of stream gradient within reaches of the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks.

Stream Gradient Categories	Numeric Rating	Stream Gradient Range	Explanation/Rating Criteria
High Quality	5	< 1.25% (Dec - May) 1.25 – 2.50% (June – Nov)	Stream gradient that likely does not limit the quality or quantity of available habitat for bull trout at a given life stage to exhibit a certain strategy or conduct a particular action.
Good Quality	4	1.25 – 2.50% (Dec - May) >2.50 - 3.75% (Jun – Nov)	Stream gradient that may only slightly limit the quality or quantity of available habitat for bull trout at a given life stage to exhibit a certain strategy or conduct a particular action.
Fair Quality	3	>2.5 - 3.75% (Dec – May) >3.75 – 5.00% (Jun – Nov)	Stream gradient that may moderately limit the quality or quantity of available habitat for bull trout at a given life stage to exhibit a certain strategy or conduct a particular action.
Low Quality	2	>3.75 – 5.00% (Dec – May) > 5.00% (Jun – Nov)	Stream gradient that may negatively influence the quantity and quality of habitat within a reach for bull trout at a given life stage to exhibit a certain strategy or conduct a particular action.
Poor Quality	1	> 5.00% (Dec – May) < 1.25% (Jun – Nov)	Stream gradient, when coupled with depleted stream flows in lower basin reaches. Also high stream gradients that likely severely limit bull trout at a given life stage to exhibit a certain strategy or conduct a particular action at a given life stage.

Table 3.10. Description of elevation categories and criteria for rating the quality of elevation within reaches of the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks.

Elevation Categories	Numeric Rating	Elevation Rating Criteria	Explanation
High Quality	5	> 1421 m	Optimal elevation for bull trout at a given life stage to exhibit a certain strategy or conduct a particular action and thrive while experiencing negligible anthropogenic influences.
Good Quality	4	> 1091 – 1421 m	Elevation, albeit not optimal, that allows bull trout at a given life stage to exhibit a certain strategy or conduct a particular action and thrive while experiencing only minimal anthropogenic influences.
Fair Quality	3	> 762 m – 1091 m	Elevation that allows bull trout at a given life stage to exhibit a certain strategy or conduct a particular action while experiencing only moderate anthropogenic influences.
Low Quality	2	> 433 – 762 m	Elevation where bull trout may experience levels of anthropogenic influences that could notably impact their ability to exhibit a certain strategy or conduct a particular action at a given life stage.
Poor Quality	1	≤ 433 m	Elevation where bull trout likely experience levels of anthropogenic influences that could severely impact their ability to exhibit a certain strategy or conduct a particular action at a given life stage.

Table 3.11. Description of land use categories and criteria for rating the quality of land use within reaches of the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks.

Land Use Categories	Numeric Rating	Explanation
High Quality	5	Forested or wildlife refuge areas generally have the least detrimental impact on the quality of riverine habitat.
Good Quality	4	Land converted to agricultural uses such as orchards and vineyards likely negatively impact riverine habitat, but the impacts are likely minor relative to other anthropogenic land uses.
Fair Quality	3	Pasture land and the associated livestock are often detrimental to riparian and riverine habitat if not managed appropriately. Despite the obvious detrimental impacts, the influence of pastures and livestock on riverine habitat is likely less than other land uses.
Low Quality	2	Erosion, fertilizer, insecticides and sedimentation from cultivation all contribute to row crop agriculture being detrimental to neighboring riverine and riparian areas
Poor Quality	1	Impermeable surfaces, increased surface runoff, altered landscapes, and pollutants associated with urban development all severely impact riparian and riverine habitat.

Table 3.12. Criteria for rating geologic habitat quality within reaches of the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks.

Life Stage, Strategy or Action	Poor Quality (1)	Fair Quality (3)	High Quality (5)
Adult Spawning	Lowlands	Foothills	Uplands
Juvenile Rearing, Foraging and Growth	Lowlands	Foothills	Uplands
Fluvial Adult Upstream Migration	Uplands	Foothills	Lowlands
Adult Foraging and Maintenance	Uplands	Foothills	Lowlands
Fluvial Adult Downstream Migration	Uplands	Foothills	Lowlands
Fluvial Sub-adult Downstream Migration	Uplands	Foothills	Lowlands
Fluvial Sub-adult Lower River Evacuation	Lowlands	Foothills	Uplands
Fluvial Sub-adult Rearing, Foraging and Growth	Uplands	Foothills	Lowlands

Table 3.13. Description of sinuosity categories and criteria for rating the habitat quality that sinuosity infers within reaches of the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks.

Sinuosity Categories	Numeric Rating	Sinuosity Rating Criteria	Explanation
High Quality	5	> 1.32	Relatively high sinuosity inferring a high level of channel complexity that likely indicates high quality habitat for bull trout at a given life stage to exhibit a certain strategy or conduct a particular action and thrive.
Good Quality	4	>1.24 – 1.32	Relatively high sinuosity inferring a relatively complex river reach that likely indicates good quality habitat for bull trout at a given life stage to exhibit a certain strategy or conduct a particular action.
Fair Quality	3	>1.16 – 1.24	Moderate sinuosity inferring that channel complexity is likely moderate as well. Bull trout habitat quality is likely only fair within the given reach.
Low Quality	2	>1.08 – 1.16	Lower level of sinuosity that may infer a lower level of channel complexity, indicating relatively low quality habitat for bull trout life stages and strategies.
Poor Quality	1	≤ 1.08	Very low sinuosity, likely indicating low channel complexity and poor habitat conditions for bull trout life stages and strategies.

Table 3.14. Definitions and explanations of the scale of numbers that indicates how much more important or influential one variable is over another variable with respect to the particular life-history stage, strategy or action (adapted from Saaty 2008).

Intensity of Importance	Definition	Explanation
1	Equal Importance	Two variables contribute equally to habitat suitability
2	Weak or Slight	Data, experience and/or judgment slightly favors one variable over another
3	Weak or Slight Plus	
4	Moderate Importance	Data, experience and /or judgment moderately favors one variable over another
5	Moderate Plus	
6	Strong Importance	Data, experience and/or judgment strongly favors one variable over another
7	Strong Plus	
8	Very Strong Importance	One variable is favored very strongly over another
9	Very Strong Plus	
10	Extreme Importance	The evidence favoring one variable over another is of the highest possible order of affirmation
Reciprocals of above	If attribute *i* has one of the above non-zero numbers assigned to it when compared with activity *j*, then *j* has the reciprocal value when compared with *i*	A reasonable assumption

Table 3.15. Habitat reaches for the South Fork and mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek.

Reach ID	Reach Start (Upstream)	Reach End (Downstream)	Length (km)
SFWW1	S.F. Walla Walla River Headwaters (rkm 125.4)	Reser Creek Confluence (rkm 115.6)	9.8
SFWW2	Reser Creek Confluence (rkm 115.6)	Harris Park Bridge (rkm 95.5)	20.1
SFWW3	Harris Park Bridge (rkm 95.5)	N.F. WW River Confluence (rkm 82.9)	12.6
WW4	N.F. WW River Confluence (rkm 82.9)	Upstream End of Levee Section (rkm 78.1)	4.8
WW5	Upstream End of Levee Section (rkm 78.1)	Little Walla Walla Diversion (rkm 75.1)	3.0
WW6	Little Walla Walla Diversion (rkm 75.1)	Nursery Bridge Dam (rkm 73.1)	2.0
WW7	Nursery Bridge Dam (rkm 73.1)	Tumalum Bridge (rkm 69.3)	3.8
WW8	Tumalum Bridge (rkm 69.3)	Yellowhawk Creek Confluence (rkm 62.9)	6.4
WW9	Yellowhawk Creek Confluence (rkm 62.9)	Burlingame Dam (rkm 60.3)	2.6
WW10	Burlingame Dam (rkm 60.3)	Mill Creek Confluence (rkm 54.8)	5.6
WW11	Mill Creek Confluence (rkm 54.8)	Touchet River Confluence (rkm 31.3)	23.5
WW12	Touchet River Confluence (rkm 31.3)	Backwater from Columbia River (rkm 8.0)	23.3
WW13	Backwater from Columbia River (rkm 8.0)	Columbia River Confluence (rkm 0.0)	8.0
MC14	Mill Creek Headwaters (rkm 58.7)	City of Walla Walla Intake Dam (rkm 44.2)	14.6
MC15	City of Walla Walla Intake Dam (rkm 44.2)	Confluence of Blue Creek (rkm 29.7)	14.4
MC16	Confluence of Blue Creek (rkm 29.7)	Mill Creek Diversion Dam (rkm 20.1)	9.7
MC17	Mill Creek Diversion Dam (rkm 20.1)	Mill Creek Division Dam (rkm 18.5)	1.5
MC18	Mill Creek Division Dam (rkm 18.5)	Roosevelt St. – End Sills/Start Flume (rkm 15.2)	3.3
MC19	Roosevelt St. – End Sills/Start Flume (rkm 15.2)	End of Concrete Flume/Start of Sills (rkm 12.0)	3.2
MC20	End of Concrete Flume/Start of Sills (rkm 12.0)	End of Sills (rkm 8.9)	3.1
MC21	End of Sills (rkm 8.9)	Walla Walla River Confluence (rkm 0.0)	8.9
YHC22	Yellowhawk Cr. - Mill Cr. Division (rkm 14.5)	Walla Walla River Confluence (rkm 0.0)	14.5

Table 3.16. Summarized descriptions of each habitat reach in the South Fork and mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek.

Reach ID	Reach Attribute Summary
SFWW1	High elevation, medium-high stream gradient, forested, upland geology, no major tributary influence, no major diversions, minimal channel modification.
SFWW2	Medium elevation, medium-low gradient, forested, upland geology, major tributary influence, no major diversions, minimal channel modification.
SFWW3	Low – medium elevation, fairly low gradient, agriculture –Pasture and Orchard/Vineyard, upland geology, no major tributary influence, no major diversions, minimal channel modification.
WW4	Low elevation, fairly low gradient, agriculture –Orchard/Vineyard, foothill geology, major tributary influence (N.F. Walla Walla River), no major diversions, minimal channel modification.
WW5	Low elevation, fairly low gradient, urban development, foothill geology, major tributary influence (Couse Cr.), no major diversions, high channel modification.
WW6	Low elevation, fairly low gradient, urban development, lowland geology, no major tributary influence, major diversion (Little W.W. River Diversion), high channel modification.
WW7	Low elevation, fairly low gradient, agriculture- row crops, lowland geology, no major tributary influence, major diversion (East Side Diversion), high channel modification.
WW8	Low elevation, low gradient, agriculture- row crops, lowland geology, no major tributary influence, no major diversions, moderate channel modification.
WW9	Low elevation, low gradient, agriculture- row crops, lowland geology, major tributary influence (Yellowhawk Cr.), no major diversions, moderate channel modification.
WW10	Low elevation, low gradient, agriculture- row crops, lowland geology, no major tributary influence, major diversion (Burlingame Diversion), moderate channel modification.
WW11	Low elevation, low gradient, agriculture- row crops, lowland geology, major tributary influence (Mill Cr.), no major diversions (minor diversions – Garden City/Old Lowden #2 and pushup diversions), moderate channel modification.
WW12	Low elevation, low gradient, agriculture- row crops, lowland geology, major tributary influence (Touchet River), no major diversions, moderate channel modification.
WW13	Low elevation, low gradient, wildlife refuge, lowland geology, backwater influence, no major diversions, moderate channel modification.
MC14	Medium – fairly high elevation, fairly high – high stream gradient, forested, upland geology, no major tributary influence (Minor tributaries – Low Cr. and others), no major diversions, minimal channel modification.
MC15	Fairly low – medium elevation, fairly low stream gradient, forested and urban development, upland and foothill geology, no major tributary influence, major diversions (City of Walla Walla Intake Diversion), moderate channel modification.
MC16	Fairly low - low elevation, fairly low stream gradient, agriculture-row crops, lowland geology, major tributary influence (Blue Cr.), no major diversions, moderate channel modification.
MC17	Low elevation, fairly low stream gradient, urban development, lowland geology, no major tributary influence, major diversion (Mill Creek Diversion Dam), high channel modification.
MC18	Low elevation, fairly low stream gradient, urban development, lowland geology, no major tributary influence, major diversion (Mill Creek Division Dam), high channel modification.

MC19	Low elevation, fairly low stream gradient, urban development, lowland geology, no major tributary influence, no major diversions, severe channel modification.
MC20	Low elevation, low stream gradient, urban development, lowland geology, no major tributary influence, no major diversions, high channel modification.
MC21	Low elevation, low stream gradient, agriculture – row crops, lowland geology, no major tributary influence, no major diversions, moderate channel modification.
YHC22	Low elevation, low stream gradient, agriculture-row crops and urban development, lowland geology, no major tributary influence (minor tributaries – Cottonwood Creek and others), no major diversions (minor diversion – Garrison Cr.), moderate channel modification.

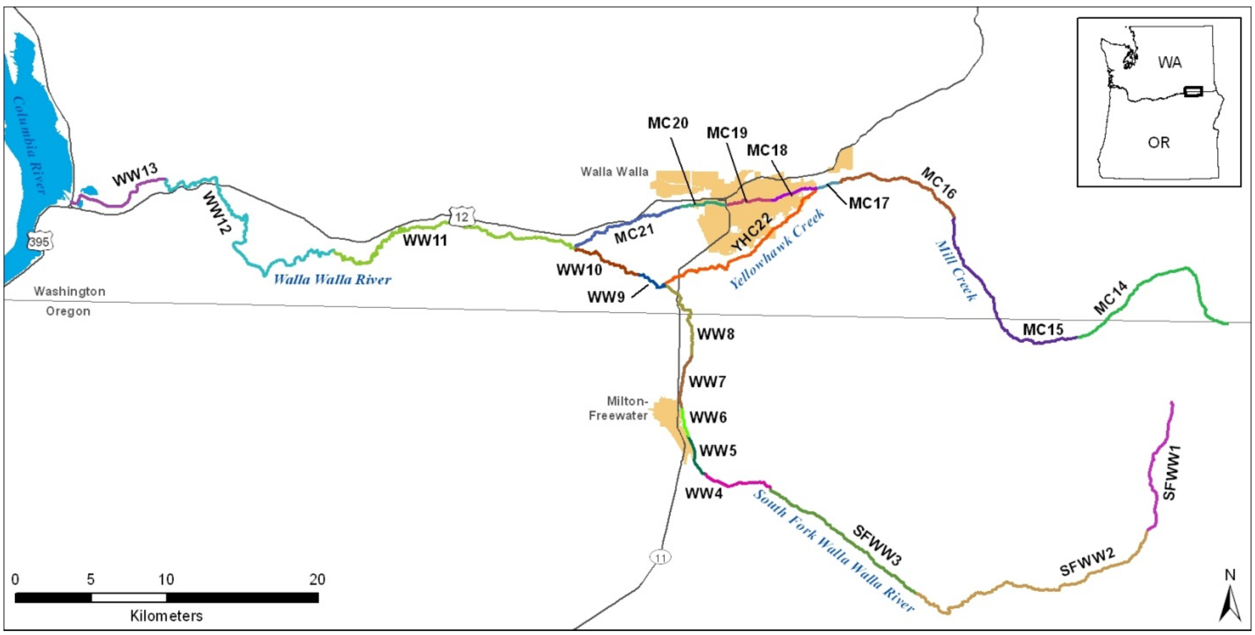

Figure 3.2. Study area map identifying and depicting the geographic locations of study reaches within the Walla Walla River and Mill Creek subbasins.

Table 3.17. Weighting factors assigned to each variable for each of the 8 identified bull trout life stages, strategies and actions.

Life Stage, Strategy or Action	Spawning	Juvenile Rearing Foraging & Growth	Fluvial Adult Upstream Migration	Adult Foraging & Maintenance	Fluvial Adult Downstream Migration	Fluvial Sub-adult Downstream Migration	Fluvial Sub-adult Upstream Migration	Fluvial. Sub-adult Rearing Foraging & Growth
Surface Flow	0.2159162	0.2144870	0.2764790	0.2211177	0.2632224	0.2114516	0.2734777	0.2082714
Ground Water	0.1092011	0.0753623	0.0459125	0.0725475	0.0501192	0.0506686	0.0572986	0.0894771
Water Temperature	0.2597441	0.2893956	0.1768333	0.2530040	0.2001522	0.2386581	0.1990558	0.2652370
Passage Impediments	0.1060755	0.0487301	0.1891403	0.0797703	0.1640810	0.1726316	0.1677920	0.0718198
Channel Modification	0.0300411	0.0395459	0.1123484	0.0823263	0.0900469	0.1128944	0.0968175	0.0958425
Riparian Zone	0.0764006	0.1370854	0.0407484	0.1140861	0.0563649	0.0591051	0.0437951	0.0974923
Stream Gradient	0.0496851	0.0400306	0.0418581	0.0277800	0.0341128	0.0330908	0.0394429	0.0286990
Elevation	0.0460842	0.0414011	0.0278833	0.0282820	0.0423262	0.0311048	0.0267521	0.0367338
Land Use	0.0336414	0.0383160	0.0422001	0.0536502	0.0490917	0.0461714	0.0491146	0.0476733
Geology	0.0338345	0.0199665	0.0167278	0.0181124	0.0200130	0.0171051	0.0194526	0.0185477
Sinuosity	0.0393762	0.0556794	0.0298688	0.0493236	0.0304697	0.0271184	0.0270011	0.0402061

Table 3.18. Monthly bull trout spawning habitat quality periodicity table for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Red, pink, light blue, blue and dark blue cells indicate poor, low, fair, good and high quality habitat respectively.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	4.15	4.15	4.15	4.15	4.41	3.94	3.94	3.94	4.46	4.46	4.20	4.15
	SFWW2	4.21	4.21	4.21	4.47	4.47	4.00	4.00	4.00	4.52	4.52	4.52	4.21
	SFWW3	4.38	4.38	4.64	4.12	3.75	3.80	3.80	3.80	3.80	4.06	4.58	4.38
	WW4	4.16	4.16	3.90	3.90	3.53	3.53	3.27	3.27	3.53	3.79	4.31	4.16
	WW5	3.77	4.03	3.51	3.51	3.14	3.14	2.88	2.88	3.14	3.14	3.40	3.77
	WW6	3.80	4.06	3.54	3.32	2.95	2.80	2.11	2.33	2.59	2.37	2.85	3.80
	WW7	3.33	3.59	3.07	2.86	2.38	1.82	1.39	1.60	1.60	1.65	2.12	3.33
	WW8	3.96	4.22	3.48	3.22	2.90	2.23	1.47	1.69	1.69	2.06	2.64	3.85
	WW9	3.93	4.19	3.56	3.41	3.19	2.30	1.87	2.09	2.09	2.61	2.93	3.93
	WW10	3.78	4.04	3.52	3.04	2.68	2.15	1.72	1.94	1.94	2.20	2.46	3.71
	WW11	4.04	4.04	3.52	3.26	3.15	2.00	1.35	1.35	1.57	1.72	2.63	3.78
	WW12	3.81	3.81	3.55	3.29	3.18	2.35	1.92	1.92	1.92	2.18	3.39	3.81
	WW13	3.69	3.69	3.43	3.18	3.18	2.34	1.91	1.91	1.91	2.17	3.38	3.69
Mill Creek Subbasin	MC14	4.28	4.28	4.28	4.54	4.02	4.07	3.81	3.81	4.07	4.07	4.59	4.28
	MC15	4.22	4.22	4.22	4.48	3.70	3.53	3.32	3.06	3.32	3.32	4.31	4.00
	MC16	3.86	4.12	3.60	3.60	3.34	3.12	2.54	2.54	2.54	2.91	3.38	3.86
	MC17	3.07	3.07	2.81	2.81	2.55	2.02	1.80	1.80	1.80	2.06	2.64	3.07
	MC18	2.94	2.94	2.68	2.68	2.10	1.53	1.10	1.10	1.10	1.36	1.84	2.73
	MC19	2.77	2.77	2.51	2.51	2.04	1.68	1.25	1.25	1.25	1.51	1.99	2.56
	MC20	2.90	2.90	2.64	2.64	2.17	1.50	1.06	1.06	1.06	1.43	1.91	2.69
	MC21	3.31	2.88	3.05	3.27	3.01	2.44	1.47	1.47	1.47	2.27	2.63	3.31
	YHC22	3.70	3.96	3.44	3.18	3.18	2.92	2.82	2.82	2.82	3.18	3.18	3.70

Poor | Low | Fair | Good | High

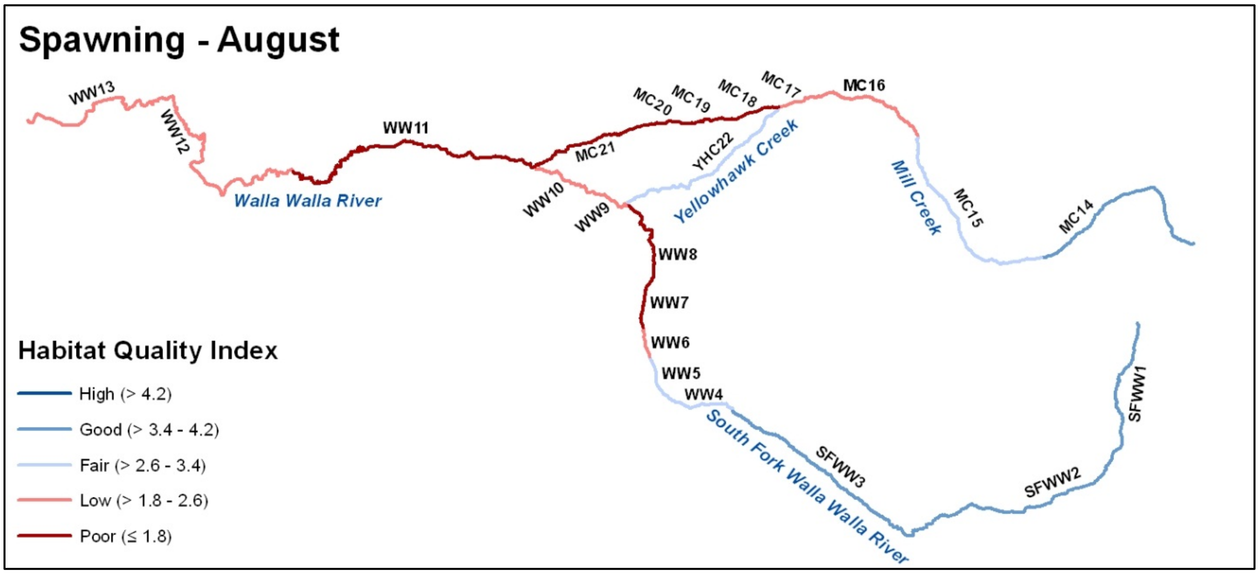

Figure 3.3. Map depicting August spawning habitat quality scores for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek.

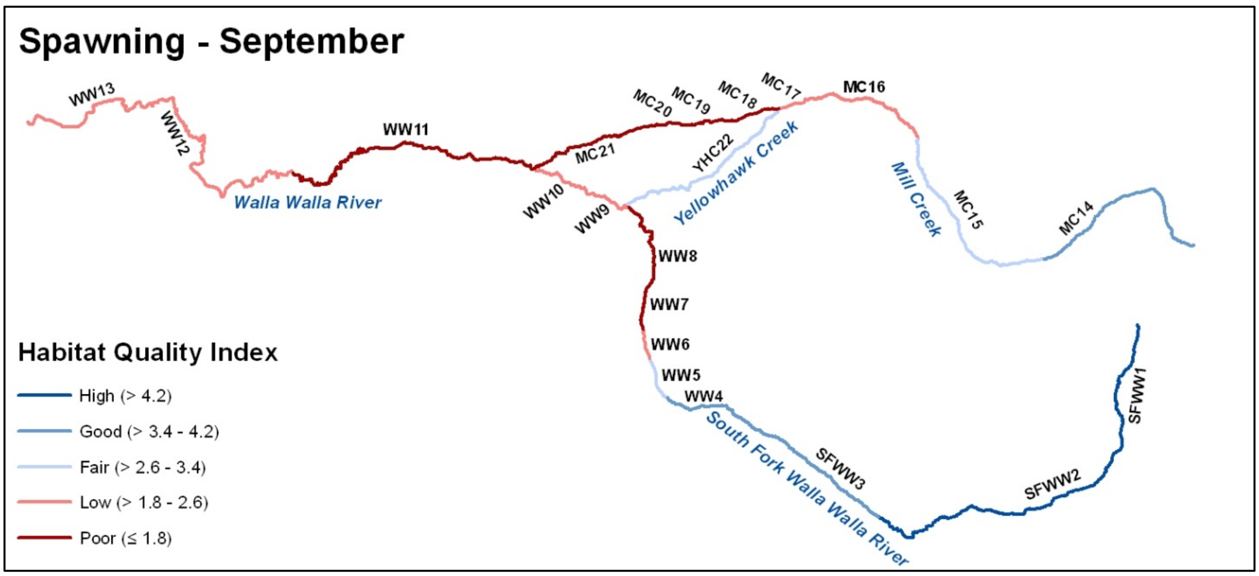

Figure 3.4. Map depicting September spawning habitat quality scores for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek.

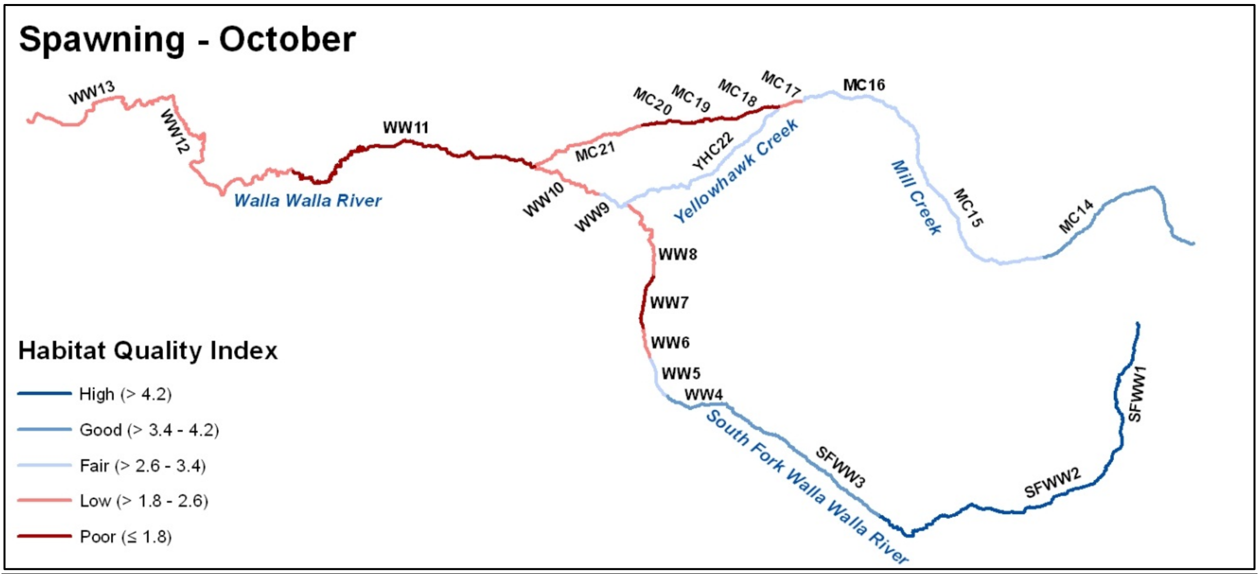

Figure 3.5. Map depicting October spawning habitat quality scores for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek.

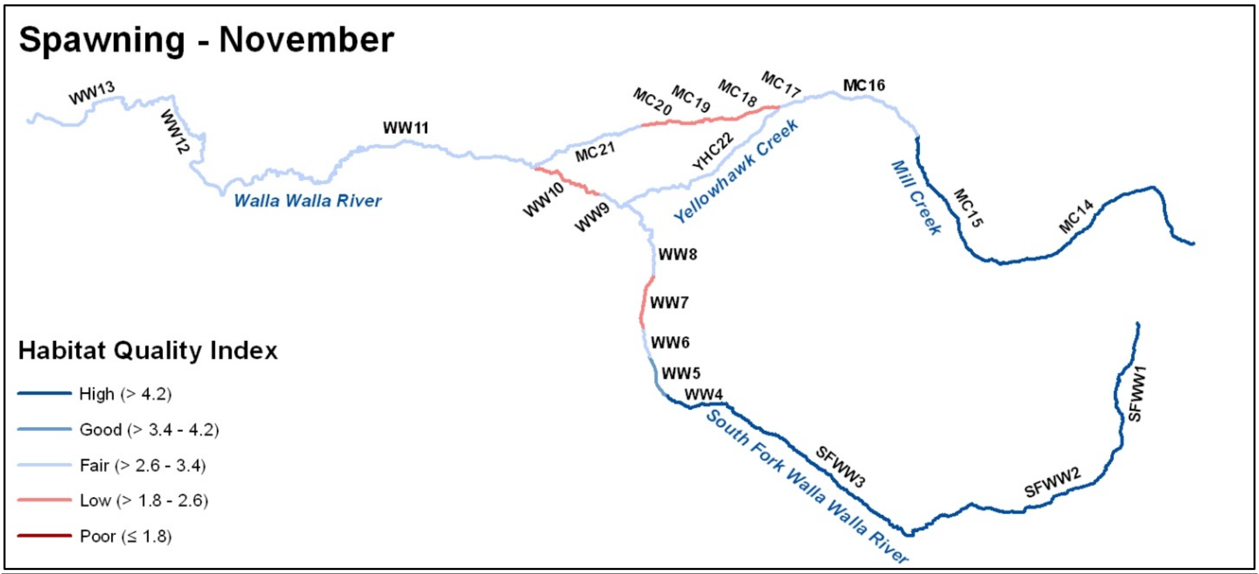

Figure 3.6. Map depicting November spawning habitat quality scores for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek.

Table 3.19. Monthly juvenile rearing, foraging and growth habitat quality periodicity table for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Red, pink, light blue, blue and dark blue cells indicate poor, low, fair, good and high quality habitat respectively.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	4.04	4.04	4.04	4.04	4.04	4.37	4.37	4.37	4.66	4.66	4.37	4.33
	SFWW2	4.12	4.12	4.12	4.12	4.41	4.45	4.45	4.45	4.45	4.45	4.16	4.12
	SFWW3	4.00	4.00	4.29	4.29	4.50	4.25	4.25	4.25	4.54	4.25	4.25	4.00
	WW4	4.00	4.00	4.29	4.29	4.50	4.25	4.25	4.25	4.54	4.25	4.25	4.00
	WW5	3.46	3.46	3.75	3.75	3.68	3.68	3.39	3.39	3.68	3.96	3.68	3.46
	WW6	3.46	3.46	3.75	3.53	3.75	3.34	2.62	2.83	3.12	3.20	3.12	3.46
	WW7	3.46	3.46	3.75	3.53	3.75	3.34	2.62	2.83	3.12	3.20	3.12	3.46
	WW8	3.68	3.68	3.84	4.04	3.58	3.03	2.02	2.24	2.53	2.89	3.16	3.63
	WW9	3.64	3.93	3.88	4.22	3.80	3.04	2.32	2.54	2.83	3.12	3.38	3.64
	WW10	3.46	3.75	3.75	3.82	3.24	2.53	2.19	2.41	2.70	2.90	2.90	3.53
	WW11	3.51	3.80	3.80	4.09	3.72	2.66	1.44	1.44	1.94	2.36	2.91	3.51
	WW12	3.52	3.52	3.81	4.10	3.73	2.56	2.13	2.13	2.13	2.71	3.43	3.52
	WW13	3.38	3.38	3.67	3.96	3.67	2.50	2.07	2.07	2.07	2.65	3.37	3.38
Mill Creek Subbasin	MC14	3.99	3.99	3.99	4.28	4.28	4.32	4.61	4.61	4.32	4.32	4.03	3.99
	MC15	3.84	3.84	3.84	4.13	4.13	3.96	3.74	3.74	4.03	4.03	3.67	3.63
	MC16	3.59	3.59	3.88	3.88	3.88	3.66	2.79	2.79	3.08	3.45	3.66	3.59
	MC17	2.73	2.73	3.02	3.02	3.02	2.27	1.76	1.76	2.05	2.63	2.85	2.73
	MC18	2.61	2.61	2.90	2.90	2.64	1.85	1.13	1.13	1.42	2.00	2.22	2.40
	MC19	2.54	2.54	2.82	2.82	2.61	1.82	1.10	1.10	1.39	1.97	2.19	2.32
	MC20	2.56	2.56	2.85	2.85	2.63	1.80	1.08	1.08	1.37	1.99	2.21	2.34
	MC21	3.14	2.71	3.43	3.64	3.64	2.86	1.63	1.63	1.92	3.01	3.05	3.14
	YHC22	3.40	3.40	3.69	3.98	3.69	3.40	2.74	2.74	3.03	3.69	3.69	3.40

Poor	Low	Fair	Good	High

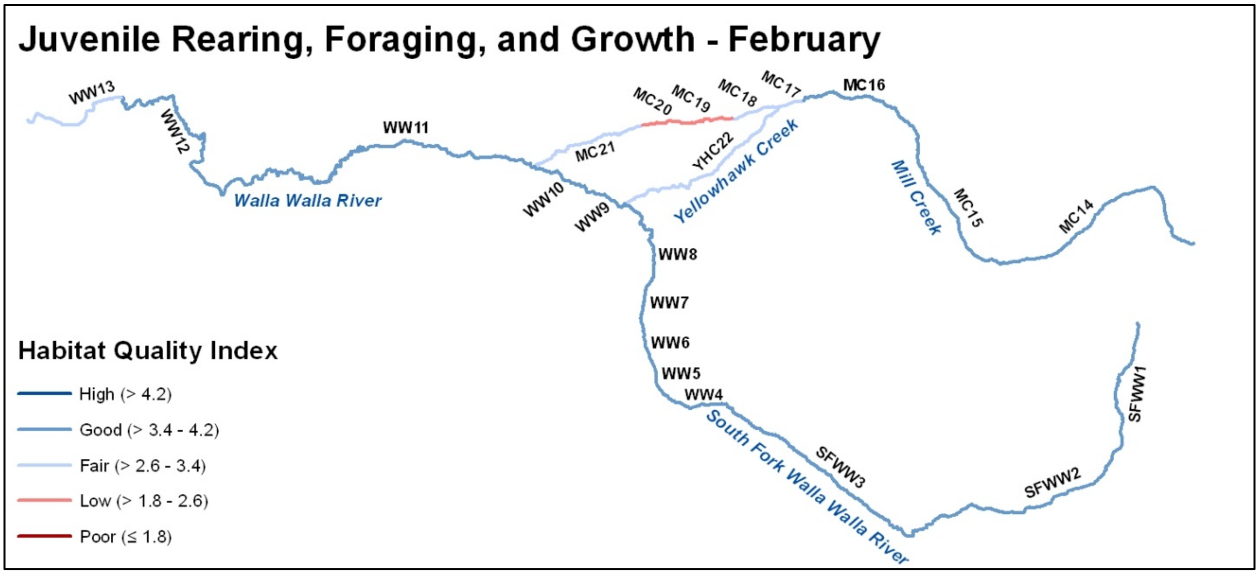

Figure 3.7. Map depicting spatial habitat quality for juvenile bull trout rearing, foraging and growth for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during February.

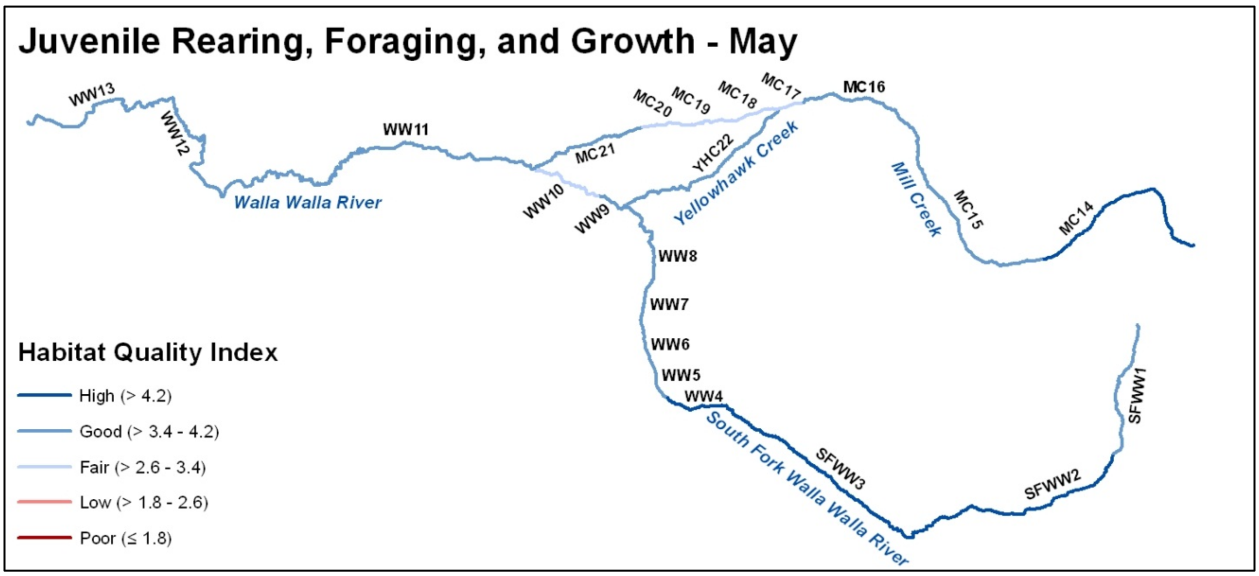

Figure 3.8. Map depicting spatial habitat quality for juvenile bull trout rearing, foraging and growth for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during May.

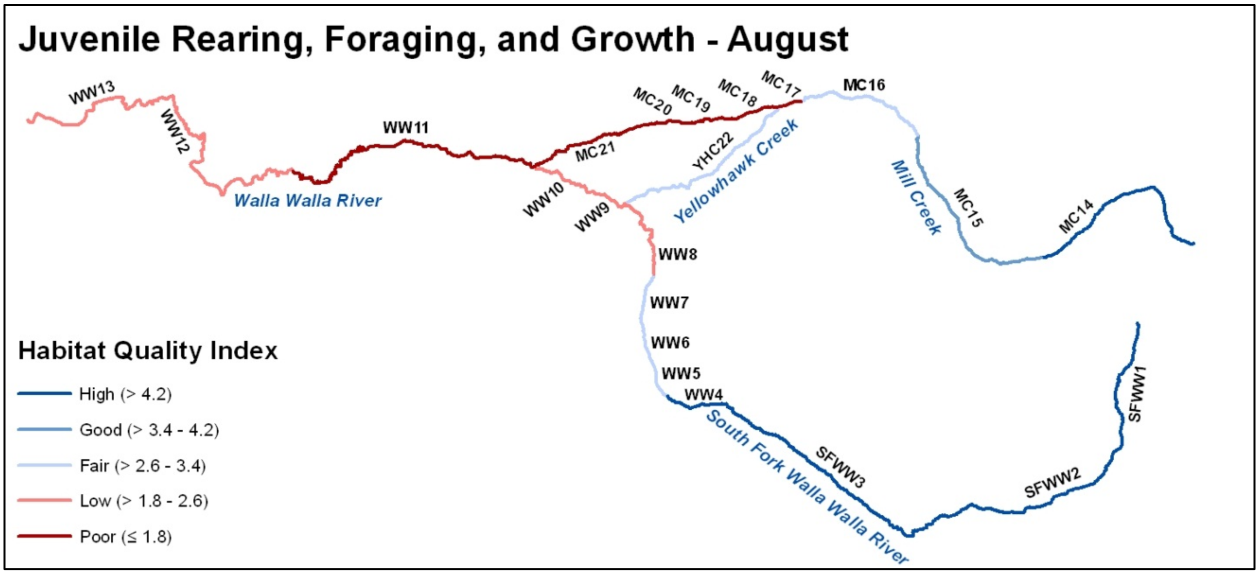

Figure 3.9. Map depicting spatial habitat quality for juvenile bull trout rearing, foraging and growth for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during August.

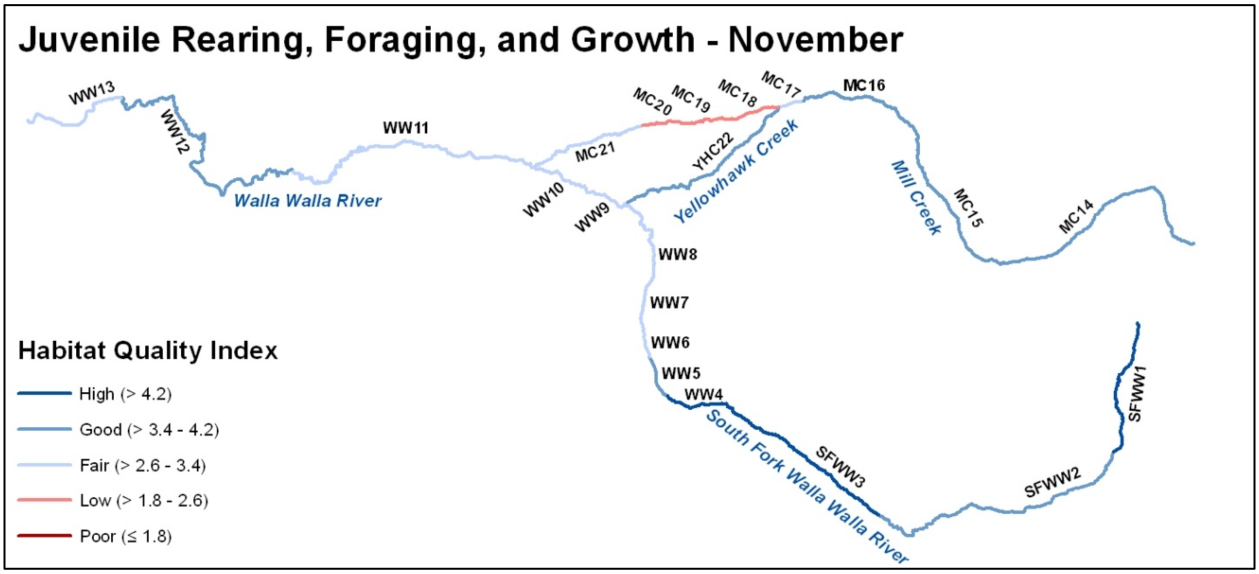

Figure 3.10. Map depicting spatial habitat quality for juvenile bull trout rearing, foraging and growth for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during November.

Table 3.20. Monthly adult fluvial upstream migration habitat quality periodicity table for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Red, pink, light blue, blue and dark blue cells indicate poor, low, fair, good and high quality habitat respectively.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	3.44	3.44	3.44	3.44	3.62	3.66	3.66	3.66	3.66	3.66	3.49	3.44
	SFWW2	3.53	3.53	3.53	3.70	3.70	3.75	3.75	3.75	3.75	3.75	3.75	3.53
	SFWW3	3.85	3.85	4.03	4.03	3.99	4.38	4.56	4.56	4.38	4.03	4.03	3.85
	WW4	3.79	3.79	3.97	3.97	4.28	4.45	4.10	4.45	4.28	3.92	3.92	3.79
	WW5	3.29	3.46	3.46	3.46	3.77	3.95	3.59	3.59	3.95	3.42	3.42	3.29
	WW6	3.25	3.42	3.42	3.32	3.46	3.51	2.60	2.88	3.23	2.78	2.70	3.25
	WW7	3.11	3.28	3.28	3.01	3.13	2.59	1.86	2.14	2.32	2.22	2.49	3.11
	WW8	3.71	3.89	3.65	3.61	3.54	2.82	1.76	2.04	2.22	2.44	2.55	3.52
	WW9	3.67	3.84	3.66	4.20	3.96	2.96	2.23	2.51	2.69	2.86	2.98	3.67
	WW10	3.59	3.77	3.77	3.85	3.48	2.85	2.16	2.43	2.61	2.75	2.39	3.49
	WW11	3.64	3.64	3.64	3.64	3.95	2.79	1.78	1.78	2.23	2.32	2.76	3.47
	WW12	3.65	3.65	3.83	3.83	4.14	3.40	2.49	2.67	2.67	3.02	3.22	3.65
	WW13	3.65	3.65	3.83	3.83	4.18	3.44	2.53	2.71	2.71	3.06	3.26	3.65
Mill Creek Subbasin	MC14	3.75	3.75	3.75	3.93	3.93	3.97	4.32	3.97	3.97	3.97	3.97	3.75
	MC15	3.61	3.61	3.61	3.79	4.14	3.91	3.81	3.81	3.63	3.28	3.55	3.33
	MC16	3.46	3.64	3.64	3.64	3.99	3.89	3.04	3.04	3.21	3.44	3.36	3.46
	MC17	2.83	2.83	3.01	3.01	3.54	2.76	2.31	2.31	2.48	2.66	2.77	2.83
	MC18	2.44	2.44	2.61	2.61	2.87	2.16	1.43	1.43	1.60	1.78	1.89	2.16
	MC19	2.66	2.47	2.46	2.46	2.71	2.19	1.46	1.46	1.64	1.82	1.93	2.38
	MC20	2.60	2.60	2.77	2.77	3.03	2.13	1.40	1.40	1.58	1.75	1.86	2.32
	MC21	2.91	2.35	3.08	3.36	3.89	3.18	1.85	1.85	2.03	2.80	2.64	2.91
	YHC22	3.41	3.58	3.58	3.58	3.94	3.76	3.54	3.54	3.72	3.94	3.58	3.41

Poor | Low | Fair | Good | High

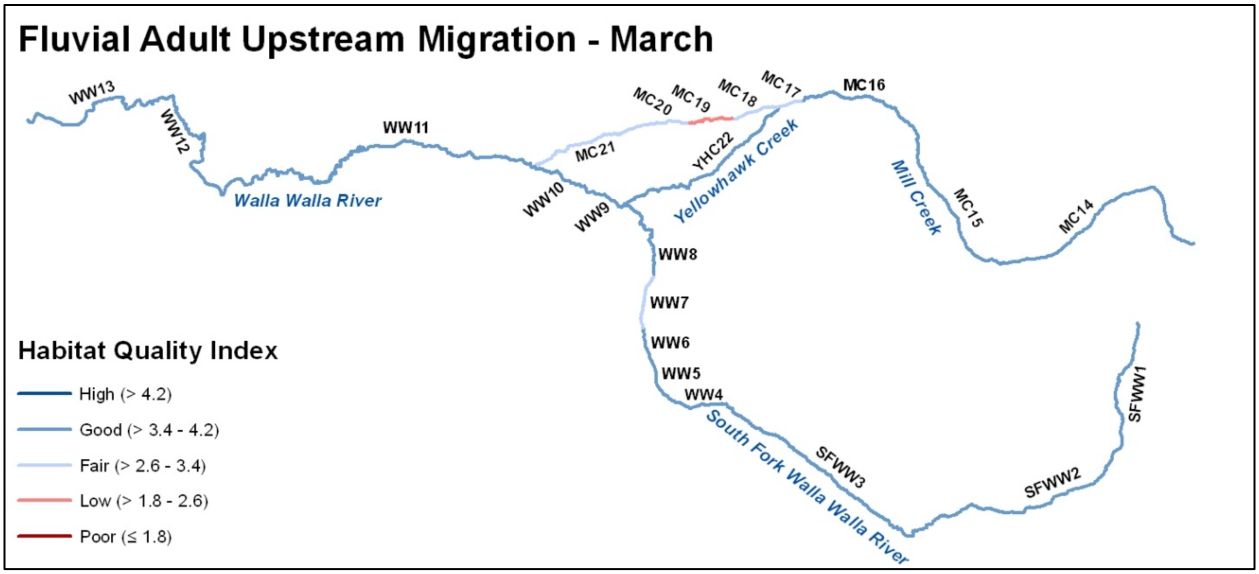

Figure 3.11. Map depicting fluvial adult upstream migration habitat quality for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during March.

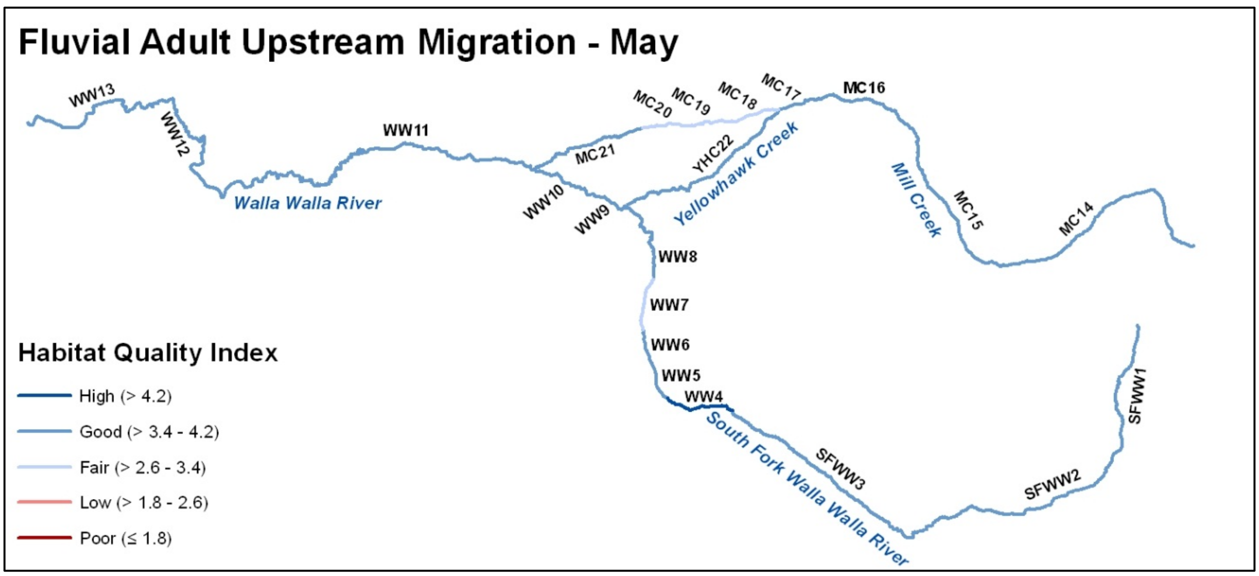

Figure 3.12. Map depicting fluvial adult upstream migration habitat quality for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during May.

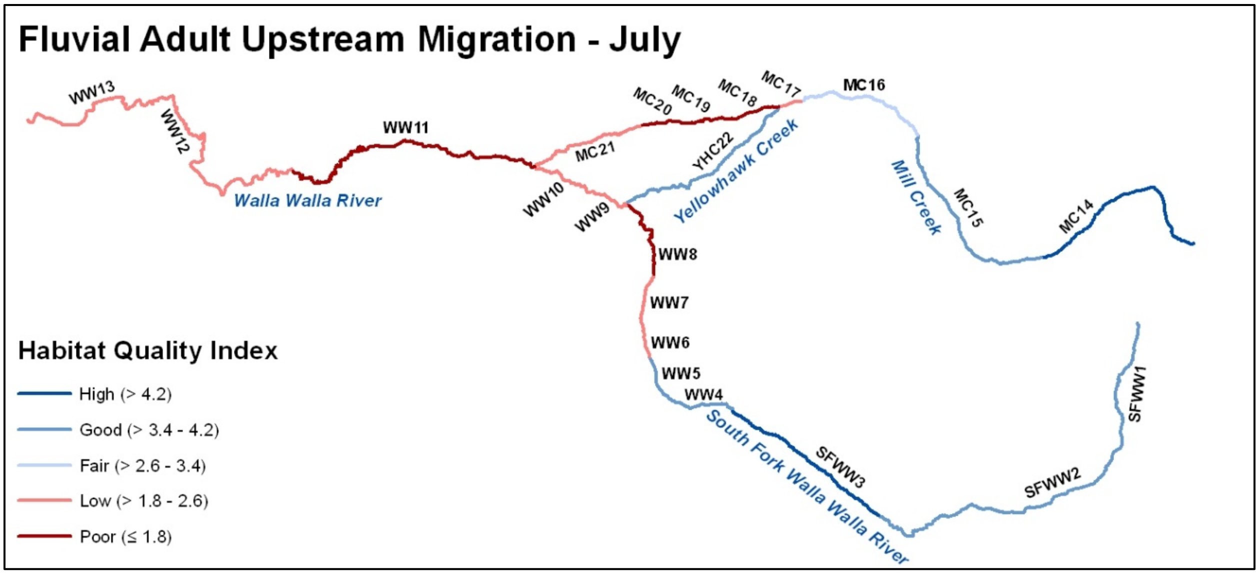

Figure 3.13. Map depicting fluvial adult upstream migration habitat quality for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during July.

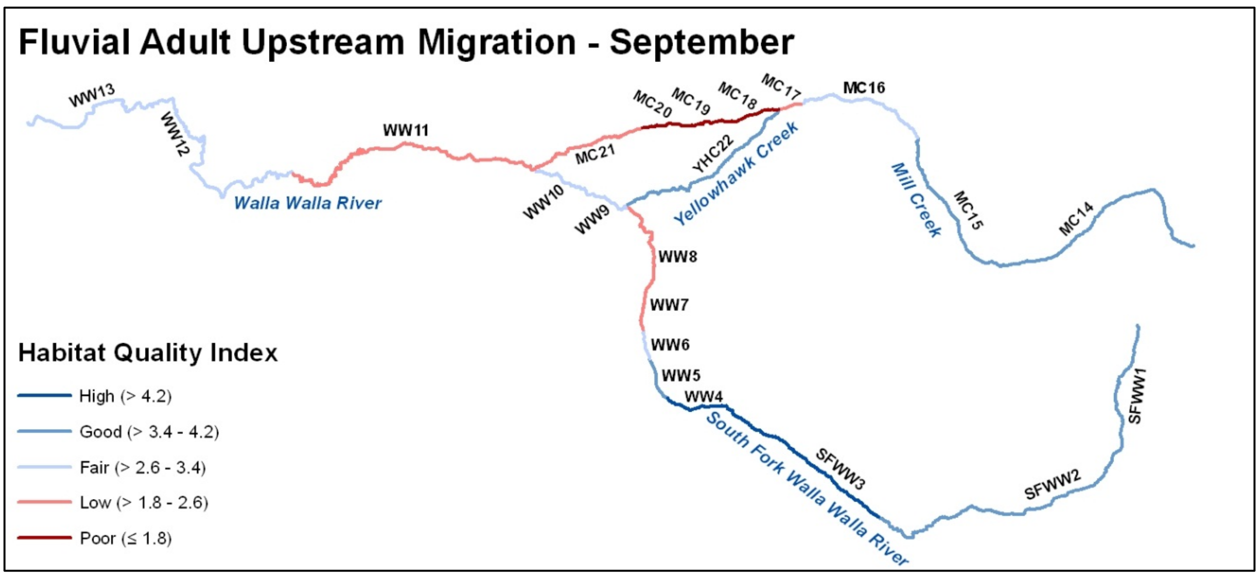

Figure 3.14. Map depicting fluvial adult upstream migration habitat quality for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during September.

Table 3.21. Monthly adult bull trout foraging and maintenance habitat quality periodicity table for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Red, pink, light blue, blue and dark blue cells indicate poor, low, fair, good and high quality habitat respectively.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	4.03	4.03	4.03	4.03	4.03	4.31	4.31	4.31	4.31	4.06	4.06	4.03
	SFWW2	4.06	4.06	4.06	4.06	4.31	4.34	4.34	4.34	4.34	4.34	4.09	4.06
	SFWW3	4.00	4.00	4.26	4.26	4.18	4.21	4.47	4.47	4.21	4.21	4.21	4.00
	WW4	3.84	3.84	4.10	4.10	4.02	4.28	4.02	4.02	4.02	4.02	4.02	3.84
	WW5	3.45	3.45	3.71	3.71	3.63	3.89	3.38	3.63	3.89	3.63	3.63	3.45
	WW6	3.45	3.45	3.70	3.48	3.40	3.57	2.63	2.85	3.35	2.88	3.10	3.45
	WW7	3.02	3.02	3.27	3.05	2.90	2.71	1.76	1.98	2.24	2.27	2.49	3.02
	WW8	3.80	3.80	3.90	3.83	3.60	3.33	2.09	2.31	2.81	2.89	3.19	3.72
	WW9	3.75	4.00	3.92	4.00	3.85	3.36	2.41	2.63	3.13	3.13	3.44	3.75
	WW10	3.55	3.80	3.80	3.58	3.58	2.91	2.29	2.51	3.01	2.94	2.94	3.58
	WW11	3.60	3.86	3.86	3.86	3.78	3.02	1.85	1.85	2.33	2.44	3.03	3.60
	WW12	3.66	3.66	3.92	4.17	3.84	3.06	2.11	2.37	2.37	2.87	3.31	3.66
	WW13	3.58	3.58	3.84	4.09	3.84	3.05	2.11	2.36	2.36	2.86	3.31	3.58
Mill Creek Subbasin	MC14	4.03	4.03	4.03	4.29	4.29	4.31	4.31	4.31	4.31	4.31	4.06	4.03
	MC15	3.66	3.66	3.66	3.91	3.91	3.72	3.75	3.75	3.50	3.50	3.47	3.44
	MC16	3.63	3.63	3.89	3.89	3.89	3.92	2.87	2.87	3.37	3.44	3.66	3.63
	MC17	2.84	2.84	3.09	3.09	2.84	2.57	2.09	2.09	2.35	2.60	2.90	2.84
	MC18	2.62	2.62	2.87	2.87	2.40	2.21	1.51	1.51	1.76	2.02	2.32	2.40
	MC19	2.64	2.56	2.74	2.74	2.26	2.15	1.45	1.45	1.71	1.96	2.26	2.42
	MC20	2.65	2.65	2.90	2.90	2.43	2.16	1.46	1.46	1.71	1.97	2.27	2.43
	MC21	3.19	2.75	3.45	3.67	3.42	3.23	2.02	2.02	2.27	3.04	3.12	3.19
	YHC22	3.50	3.50	3.76	3.76	3.76	3.76	3.18	3.18	3.43	3.76	3.76	3.50

Poor Low Fair Good High

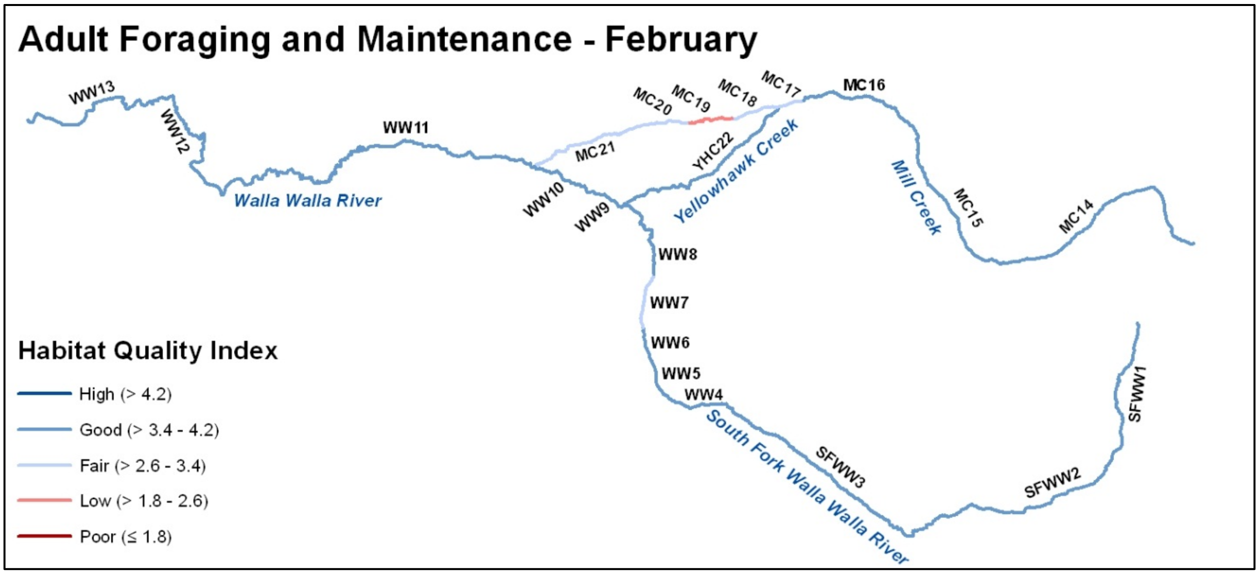

Figure 3.15. Map depicting habitat quality for adult bull trout foraging and maintenance for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during February.

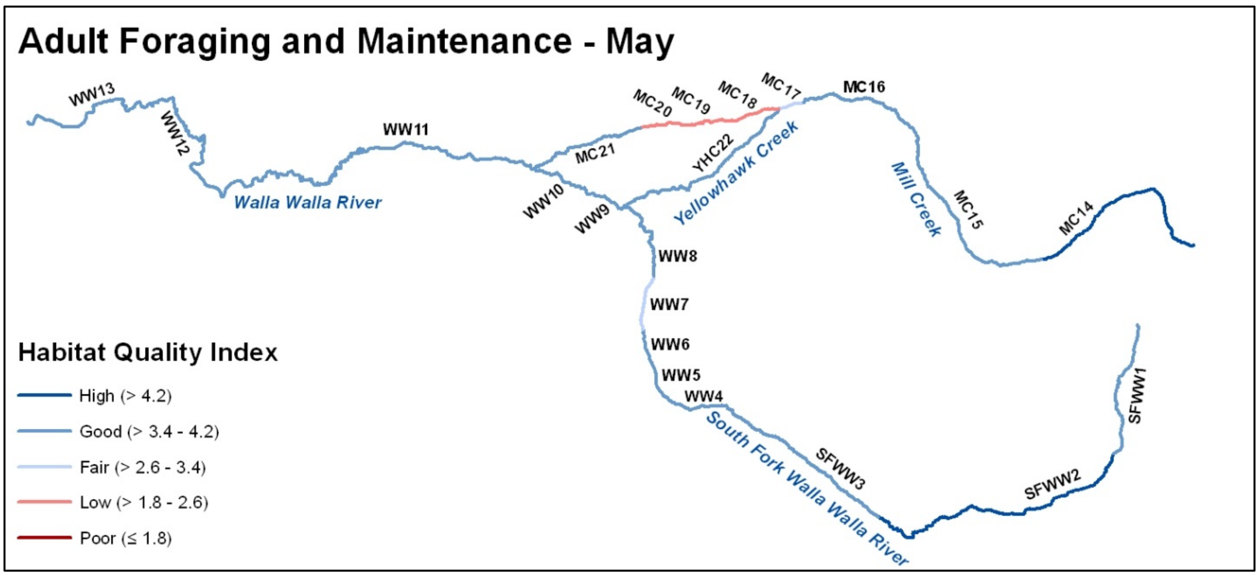

Figure 3.16. Map depicting habitat quality for adult bull trout foraging and maintenance for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during May.

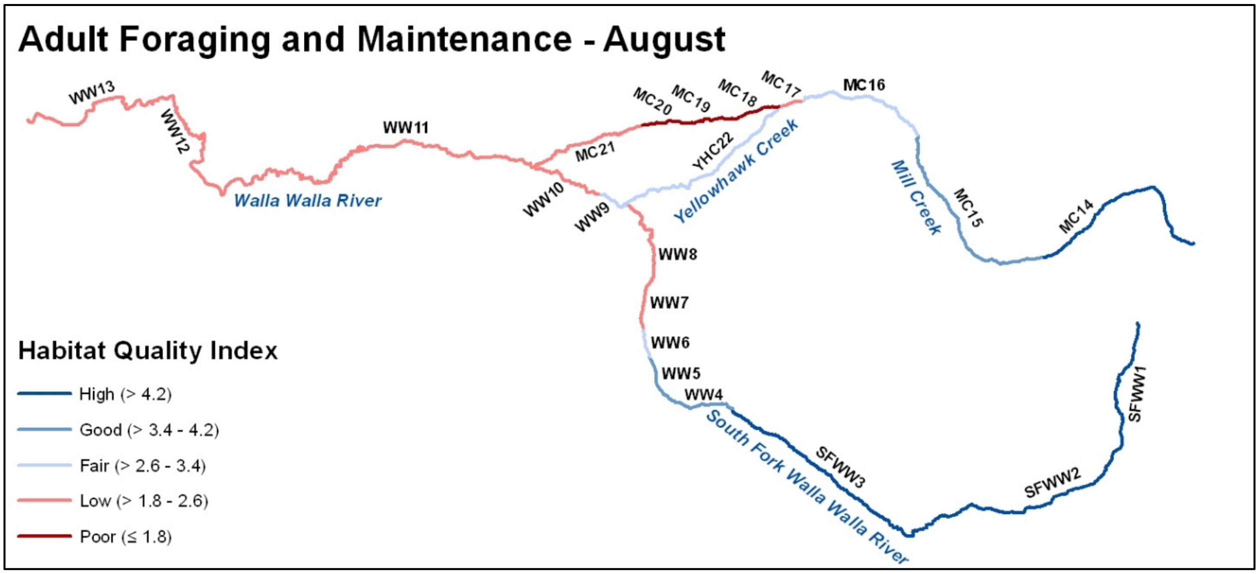

Figure 3.17. Map depicting habitat quality for adult bull trout foraging and maintenance for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during August.

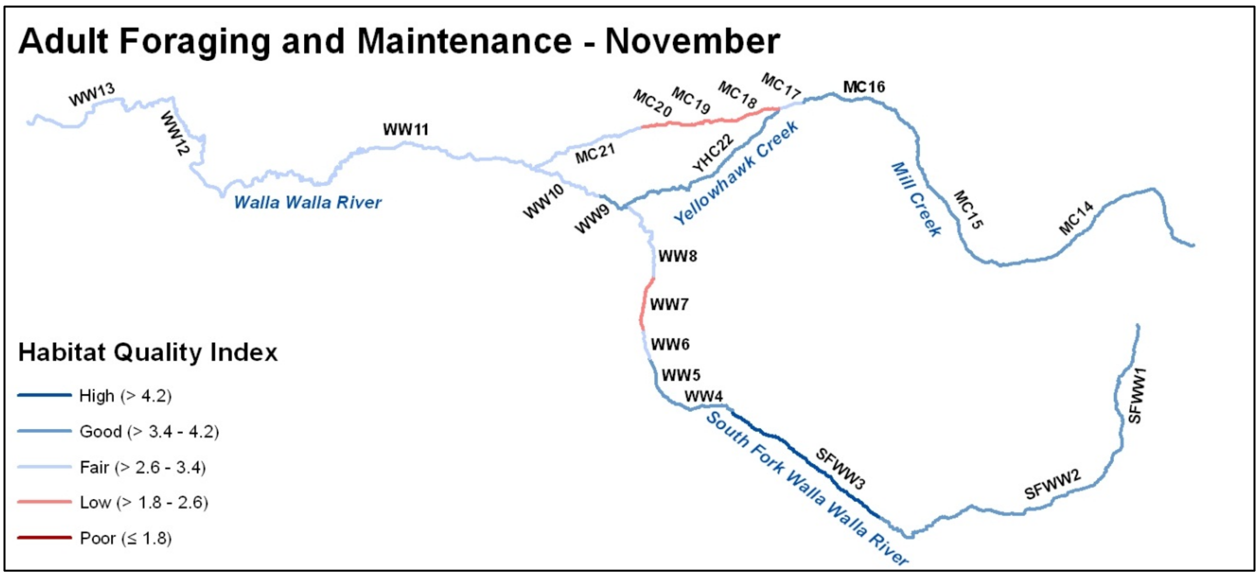

Figure 3.18. Map depicting habitat quality for adult bull trout foraging and maintenance for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during November.

Table 3.22. Monthly fluvial adult bull trout downstream migration habitat quality periodicity table for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Red, pink, light blue, blue and dark blue cells indicate poor, low, fair, good and high quality habitat respectively.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	4.20	4.20	4.20	4.20	4.20	4.43	4.43	4.43	4.43	4.23	4.23	4.20
	SFWW2	4.06	4.06	4.06	4.06	4.26	4.29	4.29	4.29	4.29	4.29	4.09	4.06
	SFWW3	4.34	4.34	4.54	4.54	4.29	4.32	4.32	4.32	4.32	4.52	4.52	4.34
	WW4	4.22	4.22	4.42	4.42	4.17	4.17	3.97	3.97	4.17	4.37	4.37	4.22
	WW5	3.78	3.78	3.98	3.98	3.73	3.73	3.53	3.53	3.73	3.73	3.93	3.78
	WW6	3.75	3.75	3.95	3.68	3.43	3.33	2.60	2.87	3.07	2.80	3.67	3.75
	WW7	3.55	3.55	3.75	3.49	3.07	2.57	1.85	2.11	2.31	2.25	2.71	3.55
	WW8	4.17	4.17	4.15	3.90	3.52	2.86	1.82	2.08	2.48	2.53	3.16	4.00
	WW9	4.12	4.32	4.15	4.12	3.90	2.97	2.25	2.51	2.71	2.91	3.54	4.12
	WW10	3.87	4.07	4.07	3.61	3.41	2.84	2.17	2.43	2.63	2.78	2.98	3.81
	WW11	3.93	4.13	4.13	3.93	3.88	2.78	1.79	1.79	2.25	2.35	3.29	3.93
	WW12	4.09	4.09	4.29	4.09	4.04	3.32	2.39	2.59	2.59	2.99	3.72	4.09
	WW13	4.08	4.08	4.28	4.08	4.08	3.36	2.43	2.63	2.63	3.03	3.76	4.08
Mill Creek Subbasin	MC14	4.30	4.30	4.30	4.50	4.50	4.53	4.33	4.33	4.53	4.53	4.33	4.30
	MC15	3.94	3.94	3.94	4.14	3.94	3.71	3.45	3.45	3.45	3.45	3.71	3.67
	MC16	3.94	3.94	4.14	4.14	3.94	3.68	2.97	2.97	3.17	3.42	3.88	3.94
	MC17	3.30	3.30	3.50	3.50	3.30	2.71	2.25	2.25	2.45	2.65	3.27	3.30
	MC18	2.94	2.94	3.14	3.14	2.68	2.18	1.45	1.45	1.65	1.85	2.48	2.68
	MC19	3.13	2.97	3.00	3.00	2.54	2.20	1.47	1.47	1.67	1.88	2.50	2.87
	MC20	3.07	3.07	3.27	3.27	2.81	2.15	1.42	1.42	1.62	1.82	2.45	2.81
	MC21	3.41	2.89	3.61	3.88	3.68	3.18	1.87	1.87	2.07	2.85	3.21	3.41
	YHC22	3.87	3.87	4.07	3.87	3.87	3.67	3.41	3.41	3.61	3.87	4.07	3.87

Poor | Low | Fair | Good | High

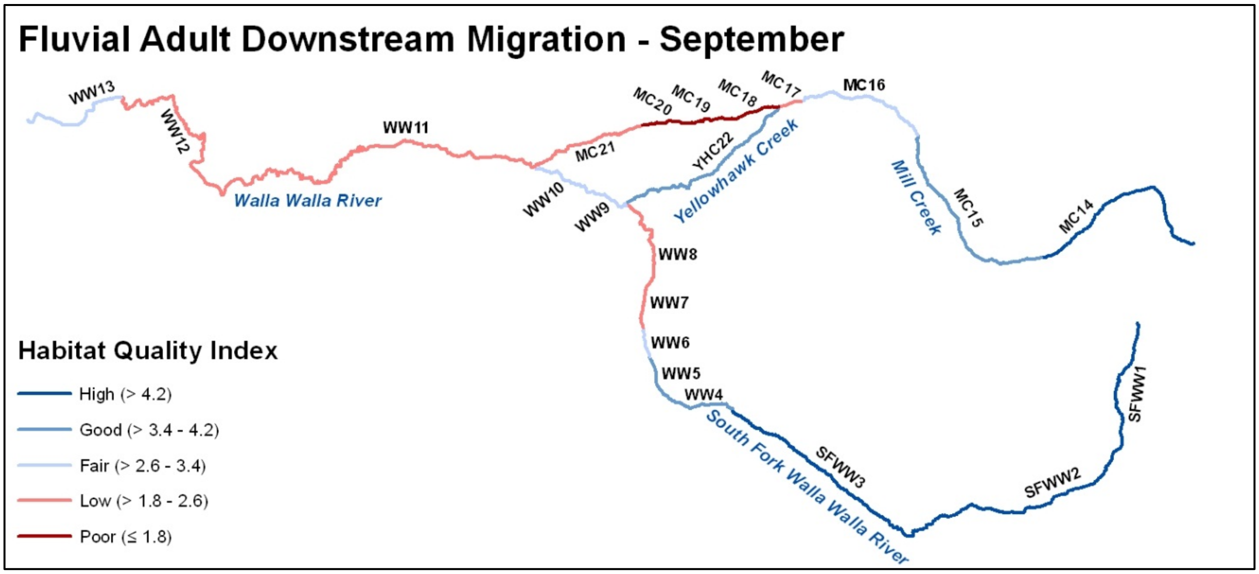

Figure 3.19. Map depicting habitat quality for fluvial adult bull trout downstream migration for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during September.

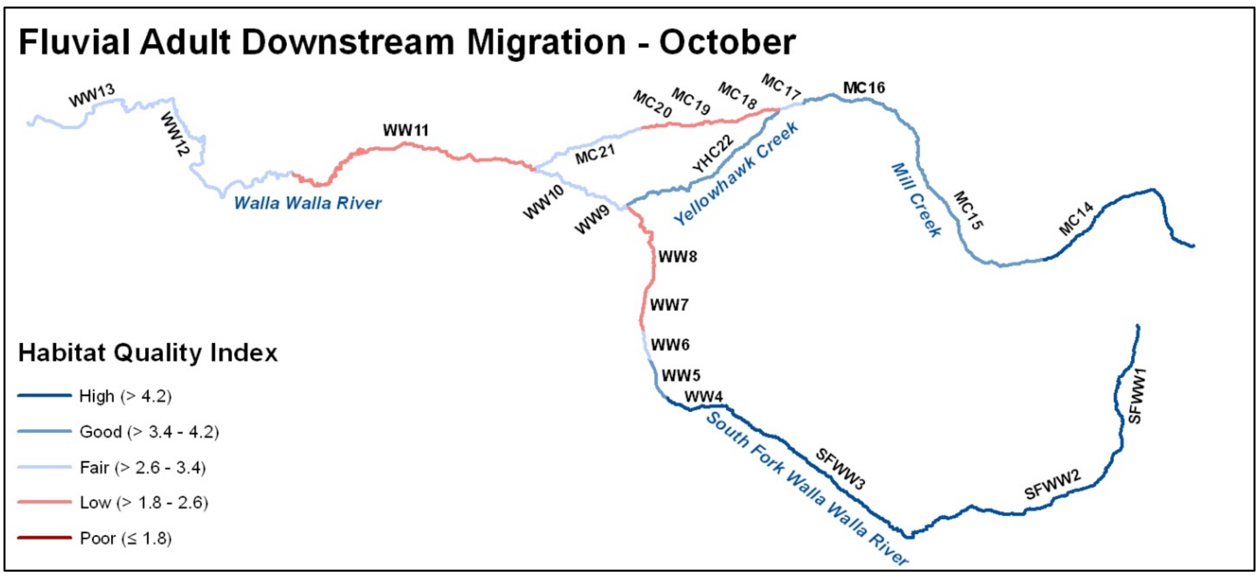

Figure 3.20. Map depicting habitat quality for fluvial adult bull trout downstream migration for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during October.

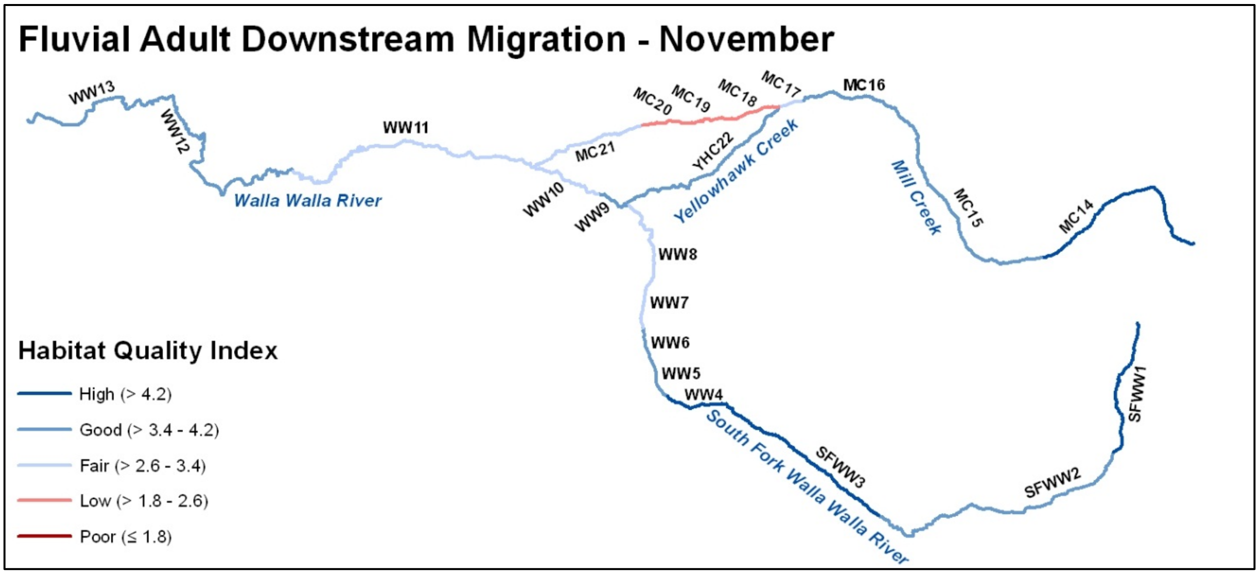

Figure 3.21. Map depicting habitat quality for fluvial adult bull trout downstream migration for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during November.

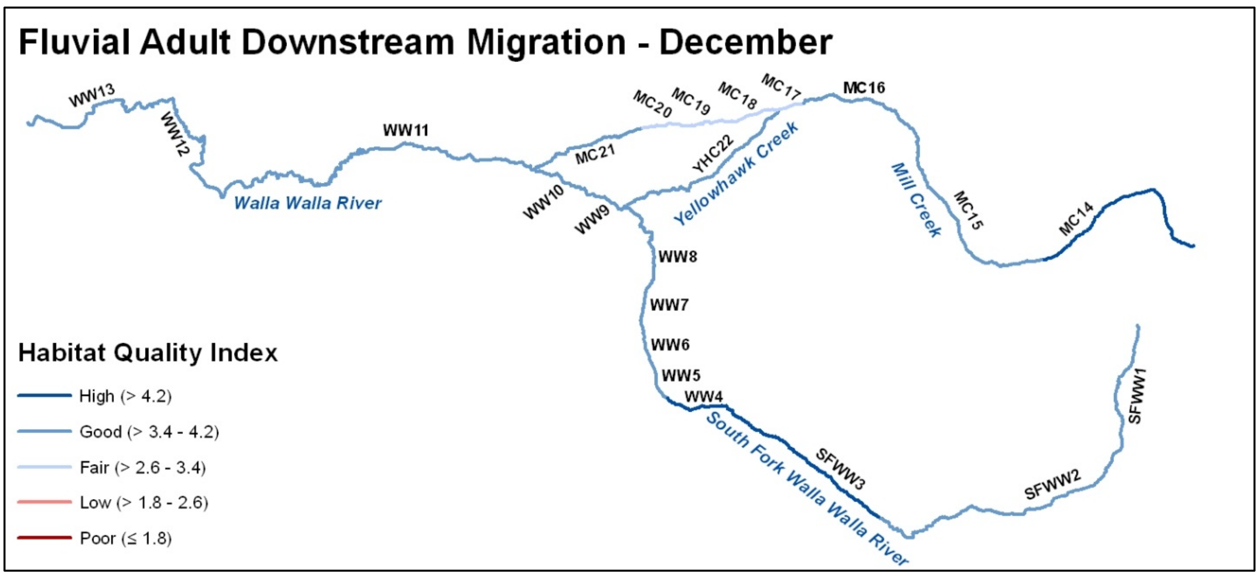

Figure 3.22. Map depicting habitat quality for fluvial adult bull trout downstream migration for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during December.

Table 3.23. Monthly fluvial sub-adult bull trout downstream migration habitat quality periodicity table for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Red, pink, light blue, blue and dark blue cells indicate poor, low, fair, good and high quality habitat respectively

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	4.17	4.17	4.17	4.17	4.17	4.44	4.44	4.44	4.44	4.20	4.20	4.17
	SFWW2	4.20	4.20	4.20	4.20	4.44	4.47	4.47	4.47	4.47	4.47	4.24	4.20
	SFWW3	4.33	4.33	4.57	4.57	4.28	4.31	4.31	4.31	4.31	4.55	4.55	4.33
	WW4	4.23	4.23	4.47	4.47	4.18	4.18	3.94	3.94	4.18	4.42	4.42	4.23
	WW5	3.90	3.90	4.14	4.14	3.85	3.85	3.61	3.61	3.85	3.85	4.09	3.90
	WW6	3.70	3.70	3.94	3.73	3.44	3.34	2.68	2.89	3.13	2.92	3.84	3.70
	WW7	3.49	3.49	3.73	3.52	3.06	2.51	1.85	2.06	2.30	2.33	2.78	3.49
	WW8	4.13	4.13	4.15	3.92	3.52	2.81	1.88	2.10	2.57	2.62	3.25	3.96
	WW9	4.09	4.32	4.15	4.09	3.86	2.93	2.27	2.48	2.72	2.96	3.58	4.09
	WW10	3.83	4.07	4.07	3.62	3.38	2.87	2.19	2.41	2.64	2.90	3.13	3.86
	WW11	3.88	4.12	4.12	3.88	3.83	2.74	1.87	1.87	2.32	2.52	3.40	3.88
	WW12	4.05	4.05	4.29	4.05	4.00	3.31	2.41	2.65	2.65	3.12	3.78	4.05
	WW13	4.03	4.03	4.27	4.03	4.03	3.34	2.44	2.68	2.68	3.16	3.82	4.03
Mill Creek Subbasin	MC14	4.45	4.45	4.45	4.69	4.69	4.72	4.49	4.49	4.72	4.72	4.49	4.45
	MC15	3.90	3.90	3.90	4.14	3.90	3.72	3.51	3.51	3.51	3.51	3.72	3.69
	MC16	3.91	3.91	4.14	4.14	3.91	3.69	2.95	2.95	3.19	3.48	3.93	3.91
	MC17	3.41	3.41	3.65	3.65	3.41	2.82	2.37	2.37	2.61	2.84	3.29	3.41
	MC18	3.08	3.08	3.32	3.32	2.87	2.15	1.49	1.49	1.73	1.97	2.59	2.87
	MC19	3.27	3.27	3.51	3.51	3.06	2.34	1.68	1.68	1.92	2.16	2.95	3.06
	MC20	3.23	3.23	3.47	3.47	3.02	2.30	1.64	1.64	1.88	2.12	2.57	3.02
	MC21	3.77	3.35	4.01	4.22	3.98	3.26	2.13	2.13	2.37	3.08	3.32	3.77
	YHC22	3.83	3.83	4.06	3.83	3.83	3.59	3.30	3.30	3.54	3.83	4.06	3.83

Legend: Poor | Low | Fair | Good | High

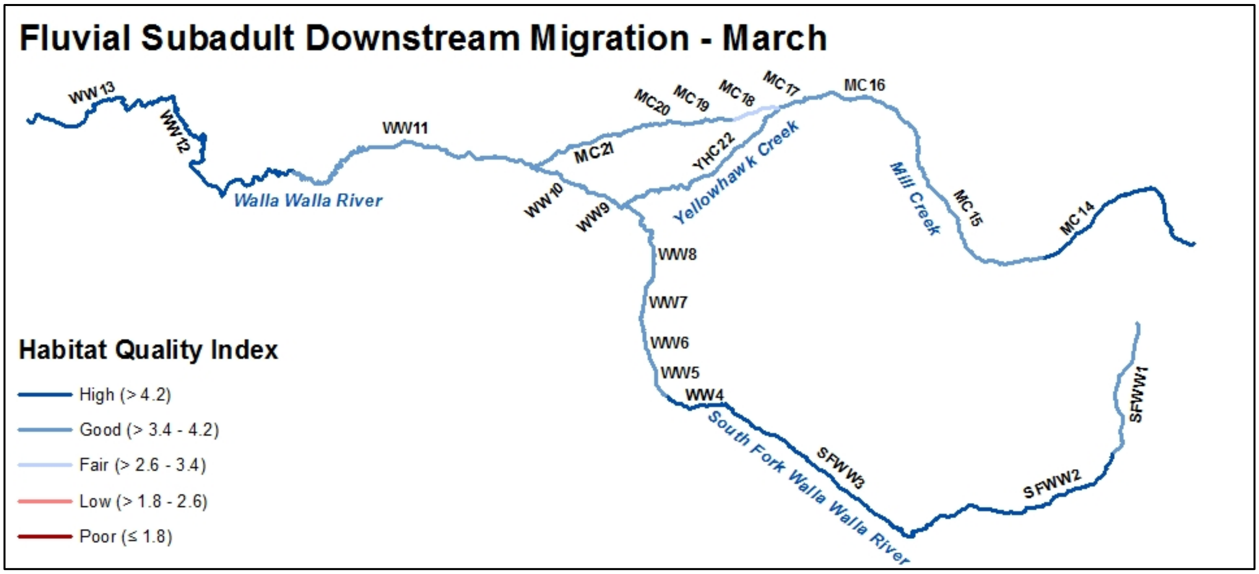

Figure 3.23. Map depicting habitat quality for fluvial sub-adult bull trout downstream migration for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during March.

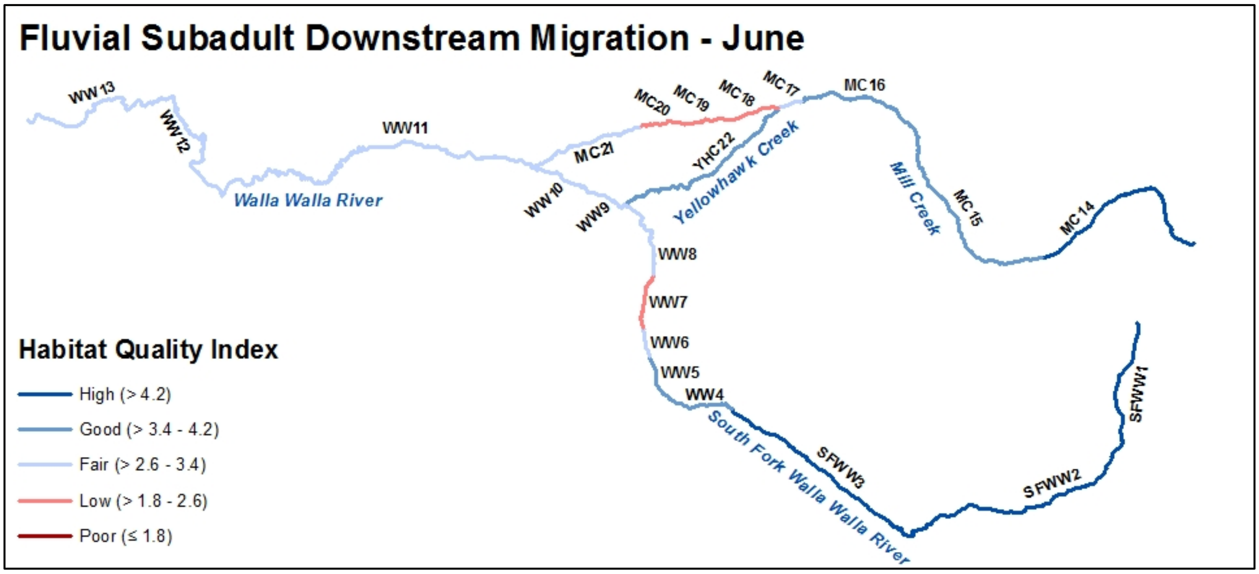

Figure 3.24. Map depicting habitat quality for fluvial sub-adult bull trout downstream migration for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during June.

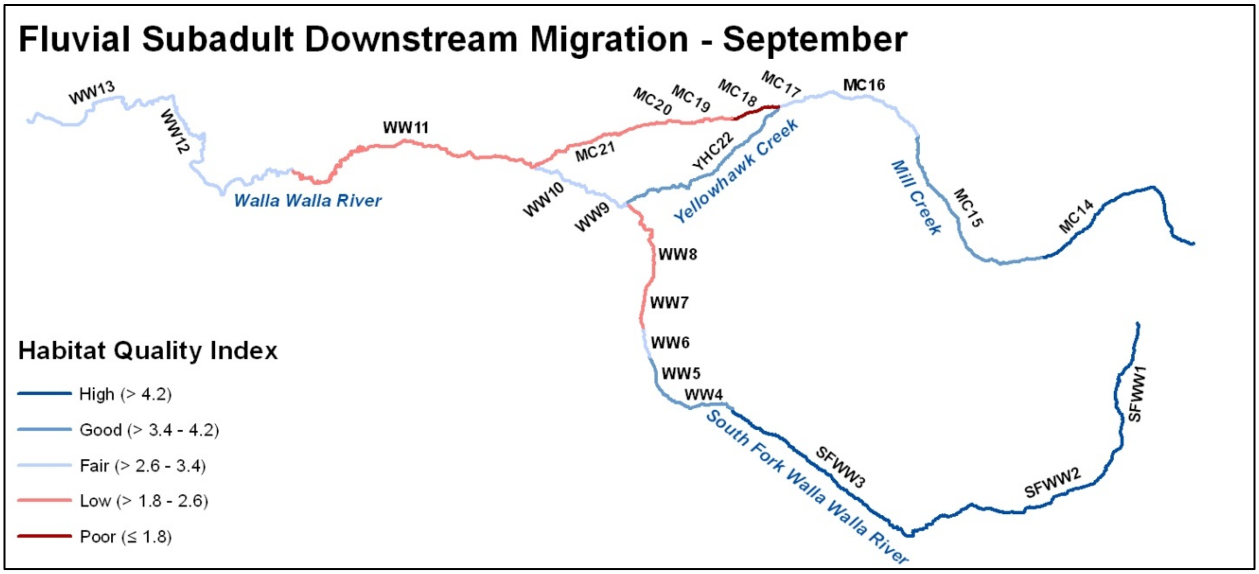

Figure 3.25. Map depicting habitat quality for fluvial sub-adult bull trout downstream migration for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during September.

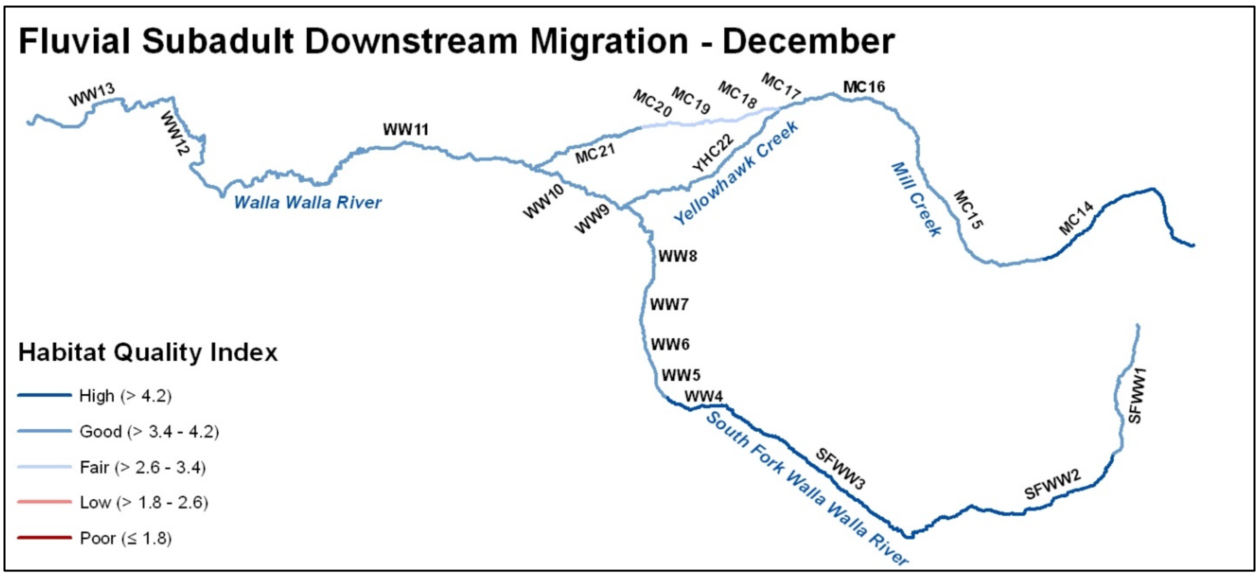

Figure 3.26. Map depicting habitat quality for fluvial sub-adult bull trout downstream migration for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during December.

Table 3.24. Monthly fluvial sub-adult bull trout upstream movement habitat quality periodicity table for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Red, pink, light blue, blue and dark blue cells indicate poor, low, fair, good and high quality habitat respectively.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	4.30	4.30	4.30	4.30	4.30	4.34	4.34	4.34	4.34	4.34	4.34	4.30
	SFWW2	4.35	4.35	4.35	4.35	4.35	4.39	4.39	4.39	4.39	4.39	4.39	4.35
	SFWW3	4.65	4.65	4.65	4.65	4.60	4.64	4.64	4.64	4.64	4.64	4.64	4.65
	WW4	4.34	4.34	4.34	4.34	4.28	4.28	4.08	4.08	4.28	4.28	4.28	4.34
	WW5	4.03	4.03	4.03	4.03	3.97	3.97	3.58	3.77	3.97	3.97	3.97	4.03
	WW6	4.00	4.00	4.00	3.73	3.67	3.38	2.44	2.71	3.11	2.84	3.28	4.00
	WW7	3.75	3.75	3.75	3.48	3.26	2.73	1.79	2.06	2.26	2.38	2.66	3.75
	WW8	4.34	4.34	4.11	4.06	3.67	2.98	1.70	1.98	2.37	2.63	3.07	4.17
	WW9	4.29	4.29	4.12	4.29	4.06	3.10	2.15	2.43	2.82	3.02	3.46	4.29
	WW10	4.20	4.20	4.20	3.93	3.56	2.77	2.07	2.34	2.74	2.89	2.89	3.93
	WW11	4.10	4.10	4.10	4.10	4.05	2.92	1.70	1.70	2.17	2.46	3.23	4.10
	WW12	4.26	4.26	4.26	4.26	4.21	3.27	2.32	2.52	2.52	3.12	3.67	4.26
	WW13	4.26	4.26	4.26	4.26	4.26	3.32	2.38	2.58	2.58	3.17	3.72	4.26
Mill Creek Subbasin	MC14	4.57	4.57	4.57	4.57	4.57	4.61	4.61	4.61	4.61	4.61	4.61	4.57
	MC15	4.40	4.40	4.40	4.40	4.40	4.17	3.89	3.89	3.89	3.89	4.17	4.13
	MC16	4.19	4.19	4.19	4.19	4.19	3.75	2.82	2.82	3.22	3.48	3.75	4.19
	MC17	3.66	3.66	3.66	3.66	3.66	2.86	2.39	2.39	2.58	2.98	3.26	3.66
	MC18	3.28	3.28	3.28	3.28	3.01	2.12	1.37	1.37	1.57	1.97	2.41	3.01
	MC19	3.30	3.30	3.30	3.30	3.03	2.31	1.56	1.56	1.76	2.16	2.43	3.03
	MC20	3.42	3.42	3.42	3.42	3.15	2.26	1.51	1.51	1.71	2.11	2.55	3.15
	MC21	3.74	3.19	3.74	4.01	4.01	3.12	1.77	1.77	1.97	2.97	3.14	3.74
	YHC22	3.88	3.88	3.88	3.88	3.88	3.68	3.23	3.23	3.43	3.88	3.88	3.88

Poor | Low | Fair | Good | High

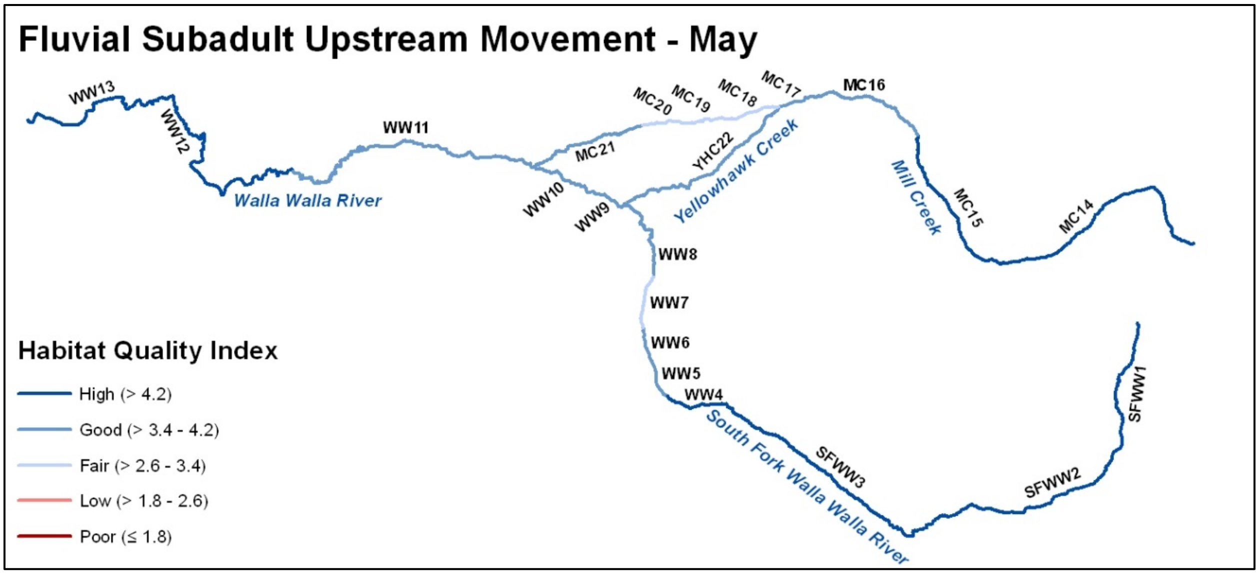

Figure 3.27. Map depicting habitat quality for sub-adult bull trout upstream movement for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during May.

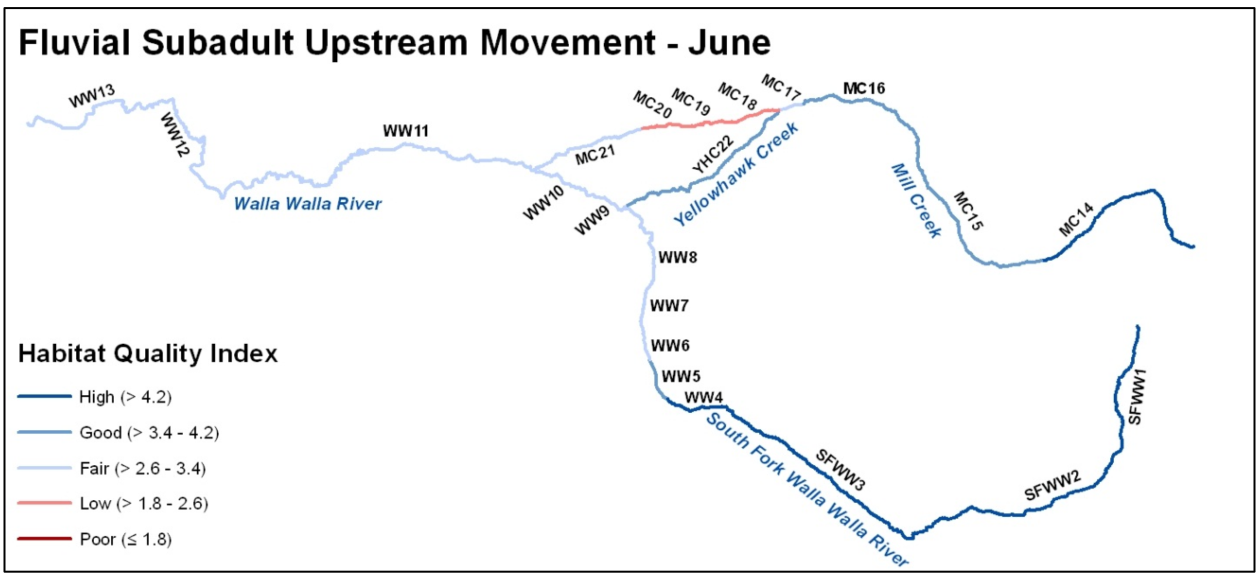

Figure 3.28. Map depicting habitat quality for sub-adult bull trout upstream movement for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during June.

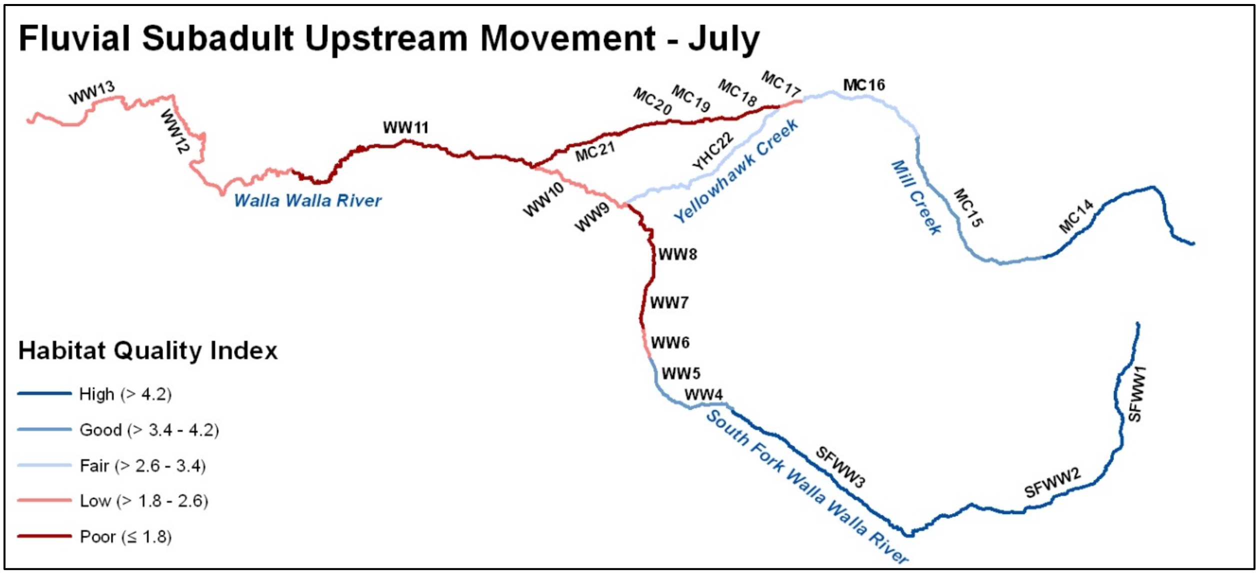

Figure 3.29. Map depicting habitat quality for sub-adult bull trout upstream movement for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during July.

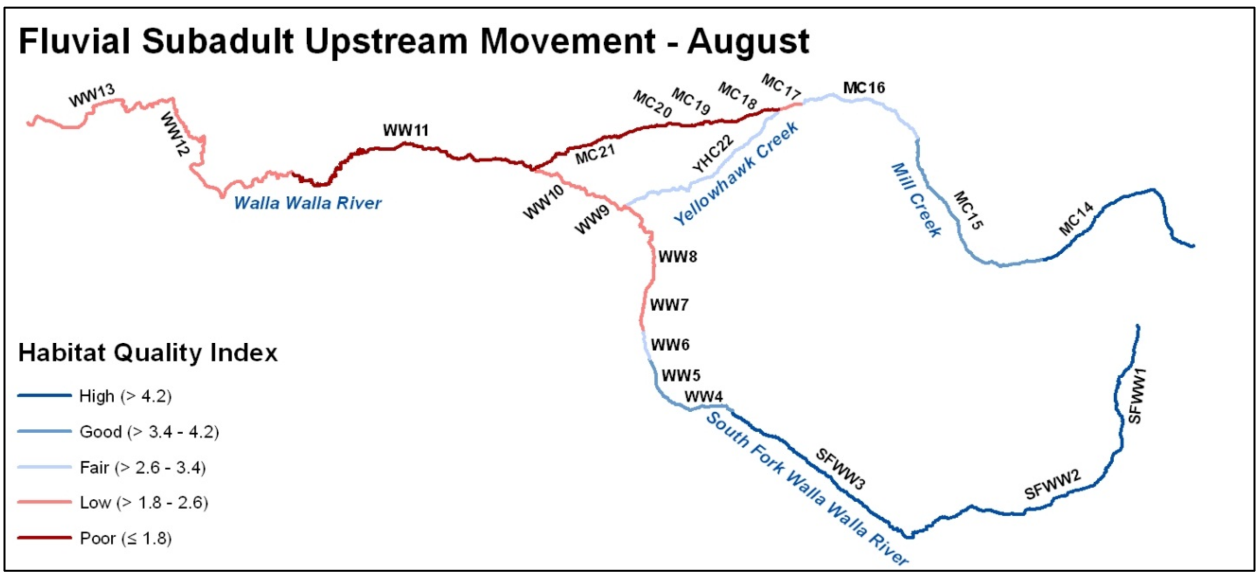

Figure 3.30. Map depicting habitat quality for sub-adult bull trout upstream movement for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during August.

Table 3.25. Monthly habitat quality periodicity table for fluvial sub-adult rearing, foraging and growth for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Red, pink, light blue, blue and dark blue cells indicate poor, low, fair, good and high quality habitat respectively.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	3.78	3.78	3.78	3.78	3.78	4.07	4.07	4.07	4.07	3.81	3.81	3.78
	SFWW2	3.80	3.80	3.80	3.80	4.07	4.09	4.09	4.09	4.09	4.09	3.83	3.80
	SFWW3	3.72	3.72	3.99	3.99	4.16	4.19	4.46	4.46	4.19	4.46	3.93	3.72
	WW4	3.57	3.57	3.84	3.84	4.01	4.28	4.01	4.01	4.01	3.75	3.75	3.57
	WW5	3.13	3.13	3.39	3.39	3.57	3.83	3.30	3.57	3.83	3.57	3.30	3.13
	WW6	3.14	3.14	3.41	3.20	3.37	3.55	2.61	2.81	3.34	2.87	2.81	3.14
	WW7	2.74	2.74	3.00	2.79	2.90	2.71	1.76	1.97	2.24	2.29	2.24	2.74
	WW8	3.45	3.45	3.56	3.78	3.54	3.28	2.04	2.25	2.78	2.87	2.88	3.38
	WW9	3.41	3.67	3.60	3.94	3.78	3.31	2.36	2.57	3.10	3.10	3.12	3.41
	WW10	3.20	3.47	3.47	3.53	3.53	2.87	2.23	2.44	2.97	2.92	2.66	3.26
	WW11	3.28	3.54	3.54	3.81	3.72	3.00	1.85	1.85	2.32	2.45	2.76	3.28
	WW12	3.31	3.31	3.57	3.84	4.01	3.00	2.05	2.32	2.32	2.85	3.00	3.31
	WW13	3.22	3.22	3.48	3.75	4.01	3.00	2.05	2.31	2.31	2.85	3.00	3.22
Mill Creek Subbasin	MC14	3.85	3.85	3.85	4.12	4.12	4.15	4.41	4.41	4.15	4.15	4.41	3.85
	MC15	3.37	3.37	3.37	3.64	3.90	3.72	3.78	3.78	3.51	3.51	3.19	3.16
	MC16	3.34	3.34	3.61	3.61	3.87	3.93	2.84	2.84	3.37	3.46	3.40	3.34
	MC17	2.62	2.62	2.88	2.88	3.41	2.63	2.16	2.16	2.42	2.69	2.63	2.62
	MC18	2.41	2.41	2.67	2.67	2.99	2.20	1.52	1.52	1.79	2.05	2.07	2.20
	MC19	2.41	2.41	2.67	2.67	2.99	2.21	1.52	1.52	1.79	2.05	2.14	2.20
	MC20	2.44	2.44	2.70	2.70	3.03	2.24	1.55	1.55	1.82	2.09	2.03	2.23
	MC21	3.03	2.61	3.29	3.50	4.03	3.24	2.06	2.06	2.32	3.09	2.83	3.03
	YHC22	3.20	3.20	3.46	3.73	3.73	3.73	3.11	3.11	3.37	3.73	3.46	3.20

Poor Low Fair Good High

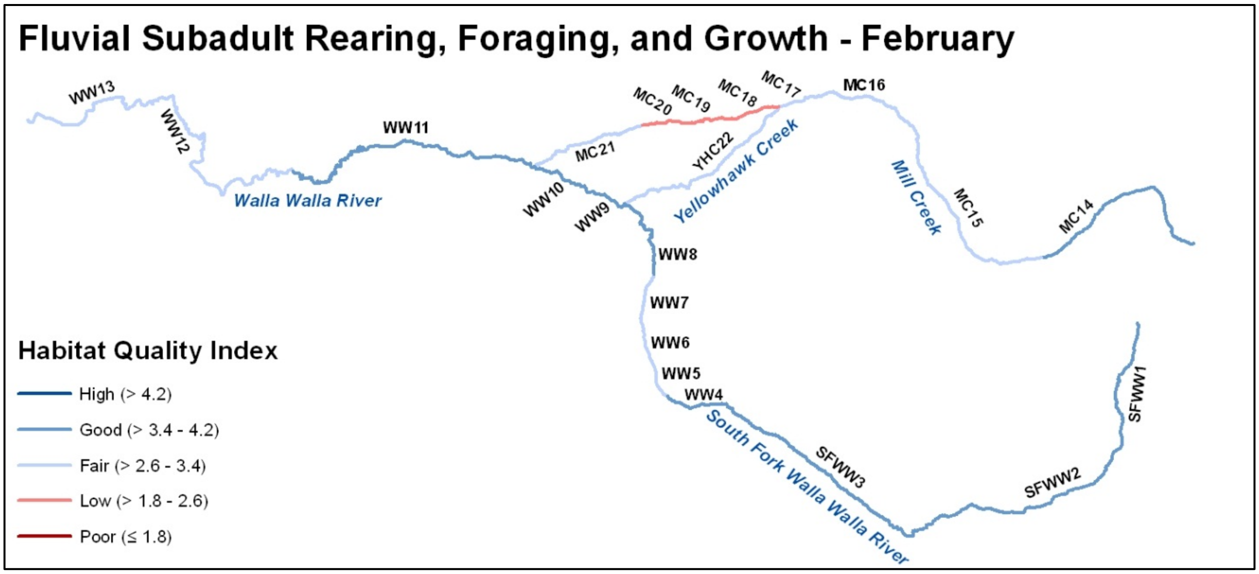

Figure 3.31. Map depicting habitat quality for sub-adult bull trout rearing, foraging and growth for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during February.

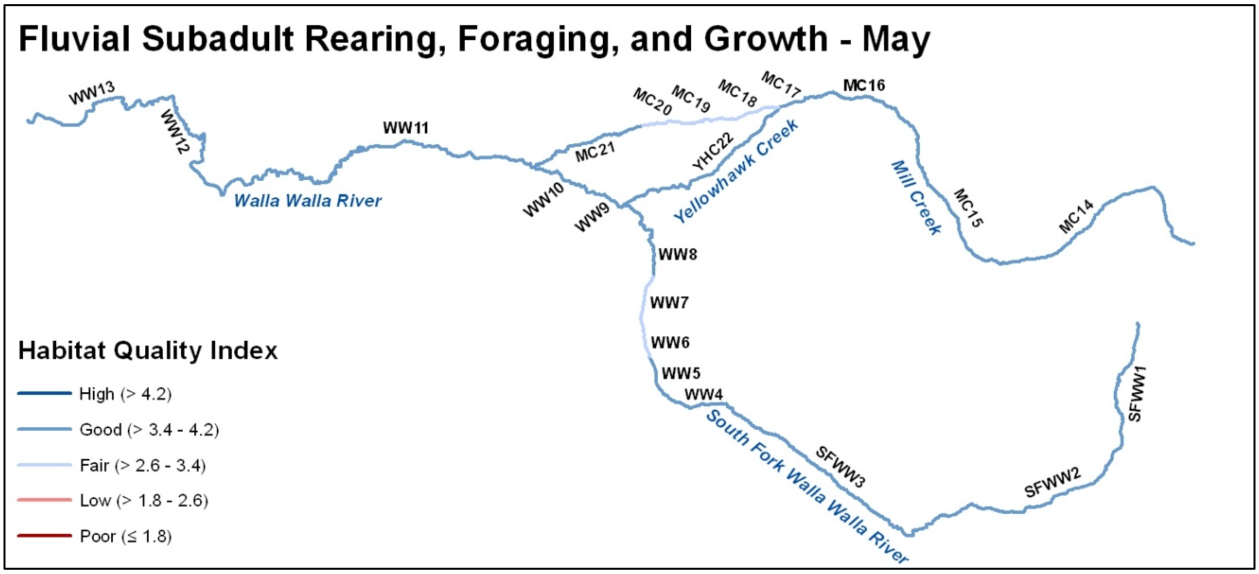

Figure 3.32. Map depicting habitat quality for sub-adult bull trout rearing, foraging and growth for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during May.

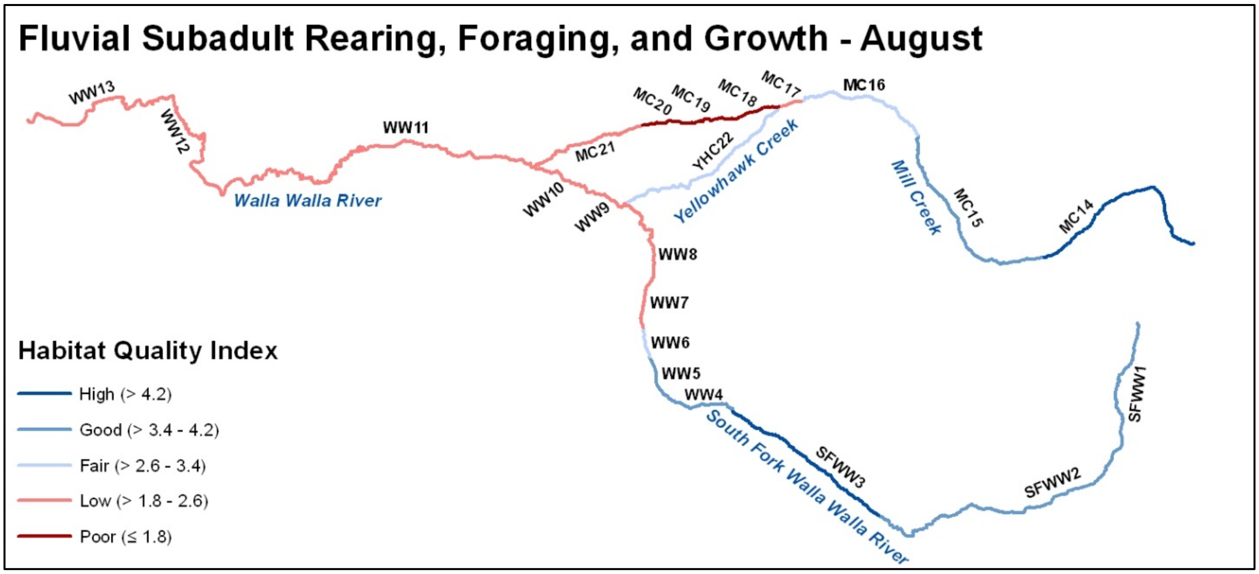

Figure 3.33. Map depicting habitat quality for sub-adult bull trout rearing, foraging and growth for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during August.

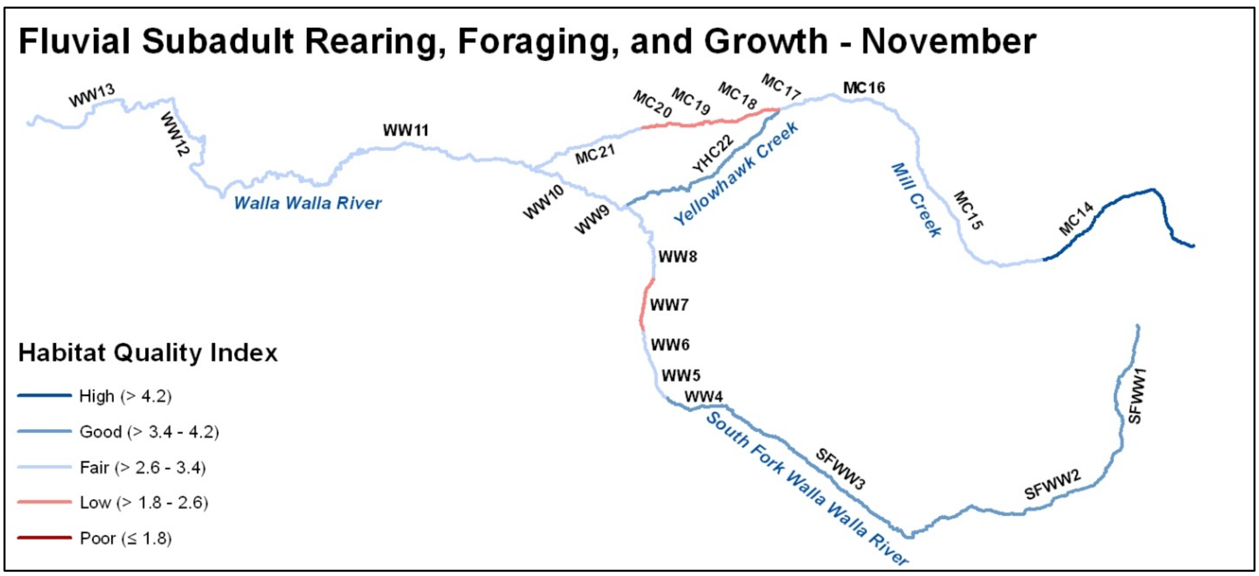

Figure 3.34. Map depicting habitat quality for sub-adult bull trout rearing, foraging and growth for all reaches in the South Fork Walla Walla River, Mainstem Walla Walla River, Mill Creek and Yellowhawk Creek during November.

Table 3.26. Monthly bull trout spawning occurrence periodicity table for reaches in the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1								2	2	2	0	
	SFWW2								2	2	2	0	
	SFWW3								0	0	0	0	
	WW4								0	0	0	0	
	WW5								0	0	0	0	
	WW6								0	0	0	0	
	WW7								0	0	0	0	
	WW8								0	0	0	0	
	WW9								0	0	0	0	
	WW10								0	0	0	0	
	WW11								0	0	0	0	
	WW12								0	0	0	0	
	WW13								0	0	0	0	
Mill Creek Subbasin	MC14								2	2	2	0	
	MC15								1	1	1	0	
	MC16								0	0	0	0	
	MC17								0	0	0	0	
	MC18								0	0	0	0	
	MC19								0	0	0	0	
	MC20								0	0	0	0	
	MC21								0	0	0	0	
	YHC22								0	0	0	0	

No Occurrence (blank) | Conceivable Occur. 0 | Low Occurrence 1 | High Occurrence 2

Table 3.27. Monthly occurrence periodicity table for reaches in the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin for juvenile bull trout rearing, foraging and growth.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	2	2	2	2	2	2	2	2	2	2	2	2
	SFWW2	2	2	2	2	2	2	2	2	2	2	2	2
	SFWW3	1	1	1	1	1	1	1	1	1	1	1	1
	WW4	0	0	0	0	0	0	0	0	0	0	0	0
	WW5	0	0	0	0	0	0	0	0	0	0	0	0
	WW6	0	0	0	0	0	0	0	0	0	0	0	0
	WW7	0	0	0	0	0	0	0	0	0	0	0	0
	WW8	0	0	0	0	0	0	0	0	0	0	0	0
	WW9	0	0	0	0	0	0	0	0	0	0	0	0
	WW10	0	0	0	0	0	0	0	0	0	0	0	0
	WW11	0	0	0	0	0	0	0	0	0	0	0	0
	WW12	0	0	0	0	0	0	0	0	0	0	0	0
	WW13	0	0	0	0	0	0	0	0	0	0	0	0
Mill Creek Subbasin	MC14	2	2	2	2	2	2	2	2	2	2	2	2
	MC15	1	1	1	1	1	1	1	1	1	1	1	1
	MC16	0	0	0	0	0	0	0	0	0	0	0	0
	MC17	0	0	0	0	0	0	0	0	0	0	0	0
	MC18	0	0	0	0	0	0	0	0	0	0	0	0
	MC19	0	0	0	0	0	0	0	0	0	0	0	0
	MC20	0	0	0	0	0	0	0	0	0	0	0	0
	MC21	0	0	0	0	0	0	0	0	0	0	0	0
	YHC22	0	0	0	0	0	0	0	0	0	0	0	0

No Occurrence [ ] Conceivable Occur. 0 Low Occurrence 1 High Occurrence 2

Table 3.28. Monthly occurrence periodicity table for reaches in the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin for fluvial adult bull trout upstream migration.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1			0	0	0	0	0	2	2	0		
	SFWW2			0	0	0	1	2	2	2	0		
	SFWW3			0	0	0	2	2	2	0	0		
	WW4			0	0	1	2	2	2	0	0		
	WW5			0	0	2	2	2	1	0	0		
	WW6			0	0	2	2	2	0	0	0		
	WW7			0	0	2	2	1	0	0	0		
	WW8			0	0	2	2	1	0	0	0		
	WW9			0	0	2	2	1	0	0	0		
	WW10			0	1	2	2	1	0	0	0		
	WW11			1	1	2	1	0	0	0	0		
	WW12			1	1	2	1	0	0	0	0		
	WW13			1	1	2	1	0	0	0	0		
Mill Creek Subbasin	MC14			0	0	0	2	2	2	1	0		
	MC15			0	0	1	2	2	2	1	0		
	MC16			0	1	2	2	1	1	0	0		
	MC17			0	1	2	2	1	0	0	0		
	MC18			0	1	2	2	1	0	0	0		
	MC19			0	1	2	1	0	0	0	0		
	MC20			1	1	2	1	0	0	0	0		
	MC21			1	1	2	1	0	0	0	0		
	YHC22				1	1	1	1	0	0	0		

No Occurrence: (blank) | Conceivable Occur.: 0 | Low Occurrence: 1 | High Occurrence: 2

Table 3.29. Monthly occurrence periodicity table for reaches in the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin for adult bull trout foraging and maintenance.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	2	2	2	2	2	2	2	2	2	2	2	2
	SFWW2	2	2	2	2	2	2	2	2	2	2	2	2
	SFWW3	2	2	2	2	2	2	2	2	1	2	2	2
	WW4	2	2	2	2	2	2	2	2	1	2	2	2
	WW5	2	2	2	2	2	2	2	1	1	2	2	2
	WW6	2	2	2	2	2	2	1	1	1	2	2	2
	WW7	2	2	2	2	2	2	1	0	1	2	2	2
	WW8	2	2	2	2	2	2	1	0	1	2	2	2
	WW9	2	2	2	2	2	2	1	0	1	2	2	2
	WW10	2	2	2	2	2	2	1	0	0	1	2	2
	WW11	2	2	2	2	2	1	0	0	0	1	2	2
	WW12	2	2	2	2	2	1	0	0	0	1	2	2
	WW13	2	2	2	2	2	1	0	0	0	1	2	2
Mill Creek Subbasin	MC14	2	2	2	2	2	2	2	2	2	2	2	2
	MC15	2	2	2	2	2	2	2	2	1	1	2	2
	MC16	2	2	2	2	2	2	1	1	0	1	2	2
	MC17	2	2	2	2	2	2	1	0	0	1	2	2
	MC18	2	2	2	2	2	2	1	0	0	1	2	2
	MC19	2	2	2	2	2	2	0	0	0	1	2	2
	MC20	2	2	2	2	2	2	0	0	0	1	2	2
	MC21	2	2	2	2	2	2	0	0	0	1	2	2
	YHC22	2	2	2	2	2	2	1	0	0	2	2	2

No Occurrence (blank) | Conceivable Occur. 0 | Low Occurrence 1 | High Occurrence 2

Table 3.30. Monthly occurrence periodicity table for reaches in the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin for fluvial adult bull trout downstream migration.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	0	0						0	2	2	1	0
	SFWW2	0	0						0	2	2	1	0
	SFWW3	1	0						0	2	2	2	1
	WW4	1	0						0	2	2	2	1
	WW5	1	0						0	2	2	2	1
	WW6	1	1						0	2	2	2	1
	WW7	1	1						0	2	2	2	1
	WW8	1	1						0	2	2	2	2
	WW9	1	1						0	1	2	2	2
	WW10	2	1						0	0	2	2	2
	WW11	2	2						0	0	1	2	2
	WW12	2	2						0	0	1	2	2
	WW13	2	2						0	0	1	2	2
Mill Creek Subbasin	MC14	0	0						0	2	2	1	0
	MC15	1	1						0	2	2	2	1
	MC16	1	1						0	2	2	2	1
	MC17	1	1						0	1	2	2	2
	MC18	1	1						0	0	2	2	2
	MC19	1	1						0	0	2	2	2
	MC20	1	1						0	0	2	2	2
	MC21	1	1						0	0	2	2	2
	YHC22	1	1						0	0	2	2	2

No Occurrence (blank) Conceivable Occur. 0 Low Occurrence 1 High Occurrence 2

Table 3.31. Monthly occurrence periodicity table for reaches in the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin for fluvial sub-adult bull trout downstream migration.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	1	1	2	2	2	2	2	2	2	2	1	1
	SFWW2	1	1	2	2	2	2	2	2	2	2	1	1
	SFWW3	1	1	2	2	2	2	2	1	1	2	2	1
	WW4	1	1	2	2	2	2	2	1	1	2	2	1
	WW5	1	1	2	2	2	2	2	1	1	2	2	1
	WW6	1	1	2	2	2	2	2	1	1	2	2	2
	WW7	1	1	2	2	2	2	2	1	1	2	2	2
	WW8	1	1	2	2	2	2	1	1	1	2	2	2
	WW9	1	1	2	2	2	2	1	1	0	2	2	2
	WW10	2	1	1	1	1	1	1	0	0	2	2	2
	WW11	2	2	1	1	1	1	1	0	0	2	2	2
	WW12	2	2	0	0	0	0	0	0	0	2	2	2
	WW13	2	2	0	0	0	0	0	0	0	2	2	2
Mill Creek Subbasin	MC14	1	1	2	2	2	2	2	2	2	2	2	2
	MC15	1	1	2	2	2	2	2	2	2	2	2	2
	MC16	1	1	2	2	2	2	2	2	2	2	2	2
	MC17	1	1	2	2	2	2	2	2	2	2	2	2
	MC18	1	1	2	2	2	2	2	1	0	1	2	2
	MC19	1	1	2	2	2	1	1	0	0	1	2	2
	MC20	1	1	2	2	2	1	1	0	0	1	2	2
	MC21	1	1	2	2	2	1	1	0	0	1	2	2
	YHC22	1	1	2	2	2	2	2	1	0	1	2	2

No Occurrence | Conceivable Occur. 0 | Low Occurrence 1 | High Occurrence 2

Table 3.32. Monthly occurrence periodicity table for reaches in the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin for fluvial sub-adult bull trout upstream movement.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1			0	0	0	0	0	0				
	SFWW2			0	0	0	0	0	0				
	SFWW3			0	0	0	0	0	0				
	WW4			0	0	0	0	0	0				
	WW5			0	0	0	1	2	2				
	WW6			0	0	0	1	2	2				
	WW7			0	0	0	1	2	2				
	WW8			0	0	0	1	2	2				
	WW9			0	0	1	2	2	1				
	WW10			0	1	2	2	2	1				
	WW11			1	1	2	2	1	1				
	WW12			1	1	2	2	0	0				
	WW13			1	1	2	2	0	0				
Mill Creek Subbasin	MC14			0	0	0	0	0	0				
	MC15			0	0	0	0	0	0				
	MC16			0	0	0	0	0	0				
	MC17			0	0	1	2	2	1				
	MC18			0	0	1	2	2	1				
	MC19			0	0	1	2	2	1				
	MC20			0	0	1	2	2	1				
	MC21			0	0	1	2	2	1				
	YHC22			0	0	1	2	2	1				

No Occurrence (blank) | Conceivable Occur. 0 | Low Occurrence 1 | High Occurrence 2

Table 3.33. Monthly occurrence periodicity table for reaches in the South Fork and Mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin for fluvial sub-adult bull trout rearing, foraging and growth.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	2	2	2	2	2	2	2	2	2	2	2	2
	SFWW2	2	2	2	2	2	2	2	2	2	2	2	2
	SFWW3	2	2	2	2	2	2	2	2	2	2	2	2
	WW4	2	2	2	2	2	2	2	2	2	2	2	2
	WW5	2	2	2	2	2	2	2	2	2	2	2	2
	WW6	2	2	2	2	2	2	2	2	2	2	2	2
	WW7	2	2	2	2	2	2	2	2	2	2	2	2
	WW8	2	2	2	2	2	2	2	1	2	2	2	2
	WW9	2	2	2	2	2	2	1	1	0	2	2	2
	WW10	2	2	2	2	2	2	1	0	0	2	2	2
	WW11	2	2	2	2	2	2	1	0	0	2	2	2
	WW12	2	2	2	2	2	2	0	0	0	2	2	2
	WW13	2	2	2	2	2	2	0	0	0	2	2	2
Mill Creek Subbasin	MC14	2	2	2	2	2	2	2	2	2	2	2	2
	MC15	2	2	2	2	2	2	2	2	2	2	2	2
	MC16	2	2	2	2	2	2	2	2	2	2	2	2
	MC17	2	2	2	2	2	2	2	2	2	2	2	2
	MC18	2	2	2	2	2	2	2	1	0	1	2	2
	MC19	2	2	2	2	2	2	2	1	0	1	2	2
	MC20	2	2	2	2	2	2	2	1	0	1	2	2
	MC21	2	2	2	2	2	2	2	1	0	1	2	2
	YHC22	2	2	2	2	2	2	2	1	0	1	2	2

No Occurrence | Conceivable Occur. 0 | Low Occurrence 1 | High Occurrence 2

Table 3.34. Mean HQSs for high, low and no bull trout occurrence when conceivable in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek for each life stage, strategy or action.

		High Occurrence		Low Occurrence		No Occurrence	
Bull Trout Life Stage, Strategy or Action	**Conceivable Occurrence (# Months)**	**Mean**	**95% CI**	**Mean**	**95% CI**	**Mean**	**95% CI**
South Fork and Mainstem Walla Walla River							
Spawning	Aug - Nov (4)	4.32	4.1 - 4.53	NA	NA	2.65	2.39 - 2.91
Juvenile Rearing, Foraging and Growth	Jan - Dec (12)	4.28	4.2 - 4.36	4.24	4.14 - 4.34	3.32	3.20 - 3.43
Fluvial Adult Upstream Migration	Mar - Oct (8)	3.70	3.49 - 3.91	3.28	2.90 - 3.65	3.17	3.0 - 3.35
Adult Foraging and Maintenance	Jan - Dec (12)	3.74	3.67 - 3.82	2.93	2.66 - 3.20	2.30	2.13 - 2.46
Fluvial Adult Downstream Migration	Aug - Feb (7)	3.69	3.5 - 3.89	3.78	3.55 - 4.00	3.34	2.99 - 3.68
Fluvial Sub-adult Downstream Migration	Jan - Dec (12)	3.82	3.69 - 3.95	3.62	3.4 - 3.83	3.09	2.74 - 3.44
Fluvial Sub-adult Upstream Movement	Mar - Aug (6)	2.93	2.55 - 3.31	3.41	2.94 - 3.87	4.04	3.86 - 4.22
Fluvial Sub-adult Rearing, Foraging and Growth	Jan - Dec (12)	3.45	3.36 - 3.53	2.25	2.02 - 2.48	2.37	2.15 - 2.59
Mill Creek							
Spawning	Aug - Nov (4)	3.98	3.81 - 4.15	3.23	3.06 - 3.40	4.45	1.69 - 2.41
Juvenile Rearing, Foraging and Growth	Jan - Dec (12)	4.23	4.1 - 4.36	3.88	3.78 - 3.98	2.54	2.36 - 2.71
Fluvial Adult Upstream Migration	Mar - Oct (8)	3.51	3.19 - 3.83	2.93	2.61 - 3.25	2.51	2.19 - 2.84
Adult Foraging and Maintenance	Jan - Dec (12)	3.24	3.08 - 3.40	2.61	2.22 - 3.00	1.90	1.63 - 2.18
Fluvial Adult Downstream Migration	Aug - Feb (7)	3.05	2.75 - 3.35	3.40	3.16 - 3.64	2.61	2.00 - 3.21
Fluvial Sub-adult Downstream Migration	Jan - Dec (12)	3.54	3.36 - 3.71	3.03	2.71 - 3.35	1.91	1.71 - 2.10
Fluvial Sub-adult Upstream Movement	Mar - Aug (6)	2.13	1.77 - 2.49	2.55	1.95 - 3.14	3.92	3.72 - 4.11
Fluvial Sub-adult Rearing, Foraging and Growth	Jan - Dec (12)	3.04	2.89 - 3.20	1.99	1.64 - 2.35	1.93	1.67 - 2.19
Yellowhawk Creek							
Spawning	Aug - Nov (4)	NA	NA	NA	NA	3.00	2.79 - 3.21
Juvenile Rearing, Foraging and Growth	Jan - Dec (12)	NA	NA	NA	NA	3.40	3.18 - 3.62
Fluvial Adult Upstream Migration	Mar - Oct (8)	NA	NA	3.71	3.53 - 3.88	3.69	3.52 - 3.87
Adult Foraging and Maintenance	Jan - Dec (12)	3.67	3.59 - 3.75	3.18	NA	3.30	3.06 - 3.55
Fluvial Adult Downstream Migration	Aug - Feb (7)	3.93	3.80 - 4.06	3.87	NA	3.51	3.32 - 3.71
Fluvial Sub-adult Downstream Migration	Jan - Dec (12)	3.78	3.58 - 3.98	3.69	3.44 - 3.95	3.54	NA
Fluvial Sub-adult Upstream Movement	Mar - Aug (6)	3.46	3.01 - 3.90	3.56	2.91 - 4.20	3.88	NA
Fluvial Sub-adult Rearing, Foraging and Growth	Jan - Dec (12)	3.42	3.25 - 3.59	3.42	2.81 - 4.02	3.37	NA

Table 3.35. Periodicity table comparing monthly spawning habitat quality scores with bull trout occurrence for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Cells outlined in red indicate when and where spawning commonly occurs, purple indicates low occurrence and green indicates reaches and months when spawning may be conceivable, but does not occur or rarely is observed.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	4.15	4.15	4.15	4.15	4.41	3.94	3.94	3.94	4.46	4.46	4.20	4.15
	SFWW2	4.21	4.21	4.21	4.47	4.47	4.00	4.00	4.00	4.52	4.52	4.52	4.21
	SFWW3	4.38	4.38	4.64	4.12	3.75	3.80	3.80	3.80	3.80	4.06	4.58	4.38
	WW4	4.16	4.16	3.90	3.90	3.53	3.53	3.27	3.27	3.53	3.79	4.31	4.16
	WW5	3.77	4.03	3.51	3.51	3.14	3.14	2.88	2.88	3.14	3.14	3.40	3.77
	WW6	3.80	4.06	3.54	3.32	2.95	2.80	2.11	2.33	2.59	2.37	2.85	3.80
	WW7	3.33	3.59	3.07	2.86	2.38	1.82	1.39	1.60	1.60	1.65	2.12	3.33
	WW8	3.96	4.22	3.48	3.22	2.90	2.23	1.47	1.69	1.69	2.06	2.64	3.85
	WW9	3.93	4.19	3.56	3.41	3.19	2.30	1.87	2.09	2.09	2.61	2.93	3.93
	WW10	3.78	4.04	3.52	3.04	2.68	2.15	1.72	1.94	1.94	2.20	2.46	3.71
	WW11	4.04	4.04	3.52	3.26	3.15	2.00	1.35	1.35	1.57	1.72	2.63	3.78
	WW12	3.81	3.81	3.55	3.29	3.18	2.35	1.92	1.92	1.92	2.18	3.39	3.81
	WW13	3.69	3.69	3.43	3.18	3.18	2.34	1.91	1.91	1.91	2.17	3.38	3.69
Mill Creek Subbasin	MC14	4.28	4.28	4.28	4.54	4.02	4.07	3.81	3.81	4.07	4.07	4.59	4.28
	MC15	4.22	4.22	4.22	4.48	3.70	3.53	3.32	3.06	3.32	3.32	4.31	4.00
	MC16	3.86	4.12	3.60	3.60	3.34	3.12	2.54	2.54	2.54	2.91	3.38	3.86
	MC17	3.07	3.07	2.81	2.81	2.55	2.02	1.80	1.80	1.80	2.06	2.64	3.07
	MC18	2.94	2.94	2.68	2.68	2.10	1.53	1.10	1.10	1.10	1.36	1.84	2.73
	MC19	2.77	2.77	2.51	2.51	2.04	1.68	1.25	1.25	1.25	1.51	1.99	2.56
	MC20	2.90	2.90	2.64	2.64	2.17	1.50	1.06	1.06	1.06	1.43	1.91	2.69
	MC21	3.31	2.88	3.05	3.27	3.01	2.44	1.47	1.47	1.47	2.27	2.63	3.31
	YHC22	3.70	3.96	3.44	3.18	3.18	2.92	2.82	2.82	2.82	3.18	3.18	3.70

Poor Low Fair Good High

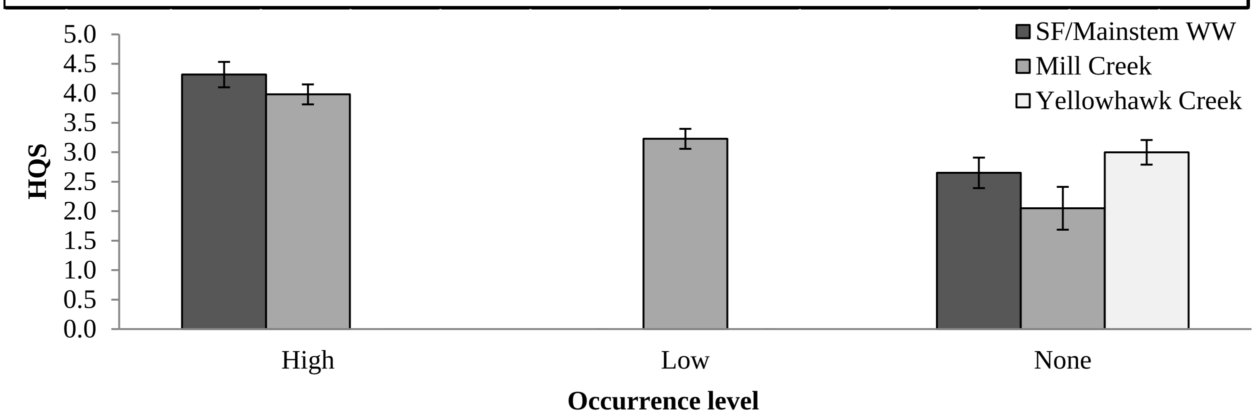

Figure 3.35. Mean habitat quality scores when bull trout spawning occurrence is high, low and not observed during time periods when occurrence is conceivable in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Table 3.36. Periodicity table comparing monthly juvenile rearing, foraging and growth habitat quality scores with juvenile bull trout occurrence for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Cells outlined in red indicate when and where juvenile bull trout commonly occur, purple indicates low occurrence and green indicates reaches where juvenile bull trout rearing, foraging and growth may be conceivable, but not occur or rarely is observed.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	4.04	4.04	4.04	4.04	4.04	4.37	4.37	4.37	4.66	4.66	4.37	4.33
	SFWW2	4.12	4.12	4.12	4.12	4.41	4.45	4.45	4.45	4.45	4.45	4.16	4.12
	SFWW3	4.00	4.00	4.29	4.29	4.50	4.25	4.25	4.25	4.54	4.25	4.25	4.00
	WW4	4.00	4.00	4.29	4.29	4.50	4.25	4.25	4.25	4.54	4.25	4.25	4.00
	WW5	3.46	3.46	3.75	3.75	3.68	3.68	3.39	3.39	3.68	3.96	3.68	3.46
	WW6	3.46	3.46	3.75	3.53	3.75	3.34	2.62	2.83	3.12	3.20	3.12	3.46
	WW7	3.46	3.46	3.75	3.53	3.75	3.34	2.62	2.83	3.12	3.20	3.12	3.46
	WW8	3.68	3.68	3.84	4.04	3.58	3.03	2.02	2.24	2.53	2.89	3.16	3.63
	WW9	3.64	3.93	3.88	4.22	3.80	3.04	2.32	2.54	2.83	3.12	3.38	3.64
	WW10	3.46	3.75	3.75	3.82	3.24	2.53	2.19	2.41	2.70	2.90	2.90	3.53
	WW11	3.51	3.80	3.80	4.09	3.72	2.66	1.44	1.44	1.94	2.36	2.91	3.51
	WW12	3.52	3.52	3.81	4.10	3.73	2.56	2.13	2.13	2.13	2.71	3.43	3.52
	WW13	3.38	3.38	3.67	3.96	3.67	2.50	2.07	2.07	2.07	2.65	3.37	3.38
Mill Creek Subbasin	MC14	3.99	3.99	3.99	4.28	4.28	4.32	4.61	4.61	4.32	4.32	4.03	3.99
	MC15	3.84	3.84	3.84	4.13	4.13	3.96	3.74	3.74	4.03	4.03	3.67	3.63
	MC16	3.59	3.59	3.88	3.88	3.88	3.66	2.79	2.79	3.08	3.45	3.66	3.59
	MC17	2.73	2.73	3.02	3.02	3.02	2.27	1.76	1.76	2.05	2.63	2.85	2.73
	MC18	2.61	2.61	2.90	2.90	2.64	1.85	1.13	1.13	1.42	2.00	2.22	2.40
	MC19	2.54	2.54	2.82	2.82	2.61	1.82	1.10	1.10	1.39	1.97	2.19	2.32
	MC20	2.56	2.56	2.85	2.85	2.63	1.80	1.08	1.08	1.37	1.99	2.21	2.34
	MC21	3.14	2.71	3.43	3.64	3.64	2.86	1.63	1.63	1.92	3.01	3.05	3.14
	YHC22	3.40	3.40	3.69	3.98	3.69	3.40	2.74	2.74	3.03	3.69	3.69	3.40

Poor | Low | Fair | Good | High

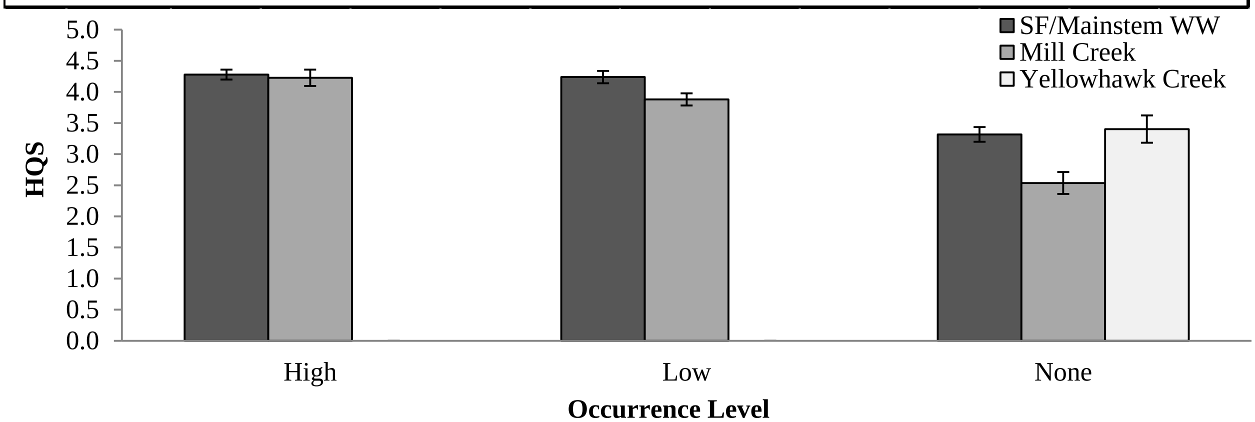

Figure 3.36. Mean habitat quality scores when occurrence of juvenile bull trout rearing, foraging and growth is high, low and not observed during time periods when occurrence is conceivable in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Table 3.37. Periodicity table comparing monthly habitat quality scores for fluvial adult upstream migration with occurrence for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Cells outlined in red indicate when and where adult upstream movement commonly occurs, purple indicates low occurrence and green indicates reaches and months when upstream movement may be conceivable, but does not occur or rarely is observed.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	3.44	3.44	3.44	3.44	3.62	3.66	3.66	3.66	3.66	3.66	3.49	3.44
	SFWW2	3.53	3.53	3.53	3.70	3.70	3.75	3.75	3.75	3.75	3.75	3.75	3.53
	SFWW3	3.85	3.85	4.03	4.03	3.99	4.38	4.56	4.56	4.38	4.03	4.03	3.85
	WW4	3.79	3.79	3.97	3.97	4.28	4.45	4.10	4.45	4.28	3.92	3.92	3.79
	WW5	3.29	3.46	3.46	3.46	3.77	3.95	3.59	3.59	3.95	3.42	3.42	3.29
	WW6	3.25	3.42	3.42	3.32	3.46	3.51	2.60	2.88	3.23	2.78	2.70	3.25
	WW7	3.11	3.28	3.28	3.01	3.13	2.59	1.86	2.14	2.32	2.22	2.49	3.11
	WW8	3.71	3.89	3.65	3.61	3.54	2.82	1.76	2.04	2.22	2.44	2.55	3.52
	WW9	3.67	3.84	3.66	4.20	3.96	2.96	2.23	2.51	2.69	2.86	2.98	3.67
	WW10	3.59	3.77	3.77	3.85	3.48	2.85	2.16	2.43	2.61	2.75	2.39	3.49
	WW11	3.64	3.64	3.64	3.64	3.95	2.79	1.78	1.78	2.23	2.32	2.76	3.47
	WW12	3.65	3.65	3.83	3.83	4.14	3.40	2.49	2.67	2.67	3.02	3.22	3.65
	WW13	3.65	3.65	3.83	3.83	4.18	3.44	2.53	2.71	2.71	3.06	3.26	3.65
Mill Creek Subbasin	MC14	3.75	3.75	3.75	3.93	3.93	3.97	4.32	3.97	3.97	3.97	3.97	3.75
	MC15	3.61	3.61	3.61	3.79	4.14	3.91	3.81	3.81	3.63	3.28	3.55	3.33
	MC16	3.46	3.64	3.64	3.64	3.99	3.89	3.04	3.04	3.21	3.44	3.36	3.46
	MC17	2.83	2.83	3.01	3.01	3.54	2.76	2.31	2.31	2.48	2.66	2.77	2.83
	MC18	2.44	2.44	2.61	2.61	2.87	2.16	1.43	1.43	1.60	1.78	1.89	2.16
	MC19	2.66	2.47	2.46	2.46	2.71	2.19	1.46	1.46	1.64	1.82	1.93	2.38
	MC20	2.60	2.60	2.77	2.77	3.03	2.13	1.40	1.40	1.58	1.75	1.86	2.32
	MC21	2.91	2.35	3.08	3.36	3.89	3.18	1.85	1.85	2.03	2.80	2.64	2.91
	YHC22	3.41	3.58	3.58	3.58	3.94	3.76	3.54	3.54	3.72	3.94	3.58	3.41

Poor | Low | Fair | Good | High

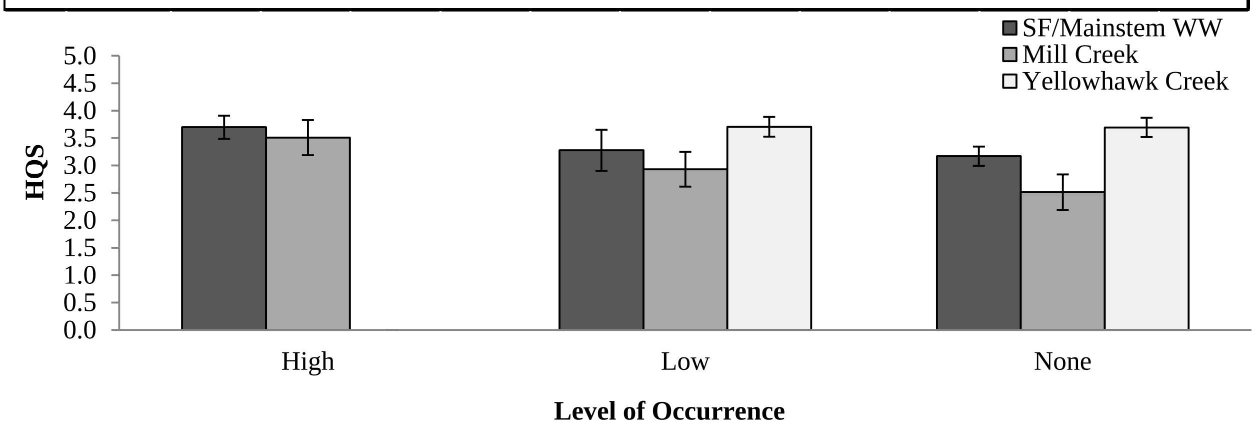

Figure 3.37Mean habitat quality scores when occurrence of adult fluvial bull trout upstream migration is high, low and not observed during time periods when occurrence is conceivable in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Table 3.38. Periodicity table comparing monthly habitat quality scores for adult foraging and maintenance with occurrence for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Cells outlined in red indicate when and where adult foraging and maintenance commonly occurs, purple indicates low occurrence and green indicates reaches and months when upstream movement may be conceivable, but does not occur or rarely is observed.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	4.03	4.03	4.03	4.03	4.03	4.31	4.31	4.31	4.31	4.06	4.06	4.03
	SFWW2	4.06	4.06	4.06	4.06	4.31	4.34	4.34	4.34	4.34	4.34	4.09	4.06
	SFWW3	4.00	4.00	4.26	4.26	4.18	4.21	4.47	4.47	4.21	4.21	4.21	4.00
	WW4	3.84	3.84	4.10	4.10	4.02	4.28	4.02	4.02	4.02	4.02	4.02	3.84
	WW5	3.45	3.45	3.71	3.71	3.63	3.89	3.38	3.63	3.89	3.63	3.63	3.45
	WW6	3.45	3.45	3.70	3.48	3.40	3.57	2.63	2.85	3.35	2.88	3.10	3.45
	WW7	3.02	3.02	3.27	3.05	2.90	2.71	1.76	1.98	2.24	2.27	2.49	3.02
	WW8	3.80	3.80	3.90	3.83	3.60	3.33	2.09	2.31	2.81	2.89	3.19	3.72
	WW9	3.75	4.00	3.92	4.00	3.85	3.36	2.41	2.63	3.13	3.13	3.44	3.75
	WW10	3.55	3.80	3.80	3.58	3.58	2.91	2.29	2.51	3.01	2.94	2.94	3.58
	WW11	3.60	3.86	3.86	3.86	3.78	3.02	1.85	1.85	2.33	2.44	3.03	3.60
	WW12	3.66	3.66	3.92	4.17	3.84	3.06	2.11	2.37	2.37	2.87	3.31	3.66
	WW13	3.58	3.58	3.84	4.09	3.84	3.05	2.11	2.36	2.36	2.86	3.31	3.58
Mill Creek Subbasin	MC14	4.03	4.03	4.03	4.29	4.29	4.31	4.31	4.31	4.31	4.31	4.06	4.03
	MC15	3.66	3.66	3.66	3.91	3.91	3.72	3.75	3.75	3.50	3.50	3.47	3.44
	MC16	3.63	3.63	3.89	3.89	3.89	3.92	2.87	2.87	3.37	3.44	3.66	3.63
	MC17	2.84	2.84	3.09	3.09	2.84	2.57	2.09	2.09	2.35	2.60	2.90	2.84
	MC18	2.62	2.62	2.87	2.87	2.40	2.21	1.51	1.51	1.76	2.02	2.32	2.40
	MC19	2.64	2.56	2.74	2.74	2.26	2.15	1.45	1.45	1.71	1.96	2.26	2.42
	MC20	2.65	2.65	2.90	2.90	2.43	2.16	1.46	1.46	1.71	1.97	2.27	2.43
	MC21	3.19	2.75	3.45	3.67	3.42	3.23	2.02	2.02	2.27	3.04	3.12	3.19
	YHC22	3.50	3.50	3.76	3.76	3.76	3.76	3.18	3.18	3.43	3.76	3.76	3.50

Poor | Low | Fair | Good | High

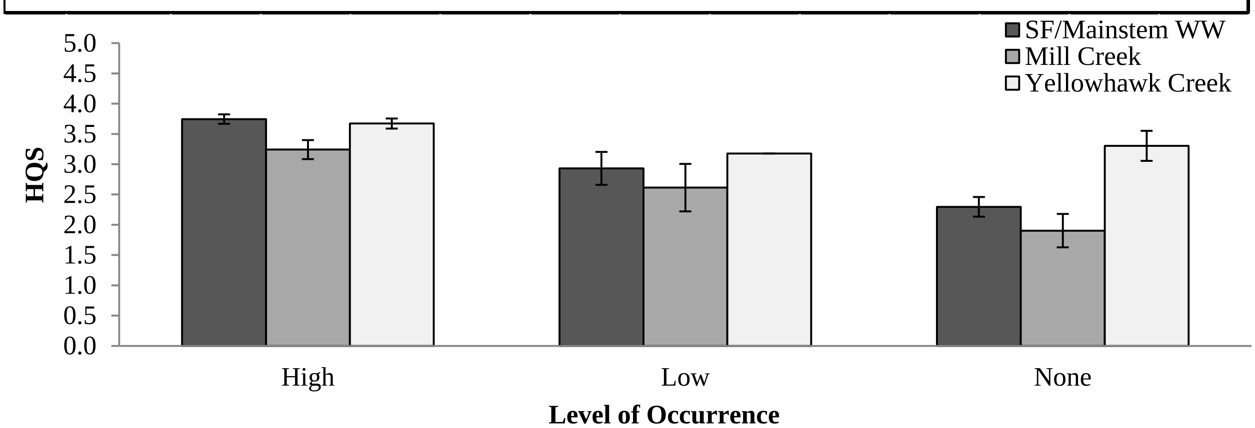

Figure 3.38. Mean habitat quality scores when occurrence of adult foraging and maintenance is high, low and not observed during time periods when occurrence is conceivable in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Table 3.39. Periodicity table comparing monthly habitat quality scores for fluvial adult downstream migration with occurrence for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Cells outlined in red indicate when and where fluvial adult downstream migration commonly occurs, purple indicates low occurrence and green indicates reaches and months when upstream movement may be conceivable, but does not occur or rarely is observed.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	4.20	4.20	4.20	4.20	4.20	4.43	4.43	4.43	4.43	4.23	4.23	4.20
	SFWW2	4.06	4.06	4.06	4.06	4.26	4.29	4.29	4.29	4.29	4.29	4.09	4.06
	SFWW3	4.34	4.34	4.54	4.54	4.29	4.32	4.32	4.32	4.32	4.52	4.52	4.34
	WW4	4.22	4.22	4.42	4.42	4.17	4.17	3.97	3.97	4.17	4.37	4.37	4.22
	WW5	3.78	3.78	3.98	3.98	3.73	3.73	3.53	3.53	3.73	3.73	3.93	3.78
	WW6	3.75	3.75	3.95	3.68	3.43	3.33	2.60	2.87	3.07	2.80	3.67	3.75
	WW7	3.55	3.55	3.75	3.49	3.07	2.57	1.85	2.11	2.31	2.25	2.71	3.55
	WW8	4.17	4.17	4.15	3.90	3.52	2.86	1.82	2.08	2.48	2.53	3.16	4.00
	WW9	4.12	4.32	4.15	4.12	3.90	2.97	2.25	2.51	2.71	2.91	3.54	4.12
	WW10	3.87	4.07	4.07	3.61	3.41	2.84	2.17	2.43	2.63	2.78	2.98	3.81
	WW11	3.93	4.13	4.13	3.93	3.88	2.78	1.79	1.79	2.25	2.35	3.29	3.93
	WW12	4.09	4.09	4.29	4.09	4.04	3.32	2.39	2.59	2.59	2.99	3.72	4.09
	WW13	4.08	4.08	4.28	4.08	4.08	3.36	2.43	2.63	2.63	3.03	3.76	4.08
Mill Creek Subbasin	MC14	4.30	4.30	4.30	4.50	4.50	4.53	4.33	4.33	4.53	4.53	4.33	4.30
	MC15	3.94	3.94	3.94	4.14	3.94	3.71	3.45	3.45	3.45	3.45	3.71	3.67
	MC16	3.94	3.94	4.14	4.14	3.94	3.68	2.97	2.97	3.17	3.42	3.88	3.94
	MC17	3.30	3.30	3.50	3.50	3.30	2.71	2.25	2.25	2.45	2.65	3.27	3.30
	MC18	2.94	2.94	3.14	3.14	2.68	2.18	1.45	1.45	1.65	1.85	2.48	2.68
	MC19	3.13	2.97	3.00	3.00	2.54	2.20	1.47	1.47	1.67	1.88	2.50	2.87
	MC20	3.07	3.07	3.27	3.27	2.81	2.15	1.42	1.42	1.62	1.82	2.45	2.81
	MC21	3.41	2.89	3.61	3.88	3.68	3.18	1.87	1.87	2.07	2.85	3.21	3.41
	YHC22	3.87	3.87	4.07	3.87	3.87	3.67	3.41	3.41	3.61	3.87	4.07	3.87

Poor | Low | Fair | Good | High

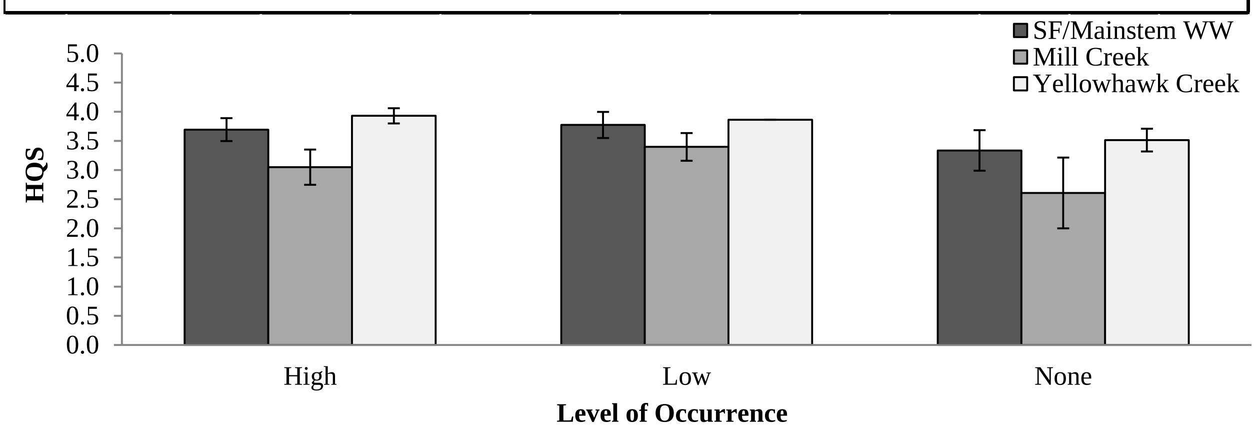

Figure 3.39. Mean habitat quality scores when occurrence of fluvial adult downstream migration is high, low and not observed during time periods when occurrence is conceivable in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Table 3.40. Periodicity table comparing monthly habitat quality scores for fluvial sub-adult downstream migration with occurrence for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Cells outlined in red indicate when and where fluvial sub-adult downstream migration commonly occurs, purple indicates low occurrence and green indicates reaches and months when upstream movement may be conceivable, but does not occur or rarely is observed.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	4.17	4.17	4.17	4.17	4.17	4.44	4.44	4.44	4.44	4.20	4.20	4.17
	SFWW2	4.20	4.20	4.20	4.20	4.44	4.47	4.47	4.47	4.47	4.47	4.24	4.20
	SFWW3	4.33	4.33	4.57	4.57	4.28	4.31	4.31	4.31	4.31	4.55	4.55	4.33
	WW4	4.23	4.23	4.47	4.47	4.18	4.18	3.94	3.94	4.18	4.42	4.42	4.23
	WW5	3.90	3.90	4.14	4.14	3.85	3.85	3.61	3.61	3.85	3.85	4.09	3.90
	WW6	3.70	3.70	3.94	3.73	3.44	3.34	2.68	2.89	3.13	2.92	3.84	3.70
	WW7	3.49	3.49	3.73	3.52	3.06	2.51	1.85	2.06	2.30	2.33	2.78	3.49
	WW8	4.13	4.13	4.15	3.92	3.52	2.81	1.88	2.10	2.57	2.62	3.25	3.96
	WW9	4.09	4.32	4.15	4.09	3.86	2.93	2.27	2.48	2.72	2.96	3.58	4.09
	WW10	3.83	4.07	4.07	3.62	3.38	2.87	2.19	2.41	2.64	2.90	3.13	3.86
	WW11	3.88	4.12	4.12	3.88	3.83	2.74	1.87	1.87	2.32	2.52	3.40	3.88
	WW12	4.05	4.05	4.29	4.05	4.00	3.31	2.41	2.65	2.65	3.12	3.78	4.05
	WW13	4.03	4.03	4.27	4.03	4.03	3.34	2.44	2.68	2.68	3.16	3.82	4.03
Mill Creek Subbasin	MC14	4.45	4.45	4.45	4.69	4.69	4.72	4.49	4.49	4.72	4.72	4.49	4.45
	MC15	3.90	3.90	3.90	4.14	3.90	3.72	3.51	3.51	3.51	3.51	3.72	3.69
	MC16	3.91	3.91	4.14	4.14	3.91	3.69	2.95	2.95	3.19	3.48	3.93	3.91
	MC17	3.41	3.41	3.65	3.65	3.41	2.82	2.37	2.37	2.61	2.84	3.29	3.41
	MC18	3.08	3.08	3.32	3.32	2.87	2.15	1.49	1.49	1.73	1.97	2.59	2.87
	MC19	3.27	3.27	3.51	3.51	3.06	2.34	1.68	1.68	1.92	2.16	2.95	3.06
	MC20	3.23	3.23	3.47	3.47	3.02	2.30	1.64	1.64	1.88	2.12	2.57	3.02
	MC21	3.77	3.35	4.01	4.22	3.98	3.26	2.13	2.13	2.37	3.08	3.32	3.77
	YHC22	3.83	3.83	4.06	3.83	3.83	3.59	3.30	3.30	3.54	3.83	4.06	3.83

Poor Low Fair Good High

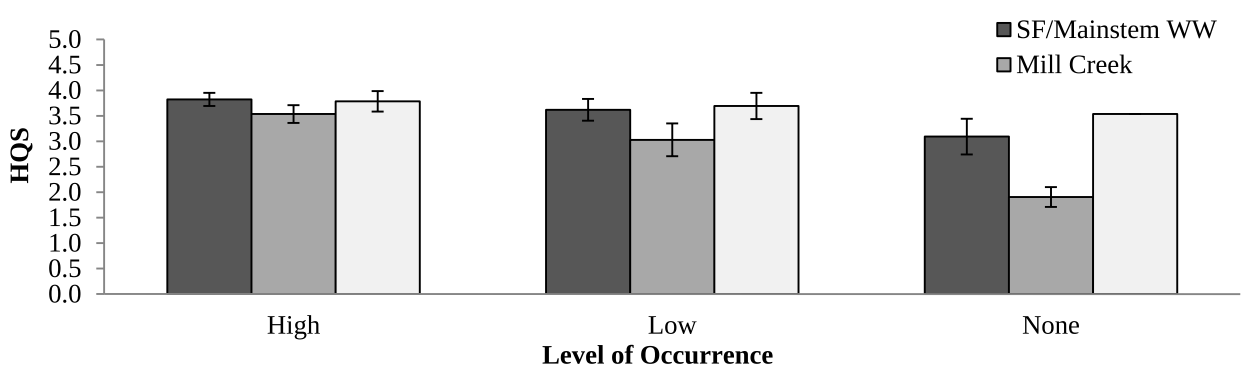

Figure 3.40. Mean habitat quality scores when occurrence of fluvial sub-adult downstream migration is high, low and not observed during time periods when occurrence is conceivable in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Table 3.41. Periodicity table comparing monthly habitat quality scores for fluvial sub-adult upstream migration with occurrence for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Cells outlined in red indicate when and where fluvial sub-adult upstream migration commonly occurs, purple indicates low occurrence and green indicates reaches and months when upstream movement may be conceivable, but does not occur or rarely is observed.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	4.30	4.30	4.30	4.30	4.30	4.34	4.34	4.34	4.34	4.34	4.34	4.30
	SFWW2	4.35	4.35	4.35	4.35	4.35	4.39	4.39	4.39	4.39	4.39	4.39	4.35
	SFWW3	4.65	4.65	4.65	4.65	4.60	4.64	4.64	4.64	4.64	4.64	4.64	4.65
	WW4	4.34	4.34	4.34	4.34	4.28	4.28	4.08	4.08	4.28	4.28	4.28	4.34
	WW5	4.03	4.03	4.03	4.03	3.97	3.97	3.58	3.77	3.97	3.97	3.97	4.03
	WW6	4.00	4.00	4.00	3.73	3.67	3.38	2.44	2.71	3.11	2.84	3.28	4.00
	WW7	3.75	3.75	3.75	3.48	3.26	2.73	1.79	2.06	2.26	2.38	2.66	3.75
	WW8	4.34	4.34	4.11	4.06	3.67	2.98	1.70	1.98	2.37	2.63	3.07	4.17
	WW9	4.29	4.29	4.12	4.29	4.06	3.10	2.15	2.43	2.82	3.02	3.46	4.29
	WW10	4.20	4.20	4.20	3.93	3.56	2.77	2.07	2.34	2.74	2.89	2.89	3.93
	WW11	4.10	4.10	4.10	4.10	4.05	2.92	1.70	1.70	2.17	2.46	3.23	4.10
	WW12	4.26	4.26	4.26	4.26	4.21	3.27	2.32	2.52	2.52	3.12	3.67	4.26
	WW13	4.26	4.26	4.26	4.26	4.26	3.32	2.38	2.58	2.58	3.17	3.72	4.26
Mill Creek Subbasin	MC14	4.57	4.57	4.57	4.57	4.57	4.61	4.61	4.61	4.61	4.61	4.61	4.57
	MC15	4.40	4.40	4.40	4.40	4.40	4.17	3.89	3.89	3.89	3.89	4.17	4.13
	MC16	4.19	4.19	4.19	4.19	4.19	3.75	2.82	2.82	3.22	3.48	3.75	4.19
	MC17	3.66	3.66	3.66	3.66	3.66	2.86	2.39	2.39	2.58	2.98	3.26	3.66
	MC18	3.28	3.28	3.28	3.28	3.01	2.12	1.37	1.37	1.57	1.97	2.41	3.01
	MC19	3.30	3.30	3.30	3.30	3.03	2.31	1.56	1.56	1.76	2.16	2.43	3.03
	MC20	3.42	3.42	3.42	3.42	3.15	2.26	1.51	1.51	1.71	2.11	2.55	3.15
	MC21	3.74	3.19	3.74	4.01	4.01	3.12	1.77	1.77	1.97	2.97	3.14	3.74
	YHC22	3.88	3.88	3.88	3.88	3.88	3.68	3.23	3.23	3.43	3.88	3.88	3.88

Poor | Low | Fair | Good | High

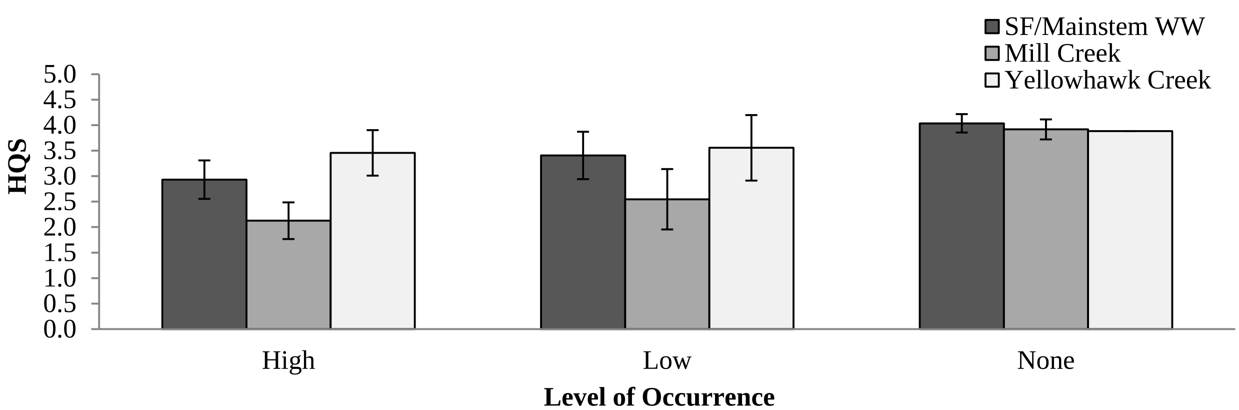

Figure 3.41. Mean habitat quality scores when occurrence of fluvial sub-adult upstream migration is high, low and not observed during time periods when occurrence is conceivable in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Table 3.42. Periodicity table comparing monthly habitat quality scores for fluvial sub-adult rearing, foraging and growth with occurrence for reaches in the South Fork and mainstem Walla Walla rivers as well as Mill and Yellowhawk creeks within the Walla Walla Basin. Cells outlined in red indicate when and where fluvial sub-adult rearing, foraging and growth commonly occurs, purple indicates low occurrence and green indicates reaches and months when upstream movement may be conceivable, but does not occur or rarely is observed.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walla Walla Subbasin	SFWW1	3.78	3.78	3.78	3.78	3.78	4.07	4.07	4.07	4.07	3.81	3.81	3.78
	SFWW2	3.80	3.80	3.80	3.80	4.07	4.09	4.09	4.09	4.09	4.09	3.83	3.80
	SFWW3	3.72	3.72	3.99	3.99	4.16	4.19	4.46	4.46	4.19	4.46	3.93	3.72
	WW4	3.57	3.57	3.84	3.84	4.01	4.28	4.01	4.01	4.01	3.75	3.75	3.57
	WW5	3.13	3.13	3.39	3.39	3.57	3.83	3.30	3.57	3.83	3.57	3.30	3.13
	WW6	3.14	3.14	3.41	3.20	3.37	3.55	2.61	2.81	3.34	2.87	2.81	3.14
	WW7	2.74	2.74	3.00	2.79	2.90	2.71	1.76	1.97	2.24	2.29	2.24	2.74
	WW8	3.45	3.45	3.56	3.78	3.54	3.28	2.04	2.25	2.78	2.87	2.88	3.38
	WW9	3.41	3.67	3.60	3.94	3.78	3.31	2.36	2.57	3.10	3.10	3.12	3.41
	WW10	3.20	3.47	3.47	3.53	3.53	2.87	2.23	2.44	2.97	2.92	2.66	3.26
	WW11	3.28	3.54	3.54	3.81	3.72	3.00	1.85	1.85	2.32	2.45	2.76	3.28
	WW12	3.31	3.31	3.57	3.84	4.01	3.00	2.05	2.32	2.32	2.85	3.00	3.31
	WW13	3.22	3.22	3.48	3.75	4.01	3.00	2.05	2.31	2.31	2.85	3.00	3.22
Mill Creek Subbasin	MC14	3.85	3.85	3.85	4.12	4.12	4.15	4.41	4.41	4.15	4.15	4.41	3.85
	MC15	3.37	3.37	3.37	3.64	3.90	3.72	3.78	3.78	3.51	3.51	3.19	3.16
	MC16	3.34	3.34	3.61	3.61	3.87	3.93	2.84	2.84	3.37	3.46	3.40	3.34
	MC17	2.62	2.62	2.88	2.88	3.41	2.63	2.16	2.16	2.42	2.69	2.63	2.62
	MC18	2.41	2.41	2.67	2.67	2.99	2.20	1.52	1.52	1.79	2.05	2.07	2.20
	MC19	2.41	2.41	2.67	2.67	2.99	2.21	1.52	1.52	1.79	2.05	2.14	2.20
	MC20	2.44	2.44	2.70	2.70	3.03	2.24	1.55	1.55	1.82	2.09	2.03	2.23
	MC21	3.03	2.61	3.29	3.50	4.03	3.24	2.06	2.06	2.32	3.09	2.83	3.03
	YHC22	3.20	3.20	3.46	3.73	3.73	3.73	3.11	3.11	3.37	3.73	3.46	3.20

Poor Low Fair Good High

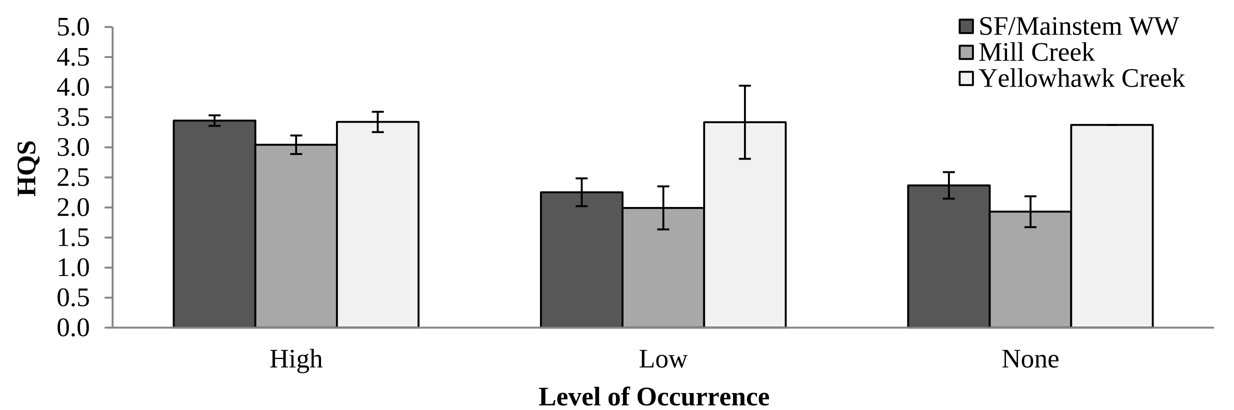

Figure 3.42. Mean habitat quality scores when occurrence of fluvial sub-adult rearing, foraging and growth is high, low and not observed during time periods when occurrence is conceivable in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.


Figure 3.43. High flow event at the downstream boundary of reach SFWW2 (Harris County Park Bridge – rkm 95.5).


Figure 3.44. Large log jam within reach SFWW2 that likely inhibits bull trout movement and likely limits migratory adult bull trout access to upstream spawning areas.

Figure 3.45. The City of Walla Walla Intake Dam and associated fish ladder at the downstream boundary of reach MC14 (rkm 44.2).

Figure 3.46. Picture depicting juvenile bull trout in off-channel habitat in the South Fork Walla Walla River.


Figure 3.47. Portion of the Walla Walla River influenced by backwater from the mainstem Columbia River (reach WW13).


Figure 3.48. Portion of the Walla Walla River (reach WW12).

Figure 3.49. Garden City-Old Lowden #2 Diversion Dam and associated fish ladder in reach WW11.

Figure 3.50. Burlingame Diversion Dam and associated fish ladder at the upstream boundary of reach WW10.

Figure 3.51. Photograph depicting one of many seasonal passage barriers that result from depleted surface flows within reaches WW8 and WW9.

Figure 3.52. Nursery Bridge Dam (rkm 73.1) on the Walla Walla River near Milton-Freewater, OR.

Figure 3.53. Levee section downstream of Nursery Bridge Dam (reach WW7) on the Walla Walla River near Milton-Freewater, OR.

Figure 3.54. Photographs depicting the inflatable dam (left), diversion canal (center) and fish ladder (right) at the Little Walla Walla Diversion facility (rkm 75.1) on the Walla Walla River near Milton-Freewater, OR.



Figure 3.55. Log jams in reaches SFWW2 (left) and SFWW1 (right).


Figure 3.56. Gose Street fish ladder in lower Mill Creek near Walla Walla, WA.


Figure 3.57. Stabilization sills in reach MC20 in lower Mill Creek near Walla Walla, WA.


Figure 3.58. Concrete flume in reach MC19 in Mill Creek near Walla Walla, WA.


Figure 3.59. Mill Creek Division Dam on Mill Creek near Walla Walla, WA.


Figure 3.60. Gabien-style concrete sills downstream of the Mill Creek Division Dam on Mill Creek near Walla Walla, WA.


Figure 3.61. Stabilization sills within reach MC17 in Mill Creek near Walla Walla, WA.


Figure 3.62. Mill Creek Diversion Dam on Mill Creek near Walla Walla, WA.

Figure 3.63. Low flow outlet and fish ladder entrance (left), eco-block separation wall (center) and impinged adult-sized bull trout (right) at the Mill Creek Diversion Dam in Mill Creek near Walla Walla, WA.

Figure 3.64. The City of Walla Walla Intake Dam in upper Mill Creek near Walla Walla, WA.

Figure 3.65. Pictured on the left, is an example of deep, slow water habitat common in the lower basin reaches in the mainstem Walla Walla River (left) near Lowden, WA. Habitat where bull trout have been located within the mainstem Columbia River upstream of McNary Dam near the Wallula Gap, WA (right).

Figure 3.66. Examples of pool-type habitat created by water control structures and diversion dams in middle and lower basin areas. Pictured are Nursery Bridge Dam (left), the Garden City-Old Lowden #2 diversion dam (center) and the Burlingame diversion dam (right) near Milton-Freewater, OR and Lowden, WA.

Figure 3.67. Scoured pools immediately downstream of stabilization sills within the flood control project in reach MC17 (approximately rkm 19) near Walla Walla, WA.

Figure 3.68. Deep water, pool-type habitat associated with Nursery Bridge Dam (rkm 73.1) in the reach WW7 within the mainstem Walla Walla River near Milton-Freewater, OR.

Figure 3.69. Example of stabilization sills near the downstream bound of reach MC18 (approximately rkm 15) as surface flows decline during early summer months in Mill Creek near Walla Walla, WA.

Figure 3.70. Examples of low flow barriers at riffles resulting from depleted instream surface flows that are common throughout the summer and early fall months within reach WW8 near Milton-Freewater, OR.

Figure 3.71. Example of unsuccessful avian predation that is commonly observed during summer sampling activities in middle basin reaches in the mainstem Walla Walla River near Milton-Freewater, OR.

Figure 3.72. Photographs of severely degraded habitat conditions within the Mill Creek Flood Control Project near Walla Walla, WA.

Figure 3.73. Improvements to fish passage in reach MC17 (left) and channel roughness/passage revisions within the concrete flume in reach MC19 in Mill Creek near Walla Walla, WA.

Appendix A: Reach Delineation

Table A1. Walla Walla River Subbasin reach delineation matrix.

Reach #	RKM	Major Tributaries	Major Diversions	Channel Modification	Land Use	Elevation	Stream Gradient	Geology
SFWW1	126			Not Modified	Forested	High	High	Uplands
	125			Not Modified	Forested	High	High	Uplands
	124	SFWWR Headwaters (rkm 125.4)		Not Modified	Forested	High	High	Uplands
	123			Not Modified	Forested	High	High	Uplands
	122			Not Modified	Forested	High	High	Uplands
	121			Not Modified	Forested	High	High	Uplands
	120			Not Modified	Forested	High	Medium	Uplands
	119			Not Modified	Forested	High	Medium	Uplands
	118			Not Modified	Forested	High	Medium	Uplands
	117			Not Modified	Forested	Medium	Medium	Uplands
	116	Reser Creek (rkm 115.6)		Not Modified	Forested	Medium	Medium	Uplands
SFWW2	115			Not Modified	Forested	Medium	Medium	Uplands
	114			Not Modified	Forested	Medium	Medium	Uplands
	113	Skiphorton Cr. (rkm 112.9)		Not Modified	Forested	Medium	Medium	Uplands
	112			Not Modified	Forested	Medium	Medium	Uplands
	111			Not Modified	Forested	Medium	Medium	Uplands
	110			Not Modified	Forested	Medium	Fairly Low	Uplands
	109			Not Modified	Forested	Medium	Fairly Low	Uplands
	108			Not Modified	Forested	Medium	Fairly Low	Uplands
	107			Not Modified	Forested	Medium	Fairly Low	Uplands
	106			Not Modified	Forested	Medium	Fairly Low	Uplands
	105			Not Modified	Forested	Medium	Fairly Low	Uplands
	104			Not Modified	Forested	Medium	Fairly Low	Uplands
	103			Not Modified	Forested	Medium	Fairly Low	Uplands
	102			Not Modified	Forested	Medium	Fairly Low	Uplands
	101			Not Modified	Forested	Medium	Fairly Low	Uplands
	100			Not Modified	Forested	Medium	Fairly Low	Uplands
	99			Not Modified	Forested	Medium	Fairly Low	Uplands
	98			Not Modified	Forested	Medium	Fairly Low	Uplands
	97	Harris Park Bridge (rkm 95.5)		Min. Modified	Forested	Medium	Fairly Low	Uplands
	96			Min. Modified	Forested	Medium	Fairly Low	Uplands
SFWW3	95			Min. Modified	Agr. - Pasture	Medium	Fairly Low	Uplands
	94			Min. Modified	Agr. - Pasture	Medium	Fairly Low	Uplands
	93			Min. Modified	Agr. - Pasture	Medium	Fairly Low	Uplands
	92			Min. Modified	Agr. - Pasture	Medium	Fairly Low	Uplands
	91			Min. Modified	Agr. - Pasture	Medium	Fairly Low	Uplands
	90			Min. Modified	Agr. - Pasture	Medium	Fairly Low	Uplands
	89			Min. Modified	Agr. - Pasture	Low	Fairly Low	Uplands
	88			Min. Modified	Agr. - Pasture	Low	Fairly Low	Uplands
	87			Min. Modified	Agr. - Orch/Vin	Low	Fairly Low	Uplands
	86			Min. Modified	Agr. - Orch/Vin	Low	Fairly Low	Uplands
	85			Min. Modified	Agr. - Orch/Vin	Low	Fairly Low	Uplands
	84	N.F. WW River (rkm 82.9)		Min. Modified	Agr. - Orch/Vin	Low	Fairly Low	Foothills
	83			Min. Modified	Agr. - Orch/Vin	Low	Fairly Low	Foothills
WW4	82			Min. Modified	Agr. - Orch/Vin	Low	Fairly Low	Foothills
	81			Min. Modified	Agr. - Orch/Vin	Low	Fairly Low	Foothills
	80			Min. Modified	Agr. - Orch/Vin	Low	Fairly Low	Foothills
	79	Couse Cr. (rkm 78.1)		Highly Modified	Agr. - Orch/Vin	Low	Fairly Low	Foothills
WW5	78			Highly Modified	Urban Devel.	Low	Fairly Low	Foothills
	77			Highly Modified	Urban Devel.	Low	Fairly Low	Foothills
	76		LWWR Diversion (rkm 75.1)	Highly Modified	Urban Devel.	Low	Fairly Low	Low Lands
WW6	75			Highly Modified	Urban Devel.	Low	Fairly Low	Low Lands
	74		East Side Diversion (rkm 73.1)	Highly Modified	Urban Devel.	Low	Fairly Low	Low Lands
WW7	73			Highly Modified	Agr. - Row Crops	Low	Fairly Low	Low Lands
	72			Highly Modified	Agr. - Row Crops	Low	Fairly Low	Low Lands
	71			Highly Modified	Agr. - Row Crops	Low	Fairly Low	Low Lands
	70	End of Levy - Tumalum Br. (rkm 69.3)		Highly Modified	Agr. - Row Crops	Low	Fairly Low	Low Lands

	69			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	68			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	67			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
WW8	66			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	65			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	64	Yellowhawk Cr. (rkm 62.9)		Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	63			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	62			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
WW9	61		Burlingame Diversion (rkm 60.3)	Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	60			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	59			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	58			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
WW10	57			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	56			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	55	Mill Creek (rkm 54.8)		Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	54			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	53			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	52			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	51		Garden City - Lowden #2	Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	50			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	49			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	48			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	47			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	46		Diversion (rkm 46)	Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	45			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
WW11	44			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	43			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	42			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	41			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	40			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	39			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	38			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	37			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	36			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	35			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	34			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	33			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	32	Touchet River (rkm 31.3)		Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	31			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	30			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	29			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	28			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	27			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	26			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	25			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	24			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	23			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	22			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	21			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
WW12	20			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	19			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	18			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	17			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	16			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	15			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	14			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	13			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	12			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	11			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	10			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	9			Moderate Mod.	Agr. - Row Crops	Low	Low	Low Lands
	8	Backwater influence (rkm 8.0)		Moderate Mod.	Wildlife Refuge	Low	Low	Low Lands
	7			Moderate Mod.	Wildlife Refuge	Low	Low	Low Lands
	6			Moderate Mod.	Wildlife Refuge	Low	Low	Low Lands
WW13	5			Moderate Mod.	Wildlife Refuge	Low	Low	Low Lands
	4			Moderate Mod.	Wildlife Refuge	Low	Low	Low Lands
	3			Moderate Mod.	Wildlife Refuge	Low	Low	Low Lands
	2			Moderate Mod.	Wildlife Refuge	Low	Low	Low Lands
	1			Moderate Mod.	Wildlife Refuge	Low	Low	Low Lands
	0			Moderate Mod.	Wildlife Refuge	Low	Low	Low Lands

Table A2. Mill Creek Subbasin reach delineation matrix.

Reach #	RKM	Major Tributaries	Major Diversions	Channel Modification	Land Use	Elevation	Stream Gradient	Geology
MC14	59			Not Modified	Forested	Fairly High	High	Uplands
	58	Mill Creek Headwaters (rkm 58.7)		Not Modified	Forested	Fairly High	High	Uplands
	57			Not Modified	Forested	Fairly High	High	Uplands
	56			Not Modified	Forested	Fairly High	High	Uplands
	55			Not Modified	Forested	Fairly High	High	Uplands
	54			Not Modified	Forested	Fairly High	High	Uplands
	53			Not Modified	Forested	Fairly High	High	Uplands
	52			Not Modified	Forested	Fairly High	High	Uplands
	51			Not Modified	Forested	Fairly High	High	Uplands
	50			Not Modified	Forested	Fairly High	Fairly Low	Uplands
	49			Not Modified	Forested	Fairly High	Fairly Low	Uplands
	48			Not Modified	Forested	Medium	Fairly Low	Uplands
	47			Not Modified	Forested	Medium	Fairly Low	Uplands
	46			Not Modified	Forested	Medium	Fairly Low	Uplands
	45		Mill Creek Intake Dam (rkm 44.2)	Not Modified	Forested	Medium	Fairly Low	Uplands
MC15	44			Moderate	Forested	Medium	Fairly Low	Uplands
	43			Moderate	Forested	Medium	Fairly Low	Uplands
	42			Moderate	Forested	Medium	Fairly Low	Uplands
	41			Moderate	Forested	Medium	Fairly Low	Uplands
	40			Moderate	Forested	Fairly Low	Fairly Low	Uplands
	39			Moderate	Forested	Fairly Low	Fairly Low	Uplands
	38			Moderate	Forested	Fairly Low	Fairly Low	Uplands
	37			Moderate	Forested	Fairly Low	Fairly Low	Uplands
	36			Moderate	Forested	Fairly Low	Fairly Low	Uplands
	35			Moderate	Forested	Fairly Low	Fairly Low	Foothills
	34			Moderate	Urban Development	Fairly Low	Fairly Low	Foothills
	33			Moderate	Urban Development	Fairly Low	Fairly Low	Foothills
	32			Moderate	Forested	Fairly Low	Fairly Low	Foothills
	31			Moderate	Forested	Fairly Low	Fairly Low	Foothills
	30	Blue Creek (rkm 29.7)		Moderate	Forested	Fairly Low	Fairly Low	Foothills
MC16	29			Moderate	Agr. - Row Crops	Fairly Low	Fairly Low	Low Lands
	28			Moderate	Agr. - Row Crops	Fairly Low	Fairly Low	Low Lands
	27			Moderate	Agr. - Row Crops	Fairly Low	Fairly Low	Low Lands
	26			Moderate	Agr. - Row Crops	Fairly Low	Fairly Low	Low Lands
	25			Moderate	Agr. - Row Crops	Low	Fairly Low	Low Lands
	24			Moderate	Agr. - Row Crops	Low	Fairly Low	Low Lands
	23			Moderate	Agr. - Row Crops	Low	Fairly Low	Low Lands
	22			Moderate	Agr. - Row Crops	Low	Fairly Low	Low Lands
	21			Moderate	Agr. - Row Crops	Low	Fairly Low	Low Lands
MC17	20		Mill Cr. Diversion (rkm 20.1)	Highly Mod.	Urban Development	Low	Fairly Low	Low Lands
	19			Highly Mod.	Urban Development	Low	Fairly Low	Low Lands
MC18	18		Mill Cr. Division Dam (rkm 18.5)	Highly Mod.	Urban Development	Low	Fairly Low	Low Lands
	17			Highly Mod.	Urban Development	Low	Fairly Low	Low Lands
	16			Highly Mod.	Urban Development	Low	Fairly Low	Low Lands
MC19	15			Severely Mod.	Urban Development	Low	Fairly Low	Low Lands
	14			Severely Mod.	Urban Development	Low	Fairly Low	Low Lands
	13			Severely Mod.	Urban Development	Low	Fairly Low	Low Lands
	12			Severely Mod.	Urban Development	Low	Fairly Low	Low Lands
MC20	11			Highly Mod.	Urban Development	Low	Fairly Low	Low Lands
	10			Highly Mod.	Urban Development	Low	Low	Low Lands
	9			Highly Mod.	Urban Development	Low	Low	Low Lands

	8			Moderate	Agr. - Row Crops	Low	Low	Low Lands
	7			Moderate	Agr. - Row Crops	Low	Low	Low Lands
	6			Moderate	Agr. - Row Crops	Low	Low	Low Lands
	5			Moderate	Agr. - Row Crops	Low	Low	Low Lands
MC21	4			Moderate	Agr. - Row Crops	Low	Low	Low Lands
	3			Moderate	Agr. - Row Crops	Low	Low	Low Lands
	2			Moderate	Agr. - Row Crops	Low	Low	Low Lands
	1			Moderate	Agr. - Row Crops	Low	Low	Low Lands
	0			Moderate	Agr. - Row Crops	Low	Low	Low Lands

Table A3. Yellowhawk Creek reach delineation matrix.

Reach #	RKM	Major Tributaries	Major Diversions	Channel Modification	Land Use	Elevation	Stream Gradient	Geology
YHC22	14	Yellowhawk Headgate (rkm 14.5)	Garrison Cr. Diversion	Moderate	Agriculture - Row Crops	Low	Low	Low Lands
	13			Moderate	Agriculture - Row Crops	Low	Low	Low Lands
	12			Moderate	Agriculture - Row Crops	Low	Low	Low Lands
	11			Moderate	Urban Development	Low	Low	Low Lands
	10			Moderate	Urban Development	Low	Low	Low Lands
	9			Moderate	Agriculture - Row Crops	Low	Low	Low Lands
	8			Moderate	Agriculture - Row Crops	Low	Low	Low Lands
	7			Moderate	Agriculture - Row Crops	Low	Low	Low Lands
	6			Moderate	Agriculture - Row Crops	Low	Low	Low Lands
	5			Moderate	Agriculture - Row Crops	Low	Low	Low Lands
	4			Moderate	Agriculture - Row Crops	Low	Low	Low Lands
	3			Moderate	Agriculture - Row Crops	Low	Low	Low Lands
	2			Moderate	Agriculture - Row Crops	Low	Low	Low Lands
	1			Moderate	Agriculture - Row Crops	Low	Low	Low Lands
	0	Confluence with Walla Walla River		Moderate	Agriculture - Row Crops	Low	Low	Low Lands

Appendix B: Primary Questionnaire

Table B1. Example of primary questionnaire for ranking variables and populating the pair wise comparison matrix.

Factor			More Importance Than…						Factor Weighting Score Equal			Less Importance Than…							Factor
HV1	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV2**
HV2	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV3**
HV3	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV4**
HV4	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV5**
HV5	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV6**
HV6	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV7**
HV7	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV8**
HV8	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV9**
HV9	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV10**
HV10	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV11**
HV1	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV3**
HV2	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV4**
HV3	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV5**
HV4	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV6**
HV5	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV7**
HV6	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV8**
HV7	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV9**
HV8	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV10**
HV9	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV11**
HV1	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV4**
HV2	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV5**
HV3	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV6**
HV4	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV7**
HV5	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV8**
HV6	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV9**
HV7	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV10**
HV8	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV11**
HV1	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV5**
HV2	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV6**
HV3	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV7**
HV4	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV8**
HV5	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV9**
HV6	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV10**
HV7	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV11**
HV1	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV6**
HV2	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV7**
HV3	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV8**
HV4	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV9**
HV5	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV10**
HV6	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV11**
HV1	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV7**
HV2	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV8**
HV3	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV9**
HV4	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV10**
HV5	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV11**
HV1	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV8**
HV2	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV9**
HV3	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV10**
HV4	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV11**
HV1	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV9**
HV2	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV10**
HV3	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV11**
HV1	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV10**
HV2	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV11**
HV1	10	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8	9	10	**HV11**

Appendix C: Reach-specific Narratives

This appendix contains descriptive details on each of the 22 delineated river reaches in the SFWWR and the WWR, as well as MC and YHC to characterize riverine habitat to help inform current bull trout status, effectiveness of recovery actions and to help prioritize and guide future recovery actions. Available biological, chemical, riparian, geomorphic and hydrologic data were used to temporally describe environmental conditions at the reach scale.

SFWW1

Located within the Umatilla National Forest, this 9.8 km, nearly pristine reach of the SFWWR includes the headwaters from approximately rkm 124 to its downstream boundary at the Reser Creek confluence (rkm 115.6). This relatively high elevation, high gradient stream segment runs through a coniferous forested canyon, characterized by steep slopes, intact riparian canopy and a complex stream channel. Although influenced by snowpack and variable seasonal precipitation, constant groundwater influx and small tributaries drive flows within this reach. Adequate, year-round streamflows and cool water temperatures provide suitable habitat conditions for all bull trout life stages and strategies. This reach is designated as critical bull trout spawning and rearing habitat and is essentially free of channel modifications and anthropogenic influences largely due to its remote disposition and limited access. The collective habitat characteristics of this reach may lessen the direct effects of changing climatic trends than in other, less pristine reaches within the Basin.

SFWW2

This 20.1 km, relatively pristine reach of the SFWWR is bounded upstream by the confluence of Reser Creek (rkm 115.6), and flows through coniferous forest canopy to Harris Park Bridge (rkm 95.5). The lower bounds of this reach marks a notable change in ownership from government owned and managed property (U. S. Forest Service, Bureau of Land Management and Umatilla County) to primarily private landownership. With this change in ownership, land use also distinctly changes from protected, forested land to primarily rural pasture for livestock. Streamflow within this reach incrementally increases downstream with the contribution from small, perennial and seasonal tributaries including: Reser, Skiphorton, Table, Burnt Cabin, Bear and Elbow Creeks. Seasonal flows are influenced by snowpack and variable precipitation. Summer base flows near the downstream end of this reach average over 100 cfs, providing reliable, year-round, cool water conditions for all bull trout life stages and strategies. This reach of the SFWWR is designated as critical bull trout spawning and rearing habitat and houses the majority of known spawning areas, which include portions of Skiphorton and Reser Creeks. Habitat conditions within this middle elevation and moderate gradient reach are characterized by intact riparian canopy and high channel complexity, ample large woody debris, as well as minimal channel confinement or modification. The relatively pristine nature and hydrologic regime of this reach may make it less prone to the direct effects of climate change than other, more modified reaches within the Basin.

SFWW3

Downstream from the Harris Park Bridge (rkm 95.5) to the confluence of the NFWWR (rkm 82.9), the steepness of canyon slopes decreases, valley bottoms widen and accordingly the stream gradient lessens. This geomorphic transition marks a shift in land-use from forested, sparsely disturbed reaches to that of agricultural pasture land, orchards and vineyards, as evidenced by cleared vegetation and altered riparian zones. Although a mixed coniferous and deciduous canopy lines most of the immediate river channel, much of the valley bottom has been cleared and the river is disconnected from its flood plain in many areas. As elevation decreases, climatic conditions generally become warmer and drier. Data collected during "seepage runs" categorized this reach of the SFWWR as primarily a gaining reach (Bower 2007). Within this 12.6 km upland reach, the presence of agricultural and rural development associates the need for irrigation, in addition to bank armoring and channel straightening to maintain fields, roads and bridges. Although surface water is tapped for livestock and irrigation purposes, withdrawals within this reach are minimal compared to further downstream reaches. Bull trout spawning may occur within this reach, but it is likely limited if it occurs at all. Habitat in this reach has been designated as critical foraging, migration and overwintering habitat for fluvial adult and sub-adult bull trout (USFWS 2010). No major tributaries contribute to flow in this reach until the NFWWR enters at the downstream boundary. The magnitude of the river and habitat characteristics within this reach may increase its resiliency to the direct effects of climate change.

WW4

From the confluence of the North and South Forks (rkm 82.9), downstream through a valley bottom amongst rolling foothills, this 4.8 km reach flows through land primarily used for orchards and vineyards. The downstream boundary of this reach (rkm 78.1) is delineated by the upstream end of a major flood control levee that represents a radical, anthropogenic change to the riverine habitat. The aquatic habitat within this relatively low elevation, low gradient stream segment is influenced by a notable increase in rural development, channel modification and the river is largely disconnect from its floodplain. Primarily deciduous riparian vegetation lines most of the river channel, but much of the valley bottom has been cleared for agricultural and rural development. Recently, a sizeable riparian restoration project, catalyzed and facilitated by the Confederated Tribes of the Umatilla Indian Reservation, was implemented within this reach. Completed by 2011, this project removed almost 800 m of levee, restoring the river's access to a portion of its historic floodplain and established a 335 m, perennial side channel to increase aquatic habitat quantity and quality within this reach. The NFWWR contributes perennial flow to the mainstem at the head of this reach, but no other significant tributaries or diversions influence instream flows. This reach is generally warmer and drier than higher elevation areas and surface water is withdrawn for agricultural needs. Habitat in this reach has been designated as critical foraging, migration and overwintering habitat for fluvial adult and sub-adult bull trout. No major tributaries contribute to flow in this reach until the NFWWR enters at the downstream boundary. The size of the river and the remaining quality of habitat may provide enough thermal buffering capacity to lessen the direct effects of climate change.

WW5

Beginning at rkm 78.1 and continuing downstream for 3 km, this extensively modified, low elevation, low gradient reach of the WWR is confined on both banks by a flood control levee. Severe channel modifications (e.g. straightening, bank armoring) and riparian vegetation removal characterize this reach. Although the levee section continues past 3 km, the Little WWR Diversion (rkm 75.1) depletes river flows during the irrigation season (April – October), marking a clear, seasonal change in macrohabitat conditions. Couse Creek, which enters the WWR near the upstream end, is the only major tributary to this reach. The WWR tracks the eastern boundary of Milton-Freewater, Oregon, and is influenced by urban development to the west and row-crops to the east. Summer water temperatures exceed those of upstream reaches, but the water volume, remnant streamside vegetation and groundwater influx somewhat buffer the effects of solar radiative heating. This reach is designated as critical foraging, migrating and overwintering habitat for bull trout.

WW6

The Little Walla Walla Diversion (rkm 75.1) seasonally diverts the majority of surface flows during the irrigation season (April to October), bypassing only enough during summer base flows to ensure a minimum of 25 cfs is measured at the end of this reach near Nursery Bridge Dam (rkm 73.1). The physical habitat within this highly modified, 2 km reach is relatively similar to the adjacent segment upstream but the seasonal lack of surface flows distinctly differentiates it. Severe straightening of the stream channel, armoring of the banks, vegetation alteration and a general lack of channel complexity characterizes this reach. Data collected during seepage runs (Bower 2007) indicated that this reach of the WWR is a losing reach. A barrier to fish migration (Smith Grade Control Sill) existed during low flows, and was removed during 2012. Summer water temperatures exceed those of upstream reaches. The remnant streamside vegetation creates only a minimal buffer to thermal heating. This combined with artificially low discharge and the loss of surface to subsurface flows in this reach results in exacerbated water temperatures. This reach is designated as critical foraging, migrating and overwintering habitat for bull trout.

WW7

The Nursery Bridge Dam (rkm 73.1) is the upstream bound of this reach. In combination with downstream levees, it provides flood control for the City of Milton-Freewater, OR and the surrounding agricultural land. The Dam consists of two permanent concrete gravity dams with a 70 foot stilling basin between them that dissipates hydrologic energy, especially during high flow events. Prior to 2001, fish passage at the Nursery Bridge Dam was considered inadequate for migratory fish species. A new fish ladder was completed in 2001 to facilitate upstream passage of bull trout and other migratory salmonids. The East Side Diversion draws water for seasonal irrigation just upstream from the Nursery Bridge Dam leaving a minimum of 25 cfs instream at the head of this reach. Seepage runs indicate that this reach is a losing reach and at times, more than half of the bypassed surface water becomes subsurface prior to reaching the end of the reach at Tumalum Bridge (rkm 69.3). The habitat within this highly modified, 3.8 km reach is similar to the adjacent, upstream segment, but is differentiated by more intensive vegetation management on and along its control structures. In addition, the levee in this reach is much larger (e.g. wider), and the highly degraded aquatic habitat is almost entirely unshaded. The lack of riparian complexity, channel modification and seasonal dewatering contribute to elevated stream temperatures within this reach.   The poor quality of riparian habitat and lack of summer discharge likely provide very little thermal buffering capacity, thus exposing this reach to many of the direct effects of climate change. This reach is designated as critical foraging, migrating and overwintering habitat for bull trout.

WW8

This 6.4 km reach of the WWR is bounded upstream by the downriver end of the flood control levee (rkm 69.3) and flows through a corridor of relatively intact riparian canopy to its confluence with YHC (rkm 62.9). Primarily row crops to the east and small, residential pastures to the west sheath the relatively narrow riparian zone. Despite being influenced by occasional erosion control measures (e.g. bank armoring), the river is allowed at least some ability to meander freely within its immediate floodplain, alternately eroding and depositing sediments. Increased sinuosity and improved riparian function distinctly differentiates this reach from the adjacent, upstream segment. Hyporheic exchange and the notable influx of groundwater contribute to its categorization as a gaining reach (Bower 2007). Thermal buffering by mature riparian vegetation and the influence of groundwater reduce the rate at which river temperatures increase through this reach.. The influence of groundwater may provide pockets of thermal refugia during winter months as well. The natural processes of scouring and subsequent deposition that occur during elevated flows, result in higher channel complexity and function within this reach. Unfortunately, severely reduced seasonal surface flows within this reach create numerous barriers at hydraulic controls (e.g. riffles). Under a more natural flow regime, the depth of surface flows at riffles would likely not impede seasonal salmonid migration. This reach is designated as critical foraging, migrating and overwintering habitat for bull trout.

WW9

From its confluence with YHC (rkm 62.9), downstream through a narrow, but relatively intact riparian zone, this reach of the WWR is bordered on both banks by primarily row crop agriculture. This 2.6 km reach terminates at the Burlingame Diversion Dam (rkm 60.3), the largest irrigation diversion in the Washington portion of the river. Seepage runs determined this portion of the WWR to be within a losing reach. Surface flow from MC is diverted into YHC at the Mill Creek Division Dam to satisfy senior water rights in addition to providing an important migration corridor for bull trout and other migratory salmonids between MC and the WWR. During summer months, almost all of the surface flow from MC is diverted to the YHC distributary and eventually discharges into the mainstem WWR at the head of this reach. This reach is critical foraging, migration and overwintering habitat for bull trout. At the onset of summer base flows, both adult and sub-adult bull trout utilize this reach to escape deteriorating habitat conditions resulting from elevated water temperatures and low surface flows. The inflow from YHC, albeit small, contributes significantly to depleted surface flows during summer and fall months, reducing the occurrence of low flow barriers and facilitating bull trout movement. Similarly, the East Little WWR seasonally contributes between approximately 5 and 20 cfs of groundwater influenced surface water to this reach. Brook trout have been observed and captured in multiple reaches within the East Big Spring Branch of the East Little Walla Walla River. Multiple year classes were observed, indicative of an established, self-sustaining brook trout population. The Bull Trout Draft Recovery Plan (USFWS 2002) identifies the presence of brook trout within a bull trout core area as a major threat to the long-term persistence and eventual recovery of bull trout populations. To date, there has been no indication that brook trout enter and occupy this reach of the WWR, possibly due to seasonal habitat limitations

WW10

This 5.6 km reach of the WWR is bounded upstream by the Burlingame Diversion Dam (rkm 60.3) and flows through corridor of relatively intact riparian canopy to its confluence with MC (rkm 54.5). The riparian zone in this reach is wider than adjacent habitat segments. Row crops dominate the landscape and seepage runs seepage runs determined that this portion of the WWR is within a losing reach. The Burlingame Dam diverts water for irrigation during the spring and early summer months, ensuring a minimum of 18 cfs is bypassed downstream. Surface flows during summer months generally are insufficient to divert water throughout much of July, August and September. Water diversion usually resumes in October and continues until January most years. This reach is critical foraging, migration and overwintering habitat for bull trout. At the onset of summer base flows, both adult and sub-adult bull trout utilize this reach to escape deteriorating habitat conditions resulting from elevated water temperatures and low surface flows in the lower river. The diversion dam is equipped with a fish ladder.

WW11

From its confluence with MC (rkm 54.8), downstream through approximately 23.5 km of row crop farmland, this low gradient, low elevation reach of the WWR is a gaining reach, designated as critical foraging, migration and overwintering habitat for bull trout. The downstream end of this reach is the Touchet River confluence (rkm 31.3). In the upper portion of this reach, riparian habitat is notably less intact and considerably narrower than the downstream portion. At approximately rkm 42, sinuosity markedly increases, side channels are common and the river is allowed to meander somewhat freely within its immediate flood plain. Although certain intra-reach habitat characteristics differ, the main attributes used to delineate habitat reaches indicate a relatively homogenous segment that differs from neighboring segments primarily due to hydrologic characteristics (e.g. major tributaries and diversions). MC is a major tributary to this reach and aside from smaller irrigation withdrawals (e.g. Garden City – Lowden #2) and temporary push-up diversions, no major diversions exist. Diversions upstream from this reach seasonally reduce surface flows within this reach, likely contributing to warmer water temperatures, migratory difficulties and possibly increasing exposure to predation.

WW12

From its confluence with the Touchet River (rkm 31.3), downstream through a willow-lined riparian zone, almost void of mature canopy trees, this reach of the WWR is bordered to the northeast by primarily row crop agriculture and to the southeast by pasture land. This approximately 23.3 km reach terminates where the river is influenced by backwater from the Columbia River (rkm 8). This low elevation, low gradient losing reach is moderately confined by bank armoring, roads and railroad tracks and is allowed to meander to some extent within its immediate flood plain. The riverbed throughout much of this reach consists of deposited gravel, cobble and silt perched upon frequently exposed basalt bedrock. During summer and fall months, upstream irrigation diversions in both the Walla Walla and Touchet rivers greatly reduce instream flows within this reach. This portion of the WWR is often subject to substantial freshets during winter and spring months due to its lower basin disposition and the influence from the Touchet River. The absence of an intact, mature riparian canopy and lack of summer discharge likely provide very little thermal buffering capacity, thus exposing this reach to many of the direct effects of climate change. This reach is designated as critical foraging, migrating and overwintering habitat for bull trout.

WW13

Almost the entire 8 km reach is located within the Wallula Unit of the McNary National Wildlife Refuge from rkm 8 to its confluence with the Columbia River (rkm 0). This low elevation, low gradient reach is heavily influenced by backwater from the Columbia River, distinguishing it from all other reaches within the Walla Walla Basin. This is a highly depositional reach due largely to the influence from the Columbia River. The relatively slow, deep channel lacks complexity and mature riparian canopy. Multiple, off-channel areas (e.g. ponds and wetlands) exist and are managed primarily for waterfowl habitat. There are no major irrigation withdrawals, only small, screened pump stations to seasonally fill ponds for waterfowl. The absence of mature riparian canopy vegetation and a lack of discharge likely provide very little thermal buffering capacity during the summer. This may expose this reach to many of the direct effects of climate change. This reach is designated as critical foraging, migrating and overwintering habitat for bull trout.

MC14

Located within the Umatilla National Forest, this 14.6 km, nearly pristine reach of MC includes the headwaters from approximately rkm 58.7 to its downstream boundary at the City of Walla Walla Intake Dam (rkm 44.2). This relatively high elevation, high gradient stream segment runs through a coniferous forested canyon, characterized by steep slopes, intact riparian canopy and a complex stream channel. Although influenced by snowpack and variable seasonal precipitation, constant groundwater influx and small tributaries drive flows within this reach. Adequate, year-round streamflows and cool water temperatures provide suitable habitat conditions for all bull trout life stages and strategies. This reach is designated as critical bull trout spawning and rearing habitat and is essentially free of channel modifications and anthropogenic influences largely due to its remote disposition and restricted access. A portion of the streamflow is diverted for municipal use at the downstream end of this reach. The collective habitat characteristics of this reach may lessen the direct effects of changing climatic trends than in other, less pristine reaches within the Basin.

MC15

This 14.4 km reach of MC is bounded upstream by the City of Walla Walla Intake Dam (rkm 44.2), and flows through coniferous forest canopy before transitioning to a primarily deciduous riparian zone before reaching the Blue Creek confluence (rkm 29.7). The lower bounds of this reach marks a notable geological change from forested uplands to rolling foothills. Private landownership is prevalent and land use is mostly rural residential with sporadic orchards and pasture land intermixed. Mill Creek flows through a short, highly channelized residential stretch from approximately rkm 34 to 33. Although mature canopy lines most of the immediate river channel, much of the valley bottom has been altered and the river is disconnected and moderately channelized, disconnecting it from its flood plain in many areas. As elevation decreases, climatic conditions generally become warmer and drier. Aside from the municipal water withdrawal at the head of this reach, other diversions for irrigation are small. Bull trout spawning near the head of this reach has been documented, but likely is limited. This reach has been designated as critical foraging, migration and overwintering habitat for fluvial adult and sub-adult bull trout (USFWS 2010). Only small tributaries contribute to surface flow in this reach until Blue Creek enters at the downstream boundary. The collective habitat characteristics within this reach, may buffer the direct effects of climate change.

MC16

Downstream from the Blue Creek confluence (rkm 29.7) to the Mill Creek Diversion Dam (rkm 20.1), the steepness of canyon slopes decreases, valley bottoms widen and accordingly the stream gradient lessens. This transition marks a shift in land-use from relatively forested, moderately disturbed reaches to that of primarily row-crop agriculture and vineyards. A largely deciduous canopy lines most of the immediate river channel, but much of the valley bottom has been cleared for farmland and the river is disconnected from its flood plain in many areas. This portion of MC has been determined to be primarily a losing reach. Aside from the influence of Blue Creek at the head of the reach, no major tributaries contribute to surface flows. The habitat characteristics within this reach, may buffer some of the direct influences associated with climate change.

MC17

The Mill Creek Diversion Dam (rkm 20.1) is the upstream bound of this reach. It is a diversion structure that marks the upstream end of the Mill Creek Flood Control Project for the City of Walla Walla, constructed in 1942 by the US Army Corps of Engineers. During extreme flood events, water is shunted to an off stream storage dam (Bennington Lake), otherwise MC surface flows enter an approximately 30 m wide flood control channel. Within this reach, there are 80 concrete stabilization sills spaced approximately 18 m apart that dissipate energy during high flows. Pools have been scoured out downstream from each of the concrete weirs providing limited, unnatural habitat. As summer streamflow drops to base levels, movement of fish though this section is severely restricted, and may confine fish to areas where temperatures may become lethal and exposure to predation will likely be increased. This reach is highly channelized, lacks complexity, is disconnected from its natural floodplain by dykes on both banks, and riparian canopy is absent. Water is diverted to YHC during all months of the year, but during summer months, the majority of MC surface flows are diverted at the Mill Creek Division Dam (rkm 18.5), effectively dewatering the downstream segment. The lack of riparian complexity and channel modification contribute to elevated stream temperatures within this reach. The poor quality of riparian habitat and lack of summer discharge likely provide very little thermal buffering capacity, thus exposing this reach to many of the direct effects of climate change. This reach is designated as critical foraging, migrating and overwintering habitat for bull trout.

MC18

The Mill Creek Division Dam (rkm 18.5) marks the upstream boundary of this reach. At this location, surface water is diverted from MC down the YHC and Garrison creek distributaries during all months of the year to augment irrigation withdrawals and to provide fish passage. As MC reaches base summer flows, almost all surface flow is diverted down YHC and Garrison Creeks, effectively dewatering the reach. This reach is similar to the upstream reach in that it is a flood control channel with concrete stabilization sills. There are 77 concrete capped gabian style sills in this reach that are spaced from 21.3 to 62.5 m apart with lengths that vary from 21.3 to 167.6 m (Burns et al. 2009). The channel widens the wetted width, limits fish movement, affects water temperatures and likely exposes bull trout to increased predation This channelized reach lacks complexity, is disconnected from its natural floodplain by dykes on both banks and riparian canopy is absent. The downstream boundary of this 3.3 km reach is at rkm 15.2, where the MC channel is transitioned into a concrete flume. This reach is designated as critical foraging, migrating and overwintering habitat for bull trout.

MC19

Beginning at rkm 15.2 and continuing downstream for 3.2 km, this extensively modified and confined reach of MC is transitioned into a concrete flume, which is an open channel with a low flow trench down the center that varies from 2.7 to 4.6 m wide and is approximately 0.5 m deep. Some portions of the channel are split while others remain a single flume. Some sections of the flume run underground and remain completely dark. As MC reaches base summer flows, almost all surface flow is diverted down YHC and Garrison Creek, largely dewatering this reach. At low flows, all of the water is contained in the trench where concrete baffles are spaced between 18.2 and 30.5 m (Burns et al. 2009). At higher discharge, water flows outside this trench along sloped overbank areas. Regardless of flume geometry and channel type, the function in terms of bull trout habitat is similar. The relative uniformity of the flume results in very low channel complexity and velocities at times impede fish movement. Holding water is lacking, no substrate exists, there is no floodplain or hyporheic interaction and very limited riparian canopy. At rkm 12.0, a transition from concrete flume to channel sills marks the downstream end of this reach. This portion of MC is designated as critical foraging, migrating and overwintering habitat for bull trout.

MC20

Mill Creek transitions from a concrete flume to channel sills at rkm 12.0, marking the upstream boundary of this reach. Within this reach, there are 145 stabilization sills (91 sheet pile and 54 concrete capped) that are spaced 21.3 m apart and are approximately 21.3 m long (Burns et al. 2009). These sills dissipate energy during high flows. Pools have been scoured out downstream from each of the concrete weirs providing limited, unnatural habitat. As summer streamflow drops to base levels, movement of fish though this section is severely restricted, and may confine fish to areas where temperatures may become lethal and exposure to predation will likely be increased. This reach is highly channelized, lacks complexity, is disconnected from its natural floodplain by dykes on both banks, and riparian canopy is absent. This portion of MC is designated as critical foraging, migrating and overwintering habitat for bull trout. The point at which MC transitions from channel sills to a more natural functioning stream reach (rkm 8.9) marks the downstream boundary of this reach.

MC21

This 8.9 km reach of MC is bounded upstream by the downriver end of the Mill Creek Flood Control Project for the City of Walla Walla (rkm 8.9) and flows through a narrow riparian corridor with intermittent mature canopy. Despite being influenced by erosion control measures (e.g. bank armoring), the low elevation, low gradient channel is allowed at least some ability to meander within its immediate floodplain. Whether this reach is a gaining or losing reach has not been determined. Increased sinuosity, improved riparian function and less channel confinement distinctly differentiates this reach from the adjacent upstream segment. The landscape is dominated by row-crop agriculture to the north and south of the riparian corridor. Severely reduced summer surface flows within this reach likely contribute to elevated water temperatures and increased predation. This portion of MC is designated as critical foraging, migrating and overwintering habitat for bull trout.

YHC22

At the Mill Creek Division Dam, surface water is diverted from MC down YHC during all months of the year to augment irrigation withdrawals and to provide passage for migrating salmonids. As MC reaches base summer flows, most of the surface flow is diverted down this 14.5 km distributary almost entirely dewatering downstream reaches in MC. Yellowhawk Creek functions as a migration corridor for bull trout and other migratory salmonids that connects upper MC with the WWR while bypassing much of the fish passage barriers in the lower Mill Creek Flood Control Project. Cottonwood and Russell Creeks are small tributaries to this reach and bull trout occupancy of these streams, albeit unlikely, is currently unknown. Other spring channel tributaries contribute to discharge within this reach. A small portion of surface flows are diverted near the head of this reach down Garrison Creek. There is a fish screen to prevent downstream migrating fish from entering Garrison Creek.

Appendix D: Summary of Habitat Quality Scores

Table D1. Summary of habitat quality conditions for bull trout spawning in the South Fork and Mainstem Walla Walla rivers. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	S.F. and Mainstem Walla Walla River - Adult Spawning													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linea r (km)	HQS (Avg.)	Linea r (km)	HQS (Avg.)	Linea r (km)	HQS (Avg.)	Linea r (km)	HQS (Avg.)	Linea r (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	3.33	4	3.91	89	4.29	33	–	0	3.92	126
February	–	0	–	0	–	0	3.98	86	4.27	39	–	0	4.04	126
March	–	0	–	0	3.07	4	3.62	89	4.42	33	–	0	3.70	126
April	–	0	–	0	3.17	73	3.82	33	4.47	20	–	0	3.52	126
May	–	0	2.38	4	3.05	74	3.77	17	4.44	30	2.38	4	3.38	122
June	–	0	2.17	73	2.97	5	3.82	47	–	0	2.17	73	3.54	52
July	1.48	39	1.95	36	3.08	8	3.91	43	–	0	1.72	75	3.58	50
August	1.55	34	2.04	42	3.08	8	3.91	43	–	0	1.85	75	3.58	50
September	1.62	34	2.09	42	3.14	3	3.66	17	4.49	30	1.91	75	3.89	50
October	1.68	27	2.20	45	2.88	6	3.92	17	4.49	30	2.05	73	3.76	53
November	–	0	2.29	9	2.97	66	3.40	3	4.40	47	2.29	9	3.53	116
December	–	0	–	0	3.33	4	3.87	89	4.29	33	–	0	3.89	126
Average HQS (All Months)	1.57		2.12		3.07		3.83		4.39		1.96		3.71	
Total Linear Distance	134		251		253		574		294		385		1121	
Total Months	12		28		33		62		20		40		115	
% of the Subbasin (linear distance)	9%		17%		17%		38%		20%		26%		74%	
% of the Subbasin (% of the Year)	8%		18%		21%		40%		13%		26%		74%	

Table D2. Summary of habitat quality conditions for bull trout spawning in Mill Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Mill Creek - Adult Spawning													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	3.00	20	3.86	10	4.25	29	–	0	3.42	59
February	–	0	–	0	2.91	20	4.12	10	4.25	29	–	0	3.40	59
March	–	0	2.51	3	2.80	17	3.60	10	4.25	29	2.51	3	3.32	56
April	–	0	2.51	3	2.85	17	3.60	10	4.51	29	2.51	3	3.43	56
May	–	0	2.21	11	3.17	19	3.86	29	–	0	2.21	11	3.51	48
June	1.57	10	2.23	10	3.12	10	3.80	29	–	0	1.83	20	3.57	39
July	1.22	19	2.17	11	3.32	14	3.81	15	–	0	1.54	30	3.56	29
August	1.22	19	2.17	11	3.06	14	3.81	15	–	0	1.54	30	3.43	29
September	1.22	19	2.17	11	3.32	14	4.07	15	–	0	1.54	30	3.69	29
October	1.43	10	2.16	10	3.11	24	4.07	15	–	0	1.73	20	3.43	39
November	–	0	1.91	10	2.89	20	–	0	4.45	29	1.91	10	3.51	49
December	–	0	2.56	3	2.95	17	3.93	24	4.28	15	2.56	3	3.42	56
Average HQS (All Months)	1.32		2.20		2.97		3.86		4.33		1.78		3.44	
Total Linear Distance	75		85		206		179		160		159		545	
Total Months	18		20		33		14		11		38		58	
% of the Subbasin (linear distance)	11%		12%		29%		25%		23%		23%		77%	
% of the Subbasin (% of the Year)	19%		21%		34%		15%		11%		40%		60%	

Table D3. Summary of habitat quality conditions for bull trout spawning in Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Yellowhawk Creek - Adult Spawning													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	–	0	3.70	15	–	0	–	0	3.70	15
February	–	0	–	0	–	0	3.96	15	–	0	–	0	3.96	15
March	–	0	–	0	–	0	3.44	15	–	0	–	0	3.44	15
April	–	0	–	0	3.18	15	–	0	–	0	–	0	3.18	15
May	–	0	–	0	3.18	15	–	0	–	0	–	0	3.18	15
June	–	0	–	0	2.92	15	–	0	–	0	–	0	2.92	15
July	–	0	–	0	2.82	15	–	0	–	0	–	0	2.82	15
August	–	0	–	0	2.82	15	–	0	–	0	–	0	2.82	15
September	–	0	–	0	2.82	15	–	0	–	0	–	0	2.82	15
October	–	0	–	0	3.18	15	–	0	–	0	–	0	3.18	15
November	–	0	–	0	3.18	15	–	0	–	0	–	0	3.18	15
December	–	0	–	0	–	0	3.70	15	–	0	–	0	3.70	15
Average HQS (All Months)	–		–		3.01		3.70		–		–		3.24	
Total Linear Distance	0		0		116		58		0		0		174	
Total Months	0		0		8		4		0		0		12	
% of the Subbasin (linear distance)	0%		0%		67%		33%		0%		0%		100%	
% of the Subbasin (% of the Year)	0%		0%		67%		33%		0%		0%		100%	

Table D4. Summary of habitat quality conditions for juvenile bull trout rearing, foraging and growth in the South Fork and Mainstem Walla Walla rivers. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	S.F. and Mainstem Walla Walla River - Juvenile Rearing, Foraging and Growth													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	3.38	8	3.69	118	–	0	–	0	3.67	126
February	–	0	–	0	3.38	8	3.77	118	–	0	–	0	3.74	126
March	–	0	–	0	–	0	3.83	108	4.29	17	–	0	3.90	126
April	–	0	–	0	–	0	3.90	106	4.26	20	–	0	3.98	126
May	–	0	–	0	3.24	6	3.75	82	4.47	38	–	0	3.87	126
June	–	0	2.53	37	3.08	38	3.68	3	4.33	47	2.53	37	3.64	89
July	1.44	24	2.15	46	2.87	9	–	0	4.33	47	2.03	69	3.71	56
August	1.44	24	2.28	46	3.02	9	–	0	4.33	47	2.14	69	3.77	56
September	–	0	2.17	61	2.94	14	3.68	3	4.55	47	2.17	61	3.74	64
October	–	0	2.36	24	2.95	52	3.96	3	4.40	47	2.36	24	3.52	102
November	–	0	–	0	3.14	52	3.75	46	4.29	27	–	0	3.54	126
December	–	0	–	0	3.38	8	3.67	108	4.33	10	–	0	3.69	126
Average HQS (All Months)	1.44		2.26		3.06		3.76		4.37		2.18		3.73	
Total Linear Distance	47		213		203		694		348		260		1246	
Total Months	2		18		34		70		32		20		136	
% of the Subbasin (linear distance)	3%		14%		13%		46%		23%		17%		83%	
% of the Subbasin (% of the Year)	1%		12%		22%		45%		21%		13%		87%	

Table D5. Summary of habitat quality conditions for juvenile bull trout rearing, foraging and growth in Mill Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Mill Creek - Juvenile Rearing, Foraging and Growth													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	2.55	6	2.83	14	3.81	39	–	0	2.55	6	3.32	52
February	–	0	2.55	6	2.69	14	3.81	39	–	0	2.55	6	3.25	52
March	–	0	–	0	2.90	11	3.78	48	–	0	–	0	3.34	59
April	–	0	–	0	2.90	11	3.88	33	4.28	15	–	0	3.44	59
May	–	0	–	0	2.73	11	3.88	33	4.28	15	–	0	3.35	59
June	1.80	3	1.98	8	2.86	9	3.81	24	4.32	15	1.93	11	3.70	48
July	1.34	20	–	0	2.79	10	3.74	14	4.61	15	1.34	20	3.71	39
August	1.34	20	–	0	2.79	10	3.74	14	4.61	15	1.34	20	3.71	39
September	1.39	10	1.99	10	3.08	10	4.03	14	4.32	15	1.63	20	3.81	39
October	–	0	1.99	10	2.82	10	3.74	24	4.32	15	1.99	10	3.49	49
November	–	0	2.20	10	2.95	10	3.79	39	–	0	2.20	10	3.45	49
December	–	0	2.35	10	2.94	10	3.73	39	–	0	2.35	10	3.41	49
Average HQS (All Months)	1.39		2.21		2.84		3.81		4.39		1.85		3.45	
Total Linear Distance	53		60		130		360		102		113		592	
Total Months	14		18		28		29		7		32		64	
% of the Subbasin (linear distance)	7%		8%		18%		51%		15%		16%		84%	
% of the Subbasin (% of the Year)	15%		19%		29%		30%		7%		33%		67%	

Table D6. Summary of habitat quality conditions for juvenile bull trout rearing, foraging and growth in Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Yellowhawk Creek - Juvenile Rearing, Foraging and Growth													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	3.40	15	–	0	–	0	–	0	3.40	15
February	–	0	–	0	3.40	15	–	0	–	0	–	0	3.40	15
March	–	0	–	0	–	0	3.69	15	–	0	–	0	3.69	15
April	–	0	–	0	–	0	3.98	15	–	0	–	0	3.98	15
May	–	0	–	0	–	0	3.69	15	–	0	–	0	3.69	15
June	–	0	–	0	3.40	15	–	0	–	0	–	0	3.40	15
July	–	0	–	0	2.74	15	–	0	–	0	–	0	2.74	15
August	–	0	–	0	2.74	15	–	0	–	0	–	0	2.74	15
September	–	0	–	0	3.03	15	–	0	–	0	–	0	3.03	15
October	–	0	–	0	–	0	3.69	15	–	0	–	0	3.69	15
November	–	0	–	0	–	0	3.69	15	–	0	–	0	3.69	15
December	–	0	–	0	3.40	15	–	0	–	0	–	0	3.40	15
Average HQS (All Months)	–		–		3.16		3.74		–		–		3.40	
Total Linear Distance	0		0		102		73		0		0		174	
Total Months	0		0		7		5		0		0		12	
% of the Subbasin (linear distance)	0%		0%		58%		42%		0%		0%		100%	
% of the Subbasin (% of the Year)	0%		0%		58%		42%		0%		0%		100%	

Table D7. Summary of habitat quality conditions for fluvial adult bull trout upstream migration in the South Fork and Mainstem Walla Walla rivers. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	S.F. and Mainstem Walla Walla River - Fluvial Adult Upstream Migration													
Habitat Quality	**Poor**		**Low**		**Fair**		**Good**		**High**		**Poor - Low**		**Fair - High**	
	HQS (Avg.)	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**
January	–	0	–	0	3.21	9	3.65	117	–	0	–	0	3.55	126
February	–	0	–	0	3.28	4	3.66	122	–	0	–	0	3.63	126
March	–	0	–	0	3.28	4	3.69	122	–	0	–	0	3.66	126
April	–	0	–	0	3.17	4	3.78	120	–	0	–	0	3.68	126
May	–	0	–	0	3.13	4	3.80	117	4.28	5	–	0	3.78	126
June	–	0	2.59	4	2.96	61	3.66	43	4.42	17	2.59	4	3.50	122
July	1.77	30	2.31	45	–	0	3.77	38	4.56	13	2.18	75	3.93	50
August	1.78	24	2.28	18	2.75	33	3.67	33	4.50	17	2.18	42	3.53	84
September	–	0	2.26	34	2.78	42	3.78	33	4.33	17	2.26	34	3.39	92
October	–	0	2.33	34	2.89	42	3.75	50	–	0	2.33	34	3.32	92
November	–	0	2.48	16	2.98	59	3.72	50	–	0	2.48	16	3.35	110
December	–	0	–	0	3.21	9	3.61	117	–	0	–	0	3.52	126
Average HQS (All Months)	1.78		2.34		2.99		3.71		4.42		2.27		3.57	
Total Linear Distance	53		151		270		960		70		204		1302	
Total Months	3		20		34		91		8		23		133	
% of the Subbasin (linear distance)	4%		10%		18%		64%		5%		14%		86%	
% of the Subbasin (% of the Year)	2%		13%		22%		58%		5%		15%		85%	

Table D8. Summary of habitat quality conditions for fluvial adult bull trout upstream migration in Mill Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Mill Creek - Fluvial Adult Upstream Migration													
Habitat Quality	**Poor**		**Low**		**Fair**		**Good**		**High**		**Poor - Low**		**Fair - High**	
	HQS (Avg.)	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**
January	–	0	2.52	6	2.80	14	3.61	39	–	0	2.52	6	3.20	52
February	–	0	2.46	19	2.83	2	3.67	39	–	0	2.46	19	3.46	40
March	–	0	2.46	3	2.87	17	3.67	39	–	0	2.46	3	3.21	56
April	–	0	2.46	3	2.94	17	3.78	39	–	0	2.46	3	3.30	56
May	–	0	–	0	2.87	10	3.90	49	–	0	–	0	3.51	59
June	–	0	2.16	10	2.97	10	3.92	39	–	0	2.16	10	3.54	49
July	1.43	10	2.08	10	3.04	10	3.81	14	4.32	15	1.69	20	3.72	39
August	1.43	10	2.08	10	3.04	10	3.89	29	–	0	1.69	20	3.60	39
September	1.61	10	2.26	10	3.21	10	3.80	29	–	0	1.87	20	3.60	39
October	1.77	6	1.82	3	2.91	10	3.70	24	–	0	1.78	10	3.23	49
November	–	0	1.90	10	2.92	10	3.76	29	–	0	1.90	10	3.26	49
December	–	0	2.29	10	3.02	10	3.60	24	–	0	2.29	10	3.26	49
Average HQS (All Months)	1.54		2.23		2.93		3.77		4.32		2.01		3.38	
Total Linear Distance	35		95		129		393		15		130		575	
Total Months	11		24		29		31		1		35		61	
% of the Subbasin (linear distance)	5%		13%		18%		56%		2%		18%		82%	
% of the Subbasin (% of the Year)	11%		25%		30%		32%		1%		36%		64%	

Table D9. Summary of habitat quality conditions for fluvial adult bull trout upstream migration in Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Yellowhawk Creek - Fluvial Adult Upstream Migration													
Habitat Quality	**Poor**		**Low**		**Fair**		**Good**		**High**		**Poor - Low**		**Fair - High**	
	HQS (Avg.)	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**	**HQS (Avg.)**	**Linear (km)**
January	–	0	–	0	–	0	3.41	15	–	0	–	0	3.41	15
February	–	0	–	0	–	0	3.58	15	–	0	–	0	3.58	15
March	–	0	–	0	–	0	3.58	15	–	0	–	0	3.58	15
April	–	0	–	0	–	0	3.58	15	–	0	–	0	3.58	15
May	–	0	–	0	–	0	3.94	15	–	0	–	0	3.94	15
June	–	0	–	0	–	0	3.76	15	–	0	–	0	3.76	15
July	–	0	–	0	–	0	3.54	15	–	0	–	0	3.54	15
August	–	0	–	0	–	0	3.54	15	–	0	–	0	3.54	15
September	–	0	–	0	–	0	3.72	15	–	0	–	0	3.72	15
October	–	0	–	0	–	0	3.94	15	–	0	–	0	3.94	15
November	–	0	–	0	–	0	3.41	15	–	0	–	0	3.58	15
December	–	0	–	0	–	0	3.41	15	–	0	–	0	3.41	15
Average HQS (All Months)	–		–		–		3.63		–		–		3.63	
Total Linear Distance	0		0		0		174		0		0		174	
Total Months	0		0		0		12		0		0		12	
% of the Subbasin (linear distance)	0%		0%		0%		100%		0%		0%		100%	
% of the Subbasin (% of the Year)	0%		0%		0%		100%		0%		0%		100%	

Table D10. Summary of habitat quality conditions for adult bull trout foraging and maintenance in the South Fork and Mainstem Walla Walla rivers. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	S.F. and Mainstem Walla Walla River - Adult Foraging and Maintenance													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	3.02	4	3.73	122	–	0	–	0	3.68	126
February	–	0	–	0	3.02	4	3.79	122	–	0	–	0	3.74	126
March	–	0	–	0	3.27	4	3.89	109	4.26	13	–	0	3.87	126
April	–	0	–	0	3.05	4	3.90	109	4.26	13	–	0	3.86	126
May	–	0	–	0	2.90	4	3.80	102	4.31	20	–	0	3.77	126
June	–	0	–	0	3.06	73	3.73	5	4.28	47	–	0	3.54	126
July	1.76	4	2.14	69	3.00	5	4.02	5	4.37	43	2.09	73	3.86	52
August	–	0	2.23	71	2.74	5	3.83	8	4.37	43	2.23	71	3.75	55
September	–	0	2.32	59	3.08	17	3.96	8	4.29	43	2.32	59	3.68	67
October	–	0	2.35	27	2.93	17	3.91	18	4.28	33	2.35	27	3.44	98
November	–	0	2.49	4	3.15	69	3.85	40	4.21	13	2.49	4	3.53	122
December	–	0	–	0	3.02	4	3.73	122	–	0	–	0	3.67	48
Average HQS (All Months)	1.76		2.25		3.03		3.82		4.31		2.22		3.69	
Total Linear Distance	4		230		208		768		265		234		1195	
Total Months	1		19		33		84		19		20		136	
% of the Subbasin (linear distance)	0%		15%		14%		51%		18%		16%		79%	
% of the Subbasin (% of the Year)	1%		12%		21%		54%		12%		13%		87%	

Table D11. Summary of habitat quality conditions for adult bull trout foraging and maintenance in Mill Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Mill Creek - Adult Foraging and Maintenance													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	2.79	20	3.78	39	–	0	–	0	3.16	59
February	–	0	2.56	3	2.72	17	3.78	39	–	0	2.56	3	3.17	56
March	–	0	–	0	2.90	11	3.76	48	–	0	–	0	3.33	59
April	–	0	–	0	2.90	11	3.82	33	4.29	15	–	0	3.42	59
May	–	0	2.36	10	2.84	2	3.74	11	4.29	15	2.36	10	3.67	49
June	–	0	2.27	11	3.23	9	3.82	24	4.31	15	2.27	11	3.79	48
July	1.48	10	2.05	10	2.87	10	3.75	14	4.31	15	1.71	20	3.64	39
August	1.48	10	2.05	10	2.87	10	3.75	14	4.31	15	1.71	20	3.64	39
September	1.73	10	2.31	10	3.37	10	3.50	14	4.31	15	1.96	20	3.73	39
October	–	0	1.98	10	2.82	10	3.47	24	4.31	15	1.98	10	3.38	49
November	–	0	2.28	10	3.01	10	3.73	39	–	0	2.28	10	3.44	49
December	–	0	2.41	10	3.02	10	3.70	39	–	0	2.41	10	3.43	49
Average HQS (All Months)	1.56		2.24		2.89		3.73		4.31		2.05		3.43	
Total Linear Distance	29		84		130		338		102		113		592	
Total Months	9		23		28		29		7		32		64	
% of the Subbasin (linear distance)	4%		12%		18%		48%		15%		16%		84%	
% of the Subbasin (% of the Year)	9%		24%		29%		30%		7%		33%		67%	

Table D12. Summary of habitat quality conditions for adult bull trout foraging and maintenance in Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Yellowhawk Creek - Adult Foraging and Maintenance													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	–	0	3.50	15	–	0	–	0	3.50	15
February	–	0	–	0	–	0	3.50	15	–	0	–	0	3.50	15
March	–	0	–	0	–	0	3.76	15	–	0	–	0	3.76	15
April	–	0	–	0	–	0	3.76	15	–	0	–	0	3.76	15
May	–	0	–	0	–	0	3.76	15	–	0	–	0	3.76	15
June	–	0	–	0	–	0	3.76	15	–	0	–	0	3.76	15
July	–	0	–	0	3.18	15	–	0	–	0	–	0	3.18	15
August	–	0	–	0	3.18	15	–	0	–	0	–	0	3.18	15
September	–	0	–	0	–	0	3.43	15	–	0	–	0	3.43	15
October	–	0	–	0	–	0	3.76	15	–	0	–	0	3.76	15
November	–	0	–	0	–	0	3.50	15	–	0	–	0	3.76	15
December	–	0	–	0	–	0	3.50	0	–	0	–	0	3.50	15
Average HQS (All Months)	–		–		3.18		3.65		–		–		3.57	
Total Linear Distance	0		0		29		131		0		0		174	
Total Months	0		0		2		10		0		0		12	
% of the Subbasin (linear distance)	0%		0%		17%		75%		0%		0%		100%	
% of the Subbasin (% of the Year)	0%		0%		17%		83%		0%		0%		100%	

Table D13. Summary of habitat quality conditions for fluvial adult bull trout downstream migration in the South Fork and Mainstem Walla Walla rivers. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	South Fork and Mainstem Walla Walla Rivers - Fluvial Adult Downstream Migration													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	–	0	3.96	108	4.28	17	–	0	4.01	126
February	–	0	–	0	–	0	3.99	106	4.29	20	–	0	4.06	126
March	–	0	–	0	–	0	4.05	77	4.38	49	–	0	4.15	126
April	–	0	–	0	–	0	3.92	108	4.48	17	–	0	4.01	126
May	–	0	–	0	3.07	4	3.84	89	4.27	33	–	0	3.85	126
June	–	0	2.57	4	3.07	71	3.95	8	4.35	43	2.57	4	3.53	122
July	1.79	24	2.15	50	2.60	2	3.75	8	4.35	43	2.10	73	3.86	52
August	1.79	24	2.34	42	2.75	10	3.75	8	4.35	43	2.25	65	3.72	60
September	–	0	2.41	57	2.76	18	3.95	8	4.35	43	2.41	57	3.55	69
October	–	0	2.38	34	2.90	42	3.73	3	4.36	47	2.38	34	3.57	92
November	–	0	–	0	3.04	39	3.78	59	4.38	27	–	0	3.69	126
December	–	0	–	0	–	0	3.94	108	4.28	17	–	0	3.99	126
Average HQS (All Months)	1.79		2.31		2.93		3.92		4.35		2.26		3.85	
Total Linear Distance	47		186		186		689		398		233		1273	
Total Months	2		19		24		77		34		21		135	
% of the Subbasin (linear distance)	3%		12%		12%		46%		26%		15%		85%	
% of the Subbasin (% of the Year)	1%		12%		15%		49%		22%		13%		87%	

Table D14. Summary of habitat quality conditions for fluvial adult bull trout downstream migration in Mill Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Mill Creek - Fluvial Adult Downstream Migration													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	3.11	11	3.76	33	4.30	15	–	0	3.50	59
February	–	0	–	0	3.03	20	3.94	24	4.30	15	–	0	3.42	59
March	–	0	–	0	3.14	10	3.80	35	4.30	15	–	0	3.61	59
April	–	0	–	0	3.14	10	3.92	35	4.50	15	–	0	3.70	59
May	–	0	2.54	3	2.93	8	3.85	33	4.50	15	2.54	3	3.55	56
June	–	0	2.17	10	2.94	10	3.69	24	4.53	15	2.17	10	3.56	49
July	1.45	10	2.06	10	2.97	10	3.45	14	4.33	15	1.69	20	3.58	39
August	1.45	10	2.06	10	2.97	10	3.45	14	4.33	15	1.69	20	3.58	39
September	1.65	10	2.26	10	3.17	10	3.45	14	4.53	15	1.89	20	3.71	39
October	–	0	1.85	10	2.75	10	3.43	24	4.53	15	1.85	10	3.38	49
November	–	0	2.48	10	3.24	10	3.79	24	4.33	15	2.48	10	3.68	49
December	–	0	–	0	2.91	11	3.68	33	4.30	15	–	0	3.37	59
Average HQS (All Months)	1.51		2.17		3.03		3.74		4.40		1.94		3.54	
Total Linear Distance	29		63		130		308		175		92		612	
Total Months	9		16		31		28		12		25		71	
% of the Subbasin (linear distance)	4%		9%		18%		44%		25%		13%		87%	
% of the Subbasin (% of the Year)	9%		17%		32%		29%		13%		26%		74%	

Table D15. Summary of habitat quality conditions for fluvial adult bull trout downstream migration in Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Yellowhawk Creek - Fluvial Adult Downstream Migration													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	–	0	3.87	15	–	0	–	0	3.87	15
February	–	0	–	0	–	0	3.87	15	–	0	–	0	3.87	15
March	–	0	–	0	–	0	4.07	15	–	0	–	0	4.07	15
April	–	0	–	0	–	0	3.87	15	–	0	–	0	3.87	15
May	–	0	–	0	–	0	3.87	15	–	0	–	0	3.87	15
June	–	0	–	0	–	0	3.67	15	–	0	–	0	3.67	15
July	–	0	–	0	–	0	3.41	15	–	0	–	0	3.41	15
August	–	0	–	0	–	0	3.41	15	–	0	–	0	3.41	15
September	–	0	–	0	–	0	3.61	15	–	0	–	0	3.61	15
October	–	0	–	0	–	0	3.87	15	–	0	–	0	3.87	15
November	–	0	–	0	–	0	3.87	15	–	0	–	0	4.07	15
December	–	0	–	0	–	0	3.87	15	–	0	–	0	3.87	15
Average HQS (All Months)	–		–		–		3.79		–		–		3.79	
Total Linear Distance	0		0		0		174		0		0		174	
Total Months	0		0		0		12		0		0		12	
% of the Subbasin (linear distance)	0%		0%		0%		100%		0%		0%		100%	
% of the Subbasin (% of the Year)	0%		0%		0%		100%		0%		0%		100%	

Table D16. Summary of habitat quality conditions for fluvial sub-adult bull trout downstream migration in the South Fork and Mainstem Walla Walla rivers. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	South Fork and Mainstem Walla Walla Rivers - Fluvial Sub-adult Downstream Migration													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	–	0	3.93	88	4.25	13	–	0	4.00	126
February	–	0	–	0	–	0	3.96	85	4.27	40	–	0	4.06	126
March	–	0	–	0	–	0	4.06	57	4.36	69	–	0	4.17	126
April	–	0	–	0	–	0	3.91	88	4.41	38	–	0	4.03	126
May	–	0	–	0	3.22	9	3.88	83	4.36	33	–	0	3.85	126
June	–	0	2.51	4	3.05	71	4.02	8	4.41	43	2.51	4	3.55	122
July	–	0	2.13	73	2.68	2	3.78	8	4.41	43	2.13	73	3.91	52
August	–	0	2.18	42	2.74	33	3.78	8	4.41	43	2.18	42	3.62	84
September	–	0	2.40	34	2.76	42	4.02	8	4.41	43	2.40	34	3.51	92
October	–	0	2.42	27	2.95	48	3.85	3	4.41	47	2.42	27	3.56	98
November	–	0	–	0	3.05	16	3.75	62	4.35	47	–	0	3.78	126
December	–	0	–	0	–	0	3.91	88	4.25	38	–	0	3.99	126
Average HQS (All Months)	–		2.24		2.94		3.92		4.36		2.24		3.85	
Total Linear Distance	0		180		221		586		494		180		1326	
Total Months	0		18		27		71		40		18		138	
% of the Subbasin (linear distance)	0%		12%		15%		39%		33%		12%		88%	
% of the Subbasin (% of the Year)	0%		12%		17%		46%		26%		12%		88%	

Table D17. Summary of habitat quality conditions for fluvial sub-adult bull trout downstream migration in Mill Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Mill Creek - Fluvial Sub-adult Downstream Migration													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	3.19	10	3.75	35	4.45	15	–	0	3.63	59
February	–	0	–	0	3.23	19	3.74	26	4.45	15	–	0	3.57	59
March	–	0	–	0	3.32	3	3.78	41	4.45	15	–	0	3.81	59
April	–	0	–	0	3.32	3	3.78	32	4.45	24	–	0	3.89	59
May	–	0	–	0	2.98	10	3.80	35	4.69	15	–	0	3.60	59
June	–	0	2.27	10	3.04	10	3.71	24	4.72	15	2.27	10	3.64	49
July	1.60	10	2.25	10	2.95	10	3.51	14	4.49	15	1.86	20	3.65	39
August	1.60	10	2.25	10	2.95	10	3.51	14	4.49	15	1.86	20	3.65	39
September	1.73	3	2.05	15	2.90	11	3.51	14	4.72	15	1.97	19	3.51	40
October	–	0	2.08	10	2.96	10	3.50	24	4.72	15	2.08	10	3.53	49
November	–	0	2.58	6	3.19	14	3.83	24	4.49	15	2.58	6	3.62	52
December	–	0	–	0	2.98	10	3.69	35	4.45	15	–	0	3.52	59
Average HQS (All Months)	1.62		2.22		3.09		3.72		4.54		2.03		3.64	
Total Linear Distance	23		62		119		317		184		84		620	
Total Months	7		15		26		35		13		22		74	
% of the Subbasin (linear distance)	3%		9%		17%		45%		26%		12%		88%	
% of the Subbasin (% of the Year)	7%		16%		27%		36%		14%		23%		77%	

Table D18. Summary of habitat quality conditions for fluvial sub-adult bull trout downstream migration in Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Yellowhawk Creek - Fluvial Sub-adult Downstream Migration													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	–	0	3.83	15	–	0	–	0	3.83	15
February	–	0	–	0	–	0	3.83	15	–	0	–	0	3.83	15
March	–	0	–	0	–	0	4.06	15	–	0	–	0	4.06	15
April	–	0	–	0	–	0	3.83	15	–	0	–	0	3.83	15
May	–	0	–	0	–	0	3.83	15	–	0	–	0	3.83	15
June	–	0	–	0	–	0	3.59	15	–	0	–	0	3.59	15
July	–	0	–	0	3.30	15	–	0	–	0	–	0	3.30	15
August	–	0	–	0	3.30	15	–	0	–	0	–	0	3.30	15
September	–	0	–	0	–	0	3.54	15	–	0	–	0	3.54	15
October	–	0	–	0	–	0	3.83	15	–	0	–	0	3.83	15
November	–	0	–	0	–	0	3.83	15	–	0	–	0	4.06	15
December	–	0	–	0	–	0	3.83	15	–	0	–	0	3.83	15
Average HQS (All Months)	–		–		3.30		3.82		–		–		3.73	
Total Linear Distance	0		0		29		145		0		0		174	
Total Months	0		0		2		10		0		0		12	
% of the Subbasin (linear distance)	0%		0%		17%		83%		0%		0%		100%	
% of the Subbasin (% of the Year)	0%		0%		17%		83%		0%		0%		100%	

Table D19. Summary of habitat quality conditions for fluvial sub-adult bull trout upstream migration in the South Fork and Mainstem Walla Walla rivers. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	South Fork and Mainstem Walla Walla Rivers - Fluvial Sub-adult Upstream Migration													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	–	0	3.97	32	4.33	93	–	0	4.22	126
February	–	0	–	0	–	0	3.97	32	4.33	93	–	0	4.22	126
March	–	0	–	0	–	0	4.02	41	4.34	84	–	0	4.19	126
April	–	0	–	0	–	0	3.89	44	4.35	81	–	0	4.14	126
May	–	0	–	0	3.26	4	3.83	43	4.33	79	–	0	4.02	126
June	–	0	–	0	3.06	75	3.97	3	4.41	47	–	0	3.54	126
July	1.73	34	2.27	42	–	0	3.83	8	4.45	43	2.07	75	4.20	50
August	1.70	24	2.32	50	2.71	2	3.93	8	4.45	43	2.23	73	3.99	52
September	–	0	2.38	65	2.89	10	3.97	3	4.41	47	2.38	65	3.79	61
October	–	0	2.42	27	2.95	48	3.97	3	4.41	47	2.42	27	3.57	98
November	–	0	–	0	3.03	41	3.71	37	4.41	47	–	0	3.66	126
December	–	0	–	0	–	0	4.00	44	4.35	126	–	0	4.19	126
Average HQS (All Months)	1.72		2.33		3.00		3.92		4.37		2.22		3.98	
Total Linear Distance	57		184		180		299		830		241		1265	
Total Months	4		18		24		43		67		22		134	
% of the Subbasin (linear distance)	4%		12%		12%		20%		55%		16%		84%	
% of the Subbasin (% of the Year)	3%		12%		15%		28%		43%		14%		86%	

Table D20. Summary of habitat quality conditions for fluvial sub-adult bull trout upstream migration in Mill Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Mill Creek - Fluvial Sub-adult Upstream Migration													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	3.29	7	3.75	23	4.48	29	–	0	3.82	59
February	–	0	–	0	3.26	15	3.76	14	4.48	29	–	0	3.75	59
March	–	0	–	0	3.29	7	3.75	23	4.48	29	–	0	3.82	59
April	–	0	–	0	3.29	7	3.82	23	4.48	29	–	0	3.85	59
May	–	0	–	0	3.06	10	3.95	20	4.48	29	–	0	3.75	59
June	–	0	2.23	10	2.99	10	3.96	24	4.61	15	2.23	10	3.70	49
July	1.55	19	2.39	2	2.82	10	3.89	14	4.61	15	1.72	20	3.77	39
August	1.55	19	2.39	2	2.82	10	3.89	14	4.61	15	1.72	20	3.77	39
September	1.68	10	2.28	10	3.22	10	3.89	14	4.61	15	1.92	20	3.91	39
October	–	0	2.08	10	2.98	10	3.68	24	4.61	15	2.08	10	3.59	49
November	–	0	2.46	10	3.20	10	3.96	24	4.61	15	2.46	10	3.78	49
December	–	0	–	0	3.06	10	3.93	35	4.57	15	–	0	3.68	59
Average HQS (All Months)	1.59		2.28		3.13		3.84		4.53		1.96		3.77	
Total Linear Distance	47		42		114		254		247		89		616	
Total Months	11		13		24		31		17		24		72	
% of the Subbasin (linear distance)	7%		6%		16%		36%		35%		13%		87%	
% of the Subbasin (% of the Year)	11%		14%		25%		32%		18%		25%		75%	

Table D21. Summary of habitat quality conditions for fluvial sub-adult bull trout upstream migration in Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Yellowhawk Creek - Fluvial Sub-adult Upstream Migration													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	–	0	3.88	15	–	0	–	0	3.88	15
February	–	0	–	0	–	0	3.88	15	–	0	–	0	3.88	15
March	–	0	–	0	–	0	3.88	15	–	0	–	0	3.88	15
April	–	0	–	0	–	0	3.88	15	–	0	–	0	3.88	15
May	–	0	–	0	–	0	3.88	15	–	0	–	0	3.88	15
June	–	0	–	0	–	0	3.68	15	–	0	–	0	3.68	15
July	–	0	–	0	3.23	15	–	0	–	0	–	0	3.23	15
August	–	0	–	0	3.23	15	–	0	–	0	–	0	3.23	15
September	–	0	–	0	–	0	3.43	15	–	0	–	0	3.43	15
October	–	0	–	0	–	0	3.88	15	–	0	–	0	3.88	15
November	–	0	–	0	–	0	3.88	15	–	0	–	0	3.88	15
December	–	0	–	0	–	0	3.88	15	–	0	–	0	3.88	15
Average HQS (All Months)	–		–		3.23		3.82		–		–		3.72	
Total Linear Distance	0		0		29		145		0		0		174	
Total Months	0		0		2		10		0		0		12	
% of the Subbasin (linear distance)	0%		0%		17%		83%		0%		0%		100%	
% of the Subbasin (% of the Year)	0%		0%		17%		83%		0%		0%		100%	

Table D22. Summary of habitat quality conditions for fluvial sub-adult bull trout rearing, foraging and growth in the South Fork and Mainstem Walla Walla rivers. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	South Fork and Mainstem Walla Walla Rivers - Fluvial Sub-adult Rearing, Foraging and Growth													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	–	0	3.93	88	4.25	38	–	0	4.00	126
February	–	0	–	0	–	0	3.96	85	4.27	40	–	0	4.06	126
March	–	0	–	0	–	0	4.06	57	4.36	69	–	0	4.17	126
April	–	0	–	0	–	0	3.91	88	4.41	38	–	0	4.03	126
May	–	0	–	0	3.22	9	3.88	83	4.36	33	–	0	3.85	126
June	–	0	2.51	4	3.05	71	4.02	8	4.41	43	2.51	4	3.55	122
July	–	0	2.13	73	2.68	2	3.78	8	4.41	43	2.13	27	3.91	52
August	–	0	2.18	42	2.74	2	3.78	8	4.41	43	2.18	19	3.94	33
September	–	0	2.40	34	2.76	42	4.02	8	4.41	43	2.40	34	3.51	42
October	–	0	2.42	27	2.95	48	3.85	3	4.41	47	2.42	27	3.56	35
November	–	0	–	0	3.05	16	3.75	62	4.35	47	–	0	3.78	126
December	–	0	–	0	–	0	3.91	39	4.25	13	–	0	3.99	126
Average HQS (All Months)	–		2.24		2.94		3.92		4.36		2.24		3.85	
Total Linear Distance	0		180		190		537		494		111		1162	
Total Months	0		18		27		101		40		18		138	
% of the Subbasin (linear distance)	0%		12%		13%		36%		33%		7%		77%	
% of the Subbasin (% of the Year)	0%		12%		17%		65%		26%		12%		88%	

Table D23. Summary of habitat quality conditions for fluvial sub-adult bull trout rearing, foraging and growth in Mill Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Mill Creek - Fluvial Sub-adult Rearing, Foraging and Growth													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	3.19	10	3.75	35	4.45	15	–	0	3.63	59
February	–	0	–	0	3.23	19	3.74	26	4.45	15	–	0	3.57	59
March	–	0	–	0	3.32	3	3.78	41	4.45	15	–	0	3.81	59
April	–	0	–	0	3.32	3	3.78	32	4.45	24	–	0	3.89	59
May	–	0	–	0	2.98	10	3.80	35	4.69	15	–	0	3.60	59
June	–	0	2.27	10	3.04	10	3.71	24	4.72	15	2.27	10	3.64	49
July	1.60	10	2.25	10	2.95	10	3.51	14	4.49	15	1.86	20	3.65	39
August	1.60	10	2.25	10	2.95	10	3.51	14	4.49	15	1.86	20	3.65	39
September	1.73	3	2.05	15	2.90	11	3.51	14	4.72	15	1.97	19	3.51	40
October	–	0	2.08	10	2.96	10	3.50	24	4.72	15	2.08	10	3.53	49
November	–	0	2.58	6	3.19	14	3.83	24	4.49	15	2.58	6	3.62	52
December	–	0	–	0	2.98	10	3.69	35	4.45	15	–	0	3.52	59
Average HQS (All Months)	1.62		2.22		3.09		3.72		4.54		2.03		3.64	
Total Linear Distance	23		62		119		317		184		84		620	
Total Months	7		15		26		35		13		22		74	
% of the Subbasin (linear distance)	3%		9%		17%		45%		26%		12%		88%	
% of the Subbasin (% of the Year)	7%		16%		27%		36%		14%		23%		77%	

Table D24. Summary of habitat quality conditions for fluvial sub-adult bull trout rearing, foraging and growth in Yellowhawk Creek. Habitat quality scores of ≤ 1.8, >1.8 – 2.6, >2.6 – 3.4, >3.4 – 4.2 and >4.2 are considered to be of poor, low, fair, good and high quality, respectively.

Subbasin/Life Stage	Yellowhawk Creek - Fluvial Sub-adult Rearing, Foraging and Growth													
Habitat Quality	Poor		Low		Fair		Good		High		Poor - Low		Fair - High	
	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)	HQS (Avg.)	Linear (km)
January	–	0	–	0	–	0	3.83	15	–	0	–	0	3.83	15
February	–	0	–	0	–	0	3.83	15	–	0	–	0	3.83	15
March	–	0	–	0	–	0	4.06	15	–	0	–	0	4.06	15
April	–	0	–	0	–	0	3.83	15	–	0	–	0	3.83	15
May	–	0	–	0	–	0	3.83	15	–	0	–	0	3.83	15
June	–	0	–	0	–	0	3.59	15	–	0	–	0	3.59	15
July	–	0	–	0	3.30	15	–	0	–	0	–	0	3.30	15
August	–	0	–	0	3.30	15	–	0	–	0	–	0	3.30	15
September	–	0	–	0	–	0	3.54	15	–	0	–	0	3.54	15
October	–	0	–	0	–	0	3.83	15	–	0	–	0	3.83	15
November	–	0	–	0	–	0	3.83	15	–	0	–	0	4.06	15
December	–	0	–	0	–	0	3.83	0	–	0	–	0	3.83	15
Average HQS (All Months)	–		–		3.30		3.82		–		–		3.73	
Total Linear Distance	0		0		29		131		0		0		174	
Total Months	0		0		2		10		0		0		12	
% of the Subbasin (linear distance)	0%		0%		17%		75%		0%		0%		100%	
% of the Subbasin (% of the Year)	0%		0%		17%		83%		0%		0%		100%	

Appendix E: Summary of Bull Trout Occurrence

Table E1. Summary of occurrence for bull trout spawning in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek.

River/Creek	SF/Mainstem WW R.				Mill Creek				Yellowhawk Creek			
Occurrence Level	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)
January	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
February	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
March	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
April	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
May	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
June	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
July	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
August	29.9	0.0	95.6	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
September	29.9	0.0	95.6	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
October	29.9	0.0	95.6	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
November	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0
December	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
Total Linear Distance	89.7	0.0	412.3	1004.0	43.8	43.2	147.8	469.6	0.0	0.0	58.0	116.0
Total Months	3	0	4	8	3	3	4	8	0	0	4	8
% Subbasin (linear distance)	6%	0%	27%	67%	6%	6%	21%	67%	0%	0%	33%	67%
% of the Subbasin (% of the Year)	25%	0%	33%	67%	25%	25%	33%	67%	0%	0%	33%	67%

Table E2. Summary of occurrence for juvenile bull trout rearing, foraging and growth in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek.

River/Creek	SF/Mainstem WW R.				Mill Creek				Yellowhawk Creek			
Occurrence Level	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)
January	29.9	12.6	83.0	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
February	29.9	12.6	83.0	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
March	29.9	12.6	83.0	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
April	29.9	12.6	83.0	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
May	29.9	12.6	83.0	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
June	29.9	12.6	83.0	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
July	29.9	12.6	83.0	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
August	29.9	12.6	83.0	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
September	29.9	12.6	83.0	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
October	29.9	12.6	83.0	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
November	29.9	12.6	83.0	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
December	29.9	12.6	83.0	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
Total Linear Distance	358.8	151.2	996.0	0.0	175.2	172.8	356.4	0.0	0.0	0.0	174.0	0.0
Total Months	12	12	12	0	12	12	12	0	0	0	12	0
% of the Subbasin (linear distance)	24%	10%	66%	0%	25%	25%	51%	0%	0%	0%	100%	0%
% of the Subbasin (% of the Year)	100%	100%	100%	0%	100%	100%	100%	0%	0%	0%	100%	0%

Table E3. Summary of occurrence for fluvial adult bull trout upstream migration in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek.

River/Creek	SF/Mainstem WW R.				Mill Creek				Yellowhawk Creek			
Occurrence Level	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)
January	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
February	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
March	0.0	54.8	70.7	0.0	0.0	12.0	46.7	0.0	0.0	0.0	14.5	0.0
April	0.0	60.4	65.1	0.0	0.0	29.7	29.0	0.0	0.0	14.5	0.0	0.0
May	78.2	4.8	42.5	0.0	29.7	14.4	14.6	0.0	0.0	14.5	0.0	0.0
June	40.8	74.9	9.8	0.0	43.5	15.2	0.0	0.0	0.0	14.5	0.0	0.0
July	42.5	18.4	64.6	0.0	29.0	14.5	15.2	0.0	0.0	14.5	0.0	0.0
August	47.3	3.0	75.2	0.0	29.0	9.7	20.0	0.0	0.0	0.0	14.5	0.0
September	29.9	0.0	95.6	0.0	0.0	29.0	29.7	0.0	0.0	0.0	14.5	0.0
October	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0
November	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
December	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
Total Linear Distance	238.7	216.3	549.0	502.0	131.2	124.5	213.9	234.8	0.0	58.0	58.0	58.0
Total Months	5	6	8	4	4	7	7	4	0	4	4	4
% of the Subbasin (linear distance)	16%	14%	37%	33%	19%	18%	30%	33%	0%	33%	33%	33%
% of the Subbasin (% of the Year)	42%	50%	67%	33%	33%	58%	58%	33%	0%	33%	33%	33%

Table E4. Summary of occurrence for adult bull trout foraging and maintenance in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek.

River/Creek	SF/Mainstem WW R.				Mill Creek				Yellowhawk Creek			
Occurrence Level	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)
January	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
February	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
March	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
April	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
May	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
June	70.7	54.8	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
July	50.3	20.4	54.8	0.0	29.0	14.5	15.2	0.0	0.0	14.5	0.0	0.0
August	47.3	5.0	73.2	0.0	29.0	9.7	20.0	0.0	0.0	0.0	14.5	0.0
September	29.9	35.2	60.4	0.0	14.6	14.4	29.7	0.0	0.0	0.0	14.5	0.0
October	65.1	60.4	0.0	0.0	14.6	44.1	0.0	0.0	14.5	0.0	0.0	0.0
November	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
December	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
Total Linear Distance	1141	175.8	188.4	0.0	556.8	82.7	64.9	0.0	130.5	14.5	29.0	0.0
Total Months	12	5	3	0	12	4	3	0	9	1	2	0
% of the Subbasin (linear distance)	76%	12%	13%	0%	79%	12%	9%	0%	75%	8%	17%	0%
% of the Subbasin (% of the Year)	100%	42%	25%	0%	100%	33%	25%	0%	75%	8%	17%	0%

Table E5. Summary of occurrence for fluvial adult bull trout downstream migration in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek.

River/Creek	SF/Mainstem WW R.				Mill Creek				Yellowhawk Creek			
Occurrence Level	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)
January	60.4	35.2	29.9	0.0	0.0	44.1	14.6	0.0	0.0	14.5	0.0	0.0
February	54.8	20.4	50.3	0.0	0.0	44.1	14.6	0.0	0.0	14.5	0.0	0.0
March	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
April	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
May	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
June	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
July	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
August	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0
September	62.5	2.6	60.4	0.0	38.7	1.5	18.5	0.0	0.0	0.0	14.5	0.0
October	70.7	54.8	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
November	95.6	29.9	0.0	0.0	44.1	14.6	0.0	0.0	14.5	0.0	0.0	0.0
December	69.4	26.2	29.9	0.0	20.0	24.1	14.6	0.0	14.5	0.0	0.0	0.0
Total Linear Distance	413.4	169.1	296.0	627.5	161.5	128.4	121.0	293.5	43.5	29.0	29.0	72.5
Total Months	6	6	5	5	4	5	5	5	3	2	2	5
% of the Subbasin (linear distance)	28%	11%	20%	42%	23%	18%	17%	42%	25%	17%	17%	42%
% of the Subbasin (% of the Year)	50%	50%	42%	42%	33%	42%	42%	42%	25%	17%	17%	42%

Table E6. Summary of occurrence for fluvial sub-adult bull trout downstream migration in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek.

River/Creek	SF/Mainstem WW R.				Mill Creek				Yellowhawk Creek			
Occurrence Level	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)
January	60.4	65.1	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0
February	54.8	70.7	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0
March	65.1	29.1	31.3	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
April	65.1	29.1	31.3	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
May	65.1	29.1	31.3	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
June	65.1	29.1	31.3	0.0	43.5	15.2	0.0	0.0	14.5	0.0	0.0	0.0
July	56.1	29.1	31.3	0.0	43.5	15.2	0.0	0.0	14.5	0.0	0.0	0.0
August	29.9	35.2	60.4	0.0	40.2	3.3	15.2	0.0	0.0	14.5	0.0	0.0
September	29.9	32.6	63.0	0.0	40.2	0.0	18.5	0.0	0.0	0.0	14.5	0.0
October	125.5	0.0	0.0	0.0	40.2	18.5	0.0	0.0	0.0	14.5	0.0	0.0
November	95.6	29.9	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
December	75.2	50.3	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
Total Linear Distance	787.8	429.3	279.9	0.0	501.1	169.6	33.7	0.0	101.5	58.0	14.5	0.0
Total Months	12	11	7	0	10	6	2	0	7	4	1	0
% of the Subbasin (linear distance)	53%	29%	19%	0%	71%	24%	5%	0%	58%	33%	8%	0%
% of the Subbasin (% of the Year)	100%	92%	58%	0%	83%	50%	17%	0%	58%	33%	8%	0%

Table E7. Summary of occurrence for fluvial sub-adult bull trout upstream migration in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek.

River/Creek	SF/Mainstem WW R.				Mill Creek				Yellowhawk Creek			
Occurrence Level	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)
January	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
February	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
March	0.0	54.8	70.7	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0
April	0.0	60.4	65.1	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0
May	60.4	2.6	62.5	0.0	0.0	20.0	38.7	0.0	0.0	14.5	0.0	0.0
June	63.0	15.2	47.3	0.0	20.0	0.0	38.7	0.0	14.5	0.0	0.0	0.0
July	23.4	23.5	78.6	0.0	20.0	0.0	38.7	0.0	14.5	0.0	0.0	0.0
August	15.2	31.7	78.6	0.0	0.0	20.0	38.7	0.0	0.0	14.5	0.0	0.0
September	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
October	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
November	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
December	0.0	0.0	0.0	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5
Total Linear Distance	162.0	188.2	402.8	753.0	40.0	40.0	272.2	352.2	29.0	29.0	29.0	87.0
Total Months	4	6	6	6	2	2	6	6	2	2	2	6
% of the Subbasin (linear distance)	11%	13%	27%	50%	6%	6%	39%	50%	17%	17%	17%	50%
% of the Subbasin (% of the Year)	33%	50%	50%	50%	17%	17%	50%	50%	17%	17%	17%	50%

Table E8. Summary of occurrence for fluvial sub-adult bull trout rearing, foraging and growth in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek.

River/Creek	SF/Mainstem WW R.				Mill Creek				Yellowhawk Creek			
Occurrence Level	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)	High Linear (km)	Low Linear (km)	Conceivable Linear (km)	None Linear (km)
January	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
February	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
March	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
April	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
May	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
June	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
July	62.5	31.7	31.3	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
August	56.1	9.0	60.4	0.0	40.2	18.5	0.0	0.0	0.0	14.5	0.0	0.0
September	62.5	0.0	63.0	0.0	40.2	0.0	18.5	0.0	0.0	0.0	14.5	0.0
October	125.5	0.0	0.0	0.0	40.2	18.5	0.0	0.0	0.0	14.5	0.0	0.0
November	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
December	125.5	0.0	0.0	0.0	58.7	0.0	0.0	0.0	14.5	0.0	0.0	0.0
Total Linear Distance	1310	40.7	154.7	0.0	648.9	37.0	18.5	0.0	130.5	29.0	14.5	0.0
Total Months	12	2	3	0	12	2	1	0	9	2	1	0
% of the Subbasin (linear distance)	87%	3%	10%	0%	92%	5%	3%	0%	75%	17%	8%	0%
% of the Subbasin (% of the Year)	100%	17%	25%	0%	100%	17%	8%	0%	75%	17%	8%	0%

Appendix F: Bull Trout Habitat Quality, Availability and Occurrence

Table F1. Percent of the total and conceivable habitat where occurrence of bull trout of each life stage is high, low or does not occur in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek.

River/Creek	Description	Total or Conceivable Habitat	Life Stage							
			Spawning	Rearing, Foraging & Growth			Upstream Migration		Downstream Migration	
			Adult	Juvenile	Sub-adult	Adult	Sub-adult	Adult	Sub-adult	Adult
SF/WW R.	% of Habitat with High Occurrence	Total	6.0%	23.8%	87.0%	75.8%	10.8%	15.8%	52.3%	27.5%
SF/WW R.	% of Habitat with Low Occurrence	Total	0.0%	10.0%	2.7%	11.3%	12.5%	14.4%	28.9%	11.2%
SF/WW R.	% of Habitat with No Occurrence	Total	94.0%	66.1%	10.3%	12.9%	76.7%	69.8%	18.8%	61.3%
SF/WW R.	% of Habitat with High Occurrence	Conceivable	47.4%	63.2%	87.0%	75.8%	34.5%	23.8%	52.3%	47.1%
SF/WW R.	% of Habitat with Low Occurrence	Conceivable	0.0%	26.6%	2.7%	11.3%	40.1%	21.5%	28.9%	19.2%
SF/WW R.	% of Habitat with No Occurrence	Conceivable	52.6%	10.1%	10.3%	12.5%	25.4%	55.0%	18.6%	33.7%
Mill Cr.	% of Habitat with High Occurrence	Total	6.2%	24.9%	92.1%	79.0%	5.7%	18.6%	71.1%	22.9%
Mill Cr.	% of Habitat with Low Occurrence	Total	6.1%	24.5%	5.3%	10.5%	5.7%	17.7%	24.1%	18.2%
Mill Cr.	% of Habitat with No Occurrence	Total	87.6%	50.6%	2.6%	10.5%	88.6%	63.7%	4.8%	58.8%
Mill Cr.	% of Habitat with High Occurrence	Conceivable	37.8%	50.3%	92.1%	79.0%	26.9%	27.9%	71.1%	39.3%
Mill Cr.	% of Habitat with Low Occurrence	Conceivable	37.2%	49.7%	5.3%	10.5%	26.9%	26.5%	24.1%	31.2%
Mill Cr.	% of Habitat with No Occurrence	Conceivable	25.0%	0.0%	2.6%	9.2%	46.1%	45.5%	4.8%	29.4%
YH Cr.	% of Habitat with High Occurrence	Total	0.0%	0.0%	75.0%	83.3%	16.7%	0.0%	58.3%	25.0%
YH Cr.	% of Habitat with Low Occurrence	Total	0.0%	0.0%	16.7%	8.3%	16.7%	33.3%	33.3%	16.7%
YH Cr.	% of Habitat with No Occurrence	Total	100.0%	100.0%	8.3%	8.3%	66.7%	66.7%	8.3%	58.3%
YH Cr.	% of Habitat with High Occurrence	Conceivable	NA	NA	75.0%	83.3%	40.0%	0.0%	58.3%	42.9%
YH Cr.	% of Habitat with Low Occurrence	Conceivable	NA	NA	16.7%	8.3%	40.0%	50.0%	33.3%	28.6%
YH Cr.	% of Habitat with No Occurrence	Conceivable	NA	NA	8.3%	16.7%	20.0%	50.0%	8.3%	28.6%

Table F2. Percent of the total habitat in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek where the occurrence of each bull trout life stage, strategy or action is conceivable.

River/Creek	Description	Life Stage							
		Spawning	Rearing, Foraging & Growth			Upstream Migration		Downstream Migration	
		Adult	Juvenile	Sub-adult	Adult	Sub-adult	Adult	Sub-adult	Adult
SF/WW R.	% of Total Habitat that is Conceivable	12.5%	37.7%	100.0%	100.0%	31.1%	66.7%	100.0%	58.4%
Mill Cr.	% of Total Habitat that is Conceivable	16.5%	49.4%	100.0%	100.0%	21.2%	66.7%	100.0%	58.4%
YH Cr.	% of Total Habitat that is Conceivable	0.0%	0.0%	100.0%	100.0%	42.0%	66.7%	100.0%	58.6%

Table F3. Percent of the total and conceivable habitat in the South Fork and Mainstem Walla Walla rivers, Mill Creek and Yellowhawk Creek that is poor-low and fair-high quality when occurrence is high, low or not observed for each bull trout life stage, strategy or action.

River/Creek	Description	Total or Conceivable Habitat	Life Stage							
			Spawning	Rearing, Foraging & Growth			Upstream Migration		Downstream Migration	
			Adult	Juvenile	Sub-adult	Adult	Sub-adult	Adult	Sub-adult	Adult
SF/WW R.	% of Fair-High Quality with High Occurrence	Total	8.0%	28.8%	99.4%	89.1%	10.4%	18.2%	56.8%	30.9%
SF/WW R.	% of Fair-High Quality with Low Occurrence	Total	0.0%	12.1%	0.0%	9.8%	10.5%	15.5%	28.2%	11.4%
SF/WW R.	% of Fair-High Quality with No Occurrence	Total	92.0%	59.1%	0.6%	1.1%	79.1%	66.3%	15.0%	57.7%
SF/WW R.	% of Poor-Low Quality with High Occurrence	Total	0.0%	0.0%	20.7%	3.3%	12.7%	2.8%	19.4%	8.8%
SF/WW R.	% of Poor-Low Quality with Low Occurrence	Total	0.0%	0.0%	17.2%	19.6%	22.9%	9.0%	34.0%	10.1%
SF/WW R.	% of Poor-Low Quality with No Occurrence	Total	100.0%	100.0%	62.0%	77.2%	64.4%	88.1%	46.6%	81.2%
SF/WW R.	% of Fair-High Quality with High Occurrence	Conceivable	47.4%	63.2%	83.8%	75.3%	28.0%	23.2%	50.0%	44.7%
SF/WW R.	% of Fair-High Quality with Low Occurrence	Conceivable	0.0%	26.6%	0.0%	8.3%	28.3%	14.3%	24.9%	16.6%
SF/WW R.	% of Fair-High Quality with No Occurrence	Conceivable	52.6%	10.1%	16.2%	16.4%	43.6%	62.5%	25.1%	38.7%
SF/WW R.	% of Poor-Low Quality with High Occurrence	Conceivable	0.0%	0.0%	20.7%	3.7%	20.6%	3.1%	19.4%	13.1%
SF/WW R.	% of Poor-Low Quality with Low Occurrence	Conceivable	0.0%	0.0%	17.2%	22.2%	37.2%	9.8%	34.0%	15.1%
SF/WW R.	% of Poor-Low Quality with No Occurrence	Conceivable	0.0%	0.0%	62.0%	74.2%	42.2%	87.1%	46.6%	71.8%
Mill Cr.	% of Fair-High Quality with High Occurrence	Total	8.0%	29.6%	98.5%	86.8%	1.7%	22.3%	78.2%	23.2%
Mill Cr.	% of Fair-High Quality with Low Occurrence	Total	7.9%	29.2%	1.5%	10.0%	3.2%	19.2%	21.8%	20.7%
Mill Cr.	% of Fair-High Quality with No Occurrence	Total	84.0%	41.2%	0.0%	3.1%	95.1%	58.6%	0.0%	56.0%
Mill Cr.	% of Poor-Low Quality with High Occurrence	Total	0.0%	0.0%	60.4%	38.2%	33.3%	2.5%	19.0%	20.9%
Mill Cr.	% of Poor-Low Quality with Low Occurrence	Total	0.0%	0.0%	23.9%	12.8%	22.5%	11.0%	40.9%	1.6%
Mill Cr.	% of Poor-Low Quality with No Occurrence	Total	100.0%	100.0%	15.7%	49.0%	44.1%	86.4%	40.1%	77.5%
Mill Cr.	% of Fair-High Quality with High Occurrence	Conceivable	37.8%	50.3%	82.0%	72.9%	7.0%	27.2%	68.9%	34.6%
Mill Cr.	% of Fair-High Quality with Low Occurrence	Conceivable	37.2%	49.7%	1.3%	8.4%	13.5%	23.5%	19.2%	30.9%
Mill Cr.	% of Fair-High Quality with No Occurrence	Conceivable	25.0%	0.0%	16.7%	18.6%	79.5%	49.3%	11.9%	34.5%
Mill Cr.	% of Poor-Low Quality with High Occurrence	Conceivable	0.0%	0.0%	60.4%	38.8%	59.7%	4.1%	19.8%	32.4%
Mill Cr.	% of Poor-Low Quality with Low Occurrence	Conceivable	0.0%	0.0%	23.9%	12.9%	40.3%	17.7%	42.5%	2.5%
Mill Cr.	% of Poor-Low Quality with No Occurrence	Conceivable	0.0%	0.0%	15.7%	48.3%	0.0%	78.2%	37.7%	65.0%
YH Cr.	% of Fair-High Quality with High Occurrence	Total	0.0%	0.0%	75.0%	83.3%	16.7%	0.0%	58.3%	25.0%
YH Cr.	% of Fair-High Quality with Low Occurrence	Total	0.0%	0.0%	16.7%	8.3%	16.7%	33.3%	33.3%	16.7%
YH Cr.	% of Fair-High Quality with No Occurrence	Total	100.0%	100.0%	8.3%	8.3%	66.7%	66.7%	8.3%	58.3%
YH Cr.	% of Poor-Low Quality with High Occurrence	Total	NA	NA	NA	NA	NA	NA	NA	NA
YH Cr.	% of Poor-Low Quality with Low Occurrence	Total	NA	NA	NA	NA	NA	NA	NA	NA
YH Cr.	% of Poor-Low Quality with No Occurrence	Total	NA	NA	NA	NA	NA	NA	NA	NA
YH Cr.	% of Fair-High Quality with High Occurrence	Conceivable	NA	NA	75.0%	83.3%	40.0%	0.0%	58.3%	42.9%
YH Cr.	% of Fair-High Quality with Low Occurrence	Conceivable	NA	NA	16.7%	8.3%	40.0%	50.0%	33.3%	28.6%
YH Cr.	% of Fair-High Quality with No Occurrence	Conceivable	NA	NA	8.3%	8.3%	20.0%	50.0%	8.3%	28.6%
YH Cr.	% of Poor-Low Quality with High Occurrence	Conceivable	NA	NA	NA	NA	NA	NA	NA	NA
YH Cr.	% of Poor-Low Quality with Low Occurrence	Conceivable	NA	NA	NA	NA	NA	NA	NA	NA
YH Cr.	% of Poor-Low Quality with No Occurrence	Conceivable	NA	NA	NA	NA	NA	NA	NA	NA

Chapter 4 : Spawning, Foraging, and Migratory Habitat Use of Bull Trout in the South Fork Walla Walla River

authored by

Darren G. Gallion
Steven L. Haeseker
Don Anglin

U.S. Fish and Wildlife Service

Introduction

Bull trout (*Salvelinus confluentus*) abundance and distribution has declined (U.S. Fish and Wildlife Service 2002) and in some areas, bull trout are believed at risk of local and regional extinctions because of ongoing habitat loss (Rieman and McIntyre 1995). Bull trout were officially listed as a Threatened Species under the Endangered Species Act (ESA) in 1998. The U.S. Fish and Wildlife Service issued a Draft Recovery Plan (U.S. Fish and Wildlife Service 2002). The Draft Recovery Plan identified the need to restore and maintain suitable habitat conditions for all bull trout life-history stages and strategies. Before “suitable habitat” can be restored or maintained, “suitable habitat” must first be defined.

Bull trout spawning typically occurs when temperatures are from 5 to 9 °C (Goetz 1989). Redd site selection is often associated with low gradient, low velocities and loose uncompacted gravel substrate and near cover (Goetz 1989, Fraley and Shepard 1989). Water depth, water velocity and substrate size and the association of cover at redd locations has been reported (James and Sexauer 1997). The influence of groundwater on redd site selection has also been investigated. Although Reiser et al. (1997) found no differences in temperature at redd locations to indicate groundwater interaction, Baxter and McPhail (1999) found females were utilizing habitat influenced by groundwater discharge and Baxter and Hauer (2000) found geomorphology and groundwater affected the distribution and abundance of bull trout spawning.

To quantify species–habitat relationships, fisheries managers have increasingly relied on physical habitat models to aid in making complex decisions (Rosenfeld et al. 2000). Habitat suitability models have been used to estimate and predict the amount of suitable and unsuitable habitat under changing flow regimes (e.g., Bovee 1982). Habitat suitability models are often developed at the microhabitat (e.g., within a 1 meter cell) or mesohabitat (riffle, run, pool) scale. Bull trout spawning microhabitat suitability curves were developed using water depth, nose velocity, substrate size, and cover data by Fernet and Bjornson (1997). However, the validity of habitat suitability models has been criticized (Vadas and Orth 2001). Predictive, quantitative, multivariate spawning habitat models are an alternative to habitat suitability models. Advantages of these models include the ability to (1) account for correlation among habitat variables, (2) include interactions among variables, (3) make quantitative predictions of abundance or probability of occurrence at given flows, and (4) identify sharp thresholds in habitat selection (Jowett and Davey 2007; Ahmadi-Nedushan et al. 2006). Furthermore, Guay et al. (2000) found a predictive model was more powerful than a habitat suitability model to predict the distribution of Atlantic salmon *Salmo salar* and a predictive model was more transferable than a habitat suitability model (Guay et al. 2003). Since a predictive, multivariate spawning habitat model for bull trout currently does not exist, we intended to build one.

To describe and assess suitable bull trout spawning habitat, we developed a predictive spawning microhabitat model for the Walla Walla Basin. Surrounding mesohabitat conditions may be important in some areas, but in the South Fork Walla Walla River (SFWWR) where conditions are generally pristine, mesohabitat variables were continuous, uniform, and of good quality. Also, the SFWWR watershed does not have any significant sources of sediment or fines, and most fines that enter the stream are likely washed downstream as a function of the gradient and annual spring freshet. Thus the presence of fines is consistently low, and similar between redd sites and other areas of the stream. As a result we developed our model with habitat data collected at the microhabitat scale, but did not include fines in our analysis.

The spawning population in the SFWWR consists of both migratory and resident bull trout. Fecund, resident, female bull trout as small as 205 mm (Budy et al. 2009) and migratory bull trout as large as 724 mm (PTAGIS 2011) have been captured in the SFWWR. Larger spawning fish are capable of moving larger substrate (Kondolf and Wolman 1993). Given the wide range of adult lengths, we believe bull trout constructing redds in the SFWWR may be selecting for different size substrate. Crisp and Carling (1989) found a correlation between redd length and fish length for some salmonids. Therefore, we chose to develop and compare habitat models for three redd size classes (small, medium and large) based on redd length. We believe small redds are likely constructed by resident bull trout, medium sized redds are a mix of both resident and migratory bull trout, and large redds are likely created by migratory bull trout.

The ability to identify resident and migratory bull trout spawning habitat may help managers recover the species. Migratory bull trout are of particular concern because they are the segment of the spawning population's productivity that ultimately provides connectivity. Although resident and migratory bull trout may give rise to one another, spawning habitat for migratory bull trout needs to exist for genetic exchange between local or core area populations. The loss of migratory life histories may increase the risk of extinction for local populations and possibly metapopulations (Rieman and Dunham 2000). Although these models have been developed in the Walla Walla Basin, if transferrable, they could be used to identify areas where habitat is compromised to focus restoration efforts. These models could also be used to quantify spawning habitat and the corresponding production potential to develop realistic recovery objectives/criteria.

Foraging and migratory habitats are also critical for ensuring the connectivity among populations as well as resiliency within populations. Because bull trout are adapted to cool water conditions across all life stages, high water temperatures could limit migration or reduce the suitability of foraging habitat. The lower Walla Walla River (WWR) is characterized by high water temperatures during the summer-fall period. These water temperatures may block migratory connectivity or reduce the suitability for foraging. To evaluate the suitability of foraging and migratory habitat in the lower WWR, we conducted surveys for bull trout presence in conjunction with temperature monitoring to quantify patterns of habitat use.

Study Site

Spawning habitat

The study was conducted on the SFWWR, a tributary to the WWR, which is a tributary to the Columbia River, approximately 9 miles downstream from the confluence of the Columbia and Snake Rivers. The study was conducted between Harris County Park and Section 20 tributary in the SFWWR, which is located in northeast Oregon (Figure 4.1). The drainage area of the SFWWR is 163 km^2. In our study area, the SFWWR is a 2nd to 3rd order stream. Mean annual stream flow at Harris County Park is 5.0 m^3/s. Past redd surveys suggest that spawning occurs primarily during September and October. Streamflow during September and October ranges from 2.2 – 5.1 m^3/s and averages 3.1 m^3/s. Streamflow was relatively consistent during our study and ranged from 2.6 – 3.4 m^3/s and averaged 2.8 m^3/s. Stream temperatures at Harris County Park during September and October of 2004 and 2005 ranged between 4.9 and 12.5 °C, and averaged 8.0 °C.

Foraging and migratory habitat

Our study area included the SFWWR from Harris County Park downstream to the mainstem WWR at the OR/WA state line, a distance of approximately 30 river kilometers (Figure 4.2).

We divided the study area into three segments that were based on changes in flow regime and habitat structure resulting, in part, from human impacts such as diversions, dikes, and channelization. Segment 1 from the OR/WA state line (rkm 67) upstream to Cemetery Bridge in Milton-Freewater, OR (rkm 76) has been the most severely impacted. The WWR Flood Control Project constructed by the U.S. Army Corps of Engineers (USACE) modified the channel of the WWR through the city of Milton-Freewater, OR. The project was completed in 1952 and consisted of numerous flood control structures. The channel was widened and straightened, and the gradient was shaped to facilitate the passage of flood waters through the city (Northwest Power and Conservation Council 2004). The Little Walla Walla Diversion at Cemetery Bridge removes approximately 66% or more of the streamflow from the mainstem WWR during the irrigation season. The resulting low summer flows in combination with physical changes associated with the flood control project contribute to elevated water temperatures that can be near lethal for salmonids during the summer through this segment.

The physical conditions in segment 2 from Cemetery Bridge upstream to the confluence of the North and South Forks (rkm 84) have not been extensively altered although some channelization has occurred, numerous small diversions are present, and the riparian zone has been reduced. Streamflows are higher in this segment during the summer than in either segments 1 or 3, the gradient becomes flatter as the river transitions from the Blue Mountains to the floodplain, and substrate particle sizes are generally smaller as a result of the lower gradient. Segment 3 in the SFWW from the confluence of the North and South forks upstream to Harris County Park (rkm 96) is similar to segment 2 with slightly less streamflow from the absence of the North Fork input, a higher gradient, larger substrate particle sizes, and a more functional riparian zone. The riparian and stream habitat conditions are relatively pristine from Harris County Park upstream where most bull trout spawning occurs.

Methods

Spawning habitat

During fall 2004 and 2005, we measured microhabitat variables at bull trout redds and randomly selected locations where redds did not occur to obtain use and non-use data to develop and validate habitat suitability models for spawning bull trout. Redds were typically identified by the presence of a pit, where gravel had been excavated and a pillow where gravel had been deposited to form a nest. Microhabitat data were partitioned into groups to represent resident, a mix of resident and migratory, and migratory bull trout based on redd length. We investigated the importance of water depth, water velocity, substrate size, and hydraulic head in bull trout redd site selection. We used logistic regression analysis (SAS ver. 9.1, 2003) to determine if the habitat variables were a significant factor in redd site selection and to build multivariate habitat models. Habitat models for each redd size were compared.

Field measurements

Redd size

Redd length was measured from the head of the pit to the tail of the pillow and were recorded as small (<0.5m), medium (0.5-1.5m), or large (> 1.5m) from redd length data.

Water depth, Water velocity, substrate size

To describe habitat selection prior to redd construction, habitat measurements are often collected at the edge of the redd pit (Wollabaek et al. 2008, Thurow and King 1994). In our study substrate size was typically measured at the redd pillow. Often, bull trout in the SFWWR recruited all appropriate sized gravel to construct the redd pillow and there wasn't enough remaining suitable substrate at the edge of the pit to describe what the substrate was prior to spawning. Since substrate size prior to spawning could not be determined at the edge of the pit, we determined substrate size based on substrate observed in the constructed pillow. Substrate was categorized into six classes by diameter (Table 4.1). To determine if substrate observed after redd construction was representative of substrate present before construction, we measured dominant substrate at sites before and after redd construction in a 3.6 km stream reach of the SFWWR.

Surveyors also measured the water depth, nose velocity, and mean column velocity at the upstream edge of the redd pit with a top-set wading rod and a Marsh-McBirney Flo-Mate Model 2000 flow meter. When measuring water velocities in eddies, the flow meter sensor was pointed directly into the current, just as a fish would be oriented (Rantz 1982).

Once data were collected at the use point (redd), a non-use point was determined by pacing a random distance (one to six steps upstream or downstream and one to six steps toward either stream bank) away from the redd where the measurements were repeated.

Hydraulic head

We conducted an exploratory investigation into the importance of groundwater in bull trout redd site selection within our study area. It was not feasible to measure hydraulic head at all redd locations, so we installed piezometers at 19 redds and 19 randomly selected non-use points. Piezometers were installed in the stream reach 2.4 km below Reser Creek. This stream reach was chosen because it had a high number of redds in past surveys. Due to the remoteness of the study area, we used a dual-tube drilling system and mini-piezometers to estimate hydraulic head similar to Baxter et al. (2003). The piezometers were allowed to equilibrate for approximately one month, at which time hydraulic head measurements were collected at use and non-use locations. Mini-piezometers were typically installed to depths between approximately 25 and 40 cm. Hydraulic head was calculated by measuring the difference in head between the water level in the piezometer and the level of the stream surface using a Solinst Mini Water Level Meter.

<u>Analysis</u>

Summary statistics

The relative frequency of each redd size encountered is reported. Analytical methods included an examination of average values of physical microhabitat variables used compared to the average values measured for the variables at non-use sites. The mean, standard deviation, minimum and maximum values are reported for use and nonuse data for water depth, mean column water velocity, and nose water velocity. We also compared frequency distributions of the substrate type and hydraulic head at redd sites to frequency distributions at non-use sites to determine if spawning bull trout were selecting specific conditions at frequencies that were different than the randomly selected non-use sites.

Logistic regression

<u>Water depth, water velocity, substrate size</u>

The statistical analyses for the spawning habitat probabilistic model were conducted using microhabitat use and non-use data from the SFWWR study area. Separate models were developed for resident and migratory bull trout, making the assumption that small redds were likely constructed by resident bull trout, large redds were constructed by migratory bull trout and medium redds were constructed by large resident and small migratory bull trout.

Analytical methods included the development of a probabilistic model that could be used to predict the suitability of instream conditions for spawning bull trout. All habitat variables were analyzed as continuous variables except for substrate size, which was collected as categorical data. We used logistic regression analysis to determine the significance of individual microhabitat variables. We used logistic regression because it is well suited for the examination of the relationship between a binary response (i.e., the presence or absence of redds) and various explanatory variables. We fit logistic models of the form:

$$\log_e\left(\frac{\pi(x)}{1-\pi(x)}\right) = \beta_0 + \beta_1 x_1 + \ldots + \beta_n x_n + \varepsilon \ ,$$

where $\pi(x)$ is the probability of redd deposition associated with habitat variables $x_1, x_2, \ldots, x_n$, and $\beta_0, \beta_1, \ldots, \beta_n$ are estimated model parameters (coefficients), and ε is a binomially-distributed error term.

We used multi-model inference techniques (Burnham and Anderson 2002) to evaluate the associations between the environmental variables and redd locations. Our objectives were to account for model selection uncertainty while achieving a balance between model parsimony and model accuracy. For all habitat variables except hydraulic head, we fit logistic models using all combinations of the substrate type, water velocity, and depth variables. The models were ranked according to AIC, the model with the minimum AIC was identified, and Akaike weights (w_i) were calculated for each model (Burnham and Anderson 2002). Using the AIC-ranked set, we calculated model-averaged predictions for the relative probability of spawning habitat use. Model-averaged predictions were calculated using:

$$\hat{\bar{\theta}} = \sum_{i=1}^{R} w_i \hat{\theta},$$

where $\hat{\bar{\theta}}$ denotes the model-averaged prediction of θ (i.e., the relative probability of spawning) across the R models and w_i denotes the Akaike weight for model i = 1, 2, …, R (Burnham and Anderson 2002).

Hydraulic head

We also used logistic regression to analyze the significance of hydraulic head. As previously described, hydraulic head was not collected at all redd locations. Due to the small sample size we were unable to conduct the univariate and multivariate analyses as we did with the remaining habitat variables. Instead, we examined the P-value to determine if hydraulic head was a significant variable for characterizing spawning habitat selection.

Foraging and migratory habitat

Field measurements

Foraging and migratory habitat data were collected using monthly snorkel surveys during August-November 2004 and July-November 2005. During 2004, we conducted snorkel surveys in 10 randomly selected pools from each of the three study segments. We determined bull trout were present in segment 3 during all months sampling was conducted. As a result, in 2005 we focused our efforts on segments 1 and 2 to refine our knowledge of the spatial and temporal distribution of bull trout and increased our effort to 15 randomly selected pools in each segment, 1 and 2. Each surveyed pool was classified as occupied if bull trout were present and unoccupied if bull trout were absent.

Temperature data

Eleven thermographs (Onset Computer, StowAway Tidbits) were deployed in the WWR and four thermographs were deployed in the SFWWR to collect stream temperature. Prior to deployment, data loggers were checked for accuracy using Oregon Watershed Enhancement Board (OWEB) water quality monitoring guidebook specifications and sampling frequency was set to 30-min intervals (OWEB 1999). Manufacturer specifications report an accuracy of +/- 0.2 ºC for the Onset StowAway Tidbit (-5 ºC to + 37 ºC). Each thermograph was placed in 1 ½-in (3.81-cm) diameter metal pipe housing, 4-in (10.16-cm) in length. The metal pipe housing was secured to the bank using ¼-in (0.635-cm) stainless steel cable. Every three months, temperature data were downloaded in the field with an Onset Optic shuttle and then transferred to a personal computer. Data were summarized using BoxCar Pro software version 4.3 (Onset Computer). Temperature data were verified using quality control measures as outlined in the OWEB protocol. Thermograph placement was based on Thermal Infrared Radiometry (TIR) data collected in August 2003 (Faux 2003) and attempted to capture water temperature increases of ~ 0.5 ºC.

Several different water temperature metrics were examined to determine the most important temperature metric to foraging and migratory bull trout: the daily minimum, daily maximum, daily average, 7 day average daily minimum, 7 day average daily maximum, and 7 day average were calculated from the thermograph nearest the pool unit sampled.

Analysis

We used linear regression to quantify the relationship between pool temperature and river kilometer with the expectation that river temperatures would incrementally increase with downstream position. The slope of the linear regression was used to quantify the degree of heating that occurred by month and year.

We used logistic regression to quantify the probability of pool occupancy. Occupancy was modeled as a function of river kilometer and separately as a function of water temperature. We calculated the AIC scores for each of the six temperature metrics to evaluate which metric best characterized pool occupancy.

Results

Spawning habitat

Field measurements

To determine if substrate observed after redd construction was representative of substrate present before construction, we measured dominant substrate at 35 sites before and after redd construction in a 3.6 km stream reach of the SFWWR during 2006 (Figure 4.3). The relative frequency of substrate categories suggest a similar pattern before and after redd construction, and a two sample paired t-test (0.42) suggest no difference. Similarly, bull trout in the Flathead River, Montana, reworked the substrate but did not alter its composition when constructing redds (Shepard and Graham 1982).

We collected water depth, water velocity, and substrate size at a total of 666 locations, 333 were collected at redds and 333 were collected at nonuse locations. Of 333 redds, habitat use information was collected at 15 small redds, 219 medium redds and 99 large redds. Hydraulic head data were also collected at a subset of locations. During piezometer installation we occasionally encountered a layer of bedrock and were unable to install the piezometer to the required depth. In those instances, we discontinued installation at that redd and proceeded to the next downstream redd. During the equilibration period between installation and data collection, 2 piezometers became dislodged. As a result, we collected hydraulic head at 18 use and 18 nonuse locations. Of the 18 use locations, habitat data were collected at medium (n=10) and large (n=8) redds, but no small redds were encountered in the stream reach where hydraulic head data were collected.

Analysis

Summary statistics

Bull trout used similar mean depths among small (0.26 m) medium (0.27 m) and large (0.32 m) redds (Table 4.2). Mean depth use at small, medium, and large redds was also similar to depths measured at associated non-use locations (0.32 m, 0.34 m, and 0.35 m, respectively). Bull trout use of nose velocities was similar between small (0.12 m), medium (0.13 m), and large (0.14 m) redds but was slower in comparison to velocities measured at the associated non-use locations (0.32 m, 0.34 m, and 0.35 m, respectively). Bull trout used slower mean column velocities at small (0.15 m) redds in comparison to medium (0.24 m) and large (0.27 m) redds. Bull trout also used slower velocities in comparison to the associated non-use locations (0.51 m, 0.58 m, and 0.59 m respectively).

We found that 100%, 87%, and 78% of the substrate sizes measured at small, medium and large bull trout redd sites were in the pebble and small gravel categories (Figure 4.4). In contrast, only 0%, 6% and 4% of the substrate sizes measured at non-use sites were in the pebble and small gravel categories.

Hydraulic head was not measured at any small redds or non-use points. Hydraulic head measurements were successfully recorded at 10 medium (0.5-1.5m) use points and 10 non-use points. We found that the hydraulic head measured at medium bull trout redd sites ranged from -6.5 to 5 cm (Figure 4.5), but 80% of those measured ranged from -1 to 1 cm, and averaged 0.10 cm. Although the range of hydraulic head measured at non-use points was narrower (-7 to 1 cm), 80% of those measured ranged from -1 to 1 cm and averaged -0.85 cm. Hydraulic head measurements were successfully recorded at 8 large (>1.5m) use points and 8 non-use points. We found that the hydraulic head measured at large bull trout redd sites ranged from -6.5 to 2 cm, but 50% of those measured ranged from -1 to 1 cm and averaged -1.06 cm. Again, although the range of hydraulic head measured at non-use points was narrower (-1 to 3 cm), 63% of those measured ranged from -1 to 1 cm and averaged 0.5 cm.

Logistic regression

Water depth, water velocity, substrate size

Logistic regression model results showed that substrate size was the most important factor for characterizing spawning habitat selection across all three redd size classes (Tables 4.3-4.5). Models without the substrate variable fit poorly, as indicated by the large delta AIC values. Bull trout displayed high selection for small gravel and pebble substrates across all three redd size classes (small, medium, large, Figure 4.6). As redd size class decreased, bull trout increasingly selected smaller substrates. The medium redd size class also selected sand substrates for spawning. For the medium and large redd size classes, slow water velocity was associated with increased spawning habitat suitability, with the highest suitability at locations with water velocity less than 0.5 m/s (Figure 4.7). Depth had little effect on spawning habitat suitability for both the medium and large size redd size classes, although the medium redd size class did show a trend of decreasing suitability with depth at shallow locations less than 0.2 m. Locations with cobble or boulder substrates were unsuitable across all three size classes.

Hydraulic head

Use and non-use hydraulic gradient data were analyzed using logistic regression, which suggested hydraulic gradient was not important in redd site selection for medium (P = 0.971) or large (P = 0.979) redds. As a result hydraulic head was not explored any further or used in model development.

Foraging and migratory habitat

<u>Field measurements</u>

Although the six temperature metrics were highly correlated with each other, the seven-day average temperature showed a slightly higher degree of correspondence with the observed patterns of occupancy than the other measures. Temperature surveys showed that stream temperatures increased progressively with downstream location in the mainstem WWR in all months (Figure 4.8). However, the greatest rates of increase occurred in July and August with temperature increasing at a rate of two degrees Celsius per five rkms distance downstream (Table 4.6).

<u>Analysis</u>

Across all years and months, we observed a decreasing probability of bull trout occupancy with distance downstream (Figure 4.9). During the July-September period, the average probability of occupancy was 3% (range: 0% - 10%) at rkm 76 (Cemetery Bridge), which is the point of main diversion for irrigation withdrawals. During the October-November period, the average probability of occupancy increased to 16% (range: 9% - 26%) at rkm 76. Across all years and months we observed a decrease in the probability of bull trout occupancy as stream temperatures increased and in any given month, the highest probabilities of bull trout occupancy were locations with the coolest water available (Figure 4.10).

Discussion

Small (<0.5m), medium (0.5-1.5m) and large (>1.5m) redds were approximately 4%, 66% and 30%, of all redds encountered, respectively. Resident sized bull trout outnumber migratory bull trout in the SFWWR (Budy et al. 2009). Although smaller, resident bull trout may be underrepresented by redd counts in the SFWWR (Al-Chokhachy et al. 2005), 4% is a very small proportion of the total redds encountered. The largest proportion (66%) of redds were medium (0.5-1.5m) sized redds. We believe medium redds were likely constructed by both migratory and resident bull trout. The remaining 30% of redds encountered were large redds and were likely constructed by relatively large, migratory bull trout.

Water depth, water velocity and substrate used by spawning bull trout in the SFWWR were similar to those reported by Reiser et al. (1997) and by Fernet and Bjornson (1997). Examining the average values and the frequency distributions of microhabitat variable use and non-use lend insight into the types of habitat bull trout constructing small, medium and large redds prefer. Although there was a minimum threshold, generally depth at bull trout red sites was similar to that at non-use sites, which may be primarily because of the overriding importance of velocity and substrate conditions. Bull trout selected for slower nose and mean column velocities than were observed at nonuse locations. Bull trout selection for slower mean water velocities was more apparent than selection for nose velocities. This may have been the result of the higher variability observed in mean column velocities. The most apparent microhabitat variable bull trout selected for was for smaller substrate sizes. Not only did bull trout constructing all redd sizes select for smaller substrate than were observed at non-use locations, but generally, there was a shift in relative frequency to larger substrates as redd size increased.

The range and distribution of hydraulic head measurements at use and non-use sites was similar at medium redds (Figure 4.5). The range and distribution of hydraulic head measurements at use and non-use sites was also similar at large redds. Similarities in range and distribution at use and non-use sites suggest bull trout are not selecting for a particular amount of groundwater influence. Furthermore, most of the hydraulic head measurements collected at medium (80%) and large (50%) redds were near 0 ranging between -1 and 1 cm, again, suggesting bull trout were not selecting for a strong influence of groundwater. Comparing the range and distribution pattern of hydraulic head measurements between medium and large redds suggest large resident and migratory bull trout are using similar hydraulic habitat. In our study, hydraulic head was not a significant factor in determining redd site selection at the microhabitat scale. Baxter and Hauer (2000) found groundwater influence important in redd site selection at larger scales (i.e., valley segment, stream reach and bedform (pool/riffle)). Although our random non-use site wasn't contained within a river reach by design, it was relatively close to the redd (less than 6 paces), and was often within the same pool/riffle unit. As a result, our sampling design would not have detected differences at the bedform scale. In our study area, at the microhabitat scale, hydraulic head was not a significant habitat variable in determining redd site selection.

Analyses showed that for each redd size category, substrate type was the most important predictor of redd site selection. Substrate type was followed by mean column velocity and depth in order of importance. The combination of substrate, mean column velocity, and depth was the best fitting model for medium redds and resulted in an AIC score of 120.0 (Table 4.4). Removal of substrate from the top candidate model increased the AIC score by 251 points. Removing mean column velocity increased the score by 4 points and resulted in the 2nd best model. Removing depth increased the AIC score by 11 points but there was little support for this model in comparison to the other two based on the AIC weights (Table 4.4).

The combination of substrate and mean column velocity was the best fitting model for large redds and resulted in an AIC score of 51.7 (Table 4.5). Removal of substrate from the top candidate model increased the AIC score by about 121 points. Removing mean column velocity increased the AIC score by about 11 points, illustrating the importance of velocity in addition to substrate size for large redds.

For all sizes of redds, predicted relative use >89% when pebble and small gravel are present and no use is predicted when cobble or boulder are present (Figure 4.6). Our results suggest that pebble and small gravel is the most suitable substrate for redd construction and can be moved by all sizes of bull trout, while cobble and boulder is unsuitable. The predicted use when large gravel substrate is present is 71% for large redds, 52% at medium redds and 0% at small redds (Figure 4.6). If redd size is correlated to fish size (Crisp and Carling 1989) and larger fish are more able to move larger substrate (Kondolf and Wolman 1993), it is possible that small bull trout building small redds are unable to move large gravel substrate because of their body size. Our model predicts no use for small redds when sand is present, but surprisingly predicted 82% use for medium redds when sand is present. Although probability of occurrence of medium redds is high (82%) when sand is present, this may be an artifact of relatively small sample size for that substrate category. Sand was observed at 9 medium redds and 2 associated non-use locations. Although sand was observed more frequently at redds than at non-use sites, overall, it was observed relatively infrequently at medium redds (4%) and associated non-use sites (1%). Subdominant substrate information was collected, but was not included in the habitat model. Subdominant substrate at the 9 use locations was pebble (7) or small gravel (2). We believe bull trout were most likely selecting for the subdominant substrate at these locations.

Predicted use decreased at medium and large redds as mean column velocity increased (Figure 4.7). Predicted use declined more rapidly at large redds than medium redds as mean column velocity increased, which is contrary to what we suspected. We believe large bull trout are constructing large redds and that they would be able to utilize or at least tolerate higher water velocities due to their larger body size. But given the wide and overlapping confidence intervals, differences between predicted use at medium and large redds was not significant.

Depth had little effect on spawning habitat suitability for both the medium and large size redd size classes, although the medium redd size class did show a trend of decreasing suitability with depth at shallow locations less than 0.2 m. With some minimum threshold, depth usually becomes secondary in importance for selection of suitable redd sites, primarily because of the overriding importance of velocity and substrate conditions.

Surveys to evaluate foraging and migratory habitat preferences showed that stream temperatures increased progressively with downstream location in the mainstem WWR in all months and that water temperatures were negatively associated with pool occupancy. The greatest rates of increase in water temperature occurred in July and August, likely due to increased solar heating in combination with reduced river flow. Reducing the heating rates and overall water temperatures would require some combination of increased riparian shading along with some form of cool water supplementation.

We observed a decreasing probability of occupancy with distance downstream from Harris Park Bridge across all surveys. This pattern was most pronounced during July-September, when there was a low probability of occupancy below rkm 76, which is the point of main diversion for irrigation withdrawals. Across all years and months we observed a decrease in the probability of bull trout occupancy as stream temperatures increased and bull trout appeared to occupy the coolest available water. The analyses highlight the importance of cool water temperatures for foraging and migratory bull trout, and quantify the thermal or physical limits that may be inhibiting migration.

Management Implications

Bull trout which are listed under ESA, exhibit multiple life-history forms. Understanding bull trout habitat relationships for each life-history forms is critical for the recovery of the species. The bull trout spawning habitat models we developed are currently only applicable to the Walla Walla Basin and will need to be tested for transferability prior to use in other basins. If transferrable, they could be used to identify areas where habitat is compromised to focus restoration efforts. These models could also be used to quantify spawning habitat and the corresponding production potential to develop realistic recovery objectives/criteria.

Although we have illustrated habitat use at the microhabitat scale, additional research is necessary to better understand interactions with other species (e.g., Spring Chinook salmon). The timing of Spring Chinook salmon spawning in the SFWWR overlaps with bull trout spawning. Although Spring Chinook salmon were present during this study, only nine Spring Chinook redds were observed above Skiphorton creek (Mahoney et al. 2006), where most bull trout spawning occurs. The degree to which the presence of spring Chinook affected habitat use by bull trout, or whether higher densities of spring Chinook would affect bull trout habitat use, is unknown.

The analyses highlight the importance of cool water temperatures for foraging and migratory bull trout, and quantify the thermal preferences. Increased riparian shading and/or cool water flow augmentation appear to be the only means to reduce temperature and thereby ameliorate the thermal conditions that appear to be constraining the amount of suitable foraging and migratory habitat in the lower WWR. These results indicate that focusing on activities to improve stream temperature conditions in the mainstem WWR will be integral for restoring the migratory component and improve the resiliency of the WWR Core Area of the bull trout population.

Literature Cited

Ahmadi-Nedushan, B., A. St-Hilaire, M. Berube, E. Robichaud, N. Thiemonge, and B. Bobee. 2006. A review of statistical methods for the evaluation of aquatic habitat suitability for instream flow assessment. River Research and Applications 22:503-523.

Al-Chokhachy, R., Budy, P., and Schaller, H. 2005. Understanding the significance of redd counts: a comparison between two methods for estimating the abundance of and monitoring bull trout populations. North American Journal of Fisheries Management 25:1505-1512.

Baxter, C., and Hauer, F.R. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences. 57:1470-1481.

Baxter, C., Hauer F.R., and Woessner W.W. 2003. Measuring groundwater–stream water exchange: new techniques for installing minipiezometers and estimating hydraulic conductivity. Transactions of the American Fisheries Society 132:493–502.

Baxter, J., and McPhail, J.D. 1999. The influence of redd site selection, groundwater upwelling, and overwinter incubation temperature on survival of bull trout (*Salvelinus confluentus*) from egg to alevin. Canadian Journal of Zoology 77:1233-1239.

Bovee, K. D. 1982. A guide to stream habitat analysis using the instream flow incremental methodology. U.S. Fish and Wildlife Service, Instream Flow Information Paper 12, Fort Collins, Colorado.

Budy, P., P.D. MacKinnon, T. Bowerman, and G.P. Thiede. 2009. Bull trout population assessment in northeastern Oregon: a template for recovery planning. 2008 Annual Progress Report to US Fish and Wildlife Service. UTCFWRU 2009(1):1-57.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information–theoretic approach. 2nd edition. Springer-Verlag. New York, N.Y.

Crisp, D.T. & Carling, P.A. 1989. Observations on siting, dimensions and structure of salmonid redds. Journal of Fish Biology 34:119–134.

Faux, R. N. 2003. Aerial surveys in the Walla Walla River Basin: Thermal infrared and color videography. Report to the U.S Fish & Wildlife Service, Columbia River Fisheries Program Office.

Fernet, D.A., and Bjornson, C.P. 1997. A delphi analysis of bull trout habitat preference criteria with comparison to information collected from Smith-Dorrien Creek, Alberta, p. 435-442. In W.C. Mackay, M.K. Brewin, and M. Monita (ed.) Friends of the bull trout conference proceedings. Bull Trout Task Force (Alberta), c/o Trout Unlimited Canada, Calgary, AB.

Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Science 63:133-143.

Goetz, F. 1989. Biology of the bull trout. United States Department of Agriculture, Forest Service, Willamette National Forest, literature review, Eugene, Oregon.

Guay, J. C., D. Boisclair, D. Rioux, M. Leclerc, M. Lapointe, and P. Legendre. 2000. Development and validation of numerical habitat models for juveniles of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 57:2065–2075.

Guay, J. C., Boisclair, D., Leclerc, M. and Lapointe, M. 2003. Assessment of the transferability of biological habitat models for Atlantic salmon parr (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 60:1398–1408.

James P.J., and Sexauer H.M. 1997. Spawning behaviour, spawning habitat and alternative mating strategies in an adfluvial population of bull trout. In: Mackay W.C., Brewin M.K. and Monita M. (eds.), Friends of the Bull Trout Conference Proceedings, pp. 325–329.

Jowett, I.G. and Davey, A.J.H. 2007. A comparison of composite habitat suitability indices and generalized additive models of invertebrate abundance and fish presence-habitat availability. Transactions of the American Fisheries Society 136:428–444.

Kondolf G.M., and M.G. Wolman. 1993. The Sizes of Salmonid Spawning Gravels. Water Resources Research, Volume 29, Nl. 7. Pages 2275-2285.

Mahoney B.D., M.B. Lambert, T.J. Olsen, E. Hoverson, P. Kissner, and J.D.M. Schwartz. 2006. Walla Walla Basin Natural Production Monitoring and Evaluation Project Progress Report, 2004-2005. Confederated Tribes of the Umatilla Indian Reservation. Report submitted to Bonneville Power Administration. Project No. 2000-039-00.

Northwest Power and Conservation Council. 2004. Walla Walla Subbasin Plan.

OWEB. July 1999. The Oregon Plan for Salmon and Watersheds. Water Quality Monitoring Technical Guidebook (version 2.0). Oregon's Watershed Enhancement Board. http://oregon.gov/OWEB/docs/pubs/wq_mon_guide.pdf.

PTAGIS (Columbia Basin PIT Tag Information System). 2011. Pacific States Marine Fisheries Commission, Portland, Oregon. Available: www.ptagis.org. (October 2011).

Rantz, S. E. 1982. Measurement and Computation of Streamflow. USGS Water Supply Paper 2175. http://water.usgs.gov/pubs/wsp/wsp2175/index.html.

Reiser, W.D., E. D. Connor, K. Binkley, K. Lynch and D. Paige. 1997. Evaluation of spawning habitat used by bull trout in the Cedar River Watershed, Washington. P. 331-338. In

Friends of the Bull Trout Conference Proceedings. Edited by W. C. Mackay, M.K. Brewin and M. Monita. Bull Trout Task Force (Alberta), c/o Trout Unlimited Canada, Calgary.

Rieman, B.E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124:285-296.

Rieman, B. E. and Dunham, J. B. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. Ecology of Freshwater Fish 9:51–64.

Rosenfeld, J., M. Porter and E. Parkinson. 2000. Habitat factors affecting the abundance and distribution of juvenile cutthroat trout (*Oncorhynchus clarki*) and coho salmon (Oncorhynchus kisutch). Canadian Journal of Fish and Aquatic Sciences 57(4):766–774.

Shepard, B.B., and Graham, P.J. 1982. Monitoring spawning bed material used by bull trout on the Glacier View District Flathead National Forest. Completion Report. Montana Department of Fish, Wildlife and Parks, Region 1, Kalispell, Montana.

Thurow, R.F., and J.G. King. 1994. Attributes of Yellowstone Cutthroat Trout Redds in a Tributary of the Snake River, Idaho, Transactions of the American Fisheries Society, 123:(1)37-50.

U.S. Fish and Wildlife Service. 2002. Chapter 11, Umatilla-Walla Walla Recovery Unit, Oregon and Washington. 153 p. In: U.S. Fish and Wildlife Service. Bull Trout (*Salvelinus confluentus*) Draft Recovery Plan. Portland, Oregon.

Vadas, R. L., and D. J. Orth. 2001. Formulations of habitat suitability models for stream fish guilds: do the standard methods work? Transactions of the American Fisheries Society 130:217–235.

Wollebæk, J., R. Thue, and J. Heggenes. 2008. Redd Site Microhabitat Utilization and Quantitative Models for Wild Large Brown Trout in Three Contrasting Boreal Rivers, North American Journal of Fisheries Management 28:1249-1258.

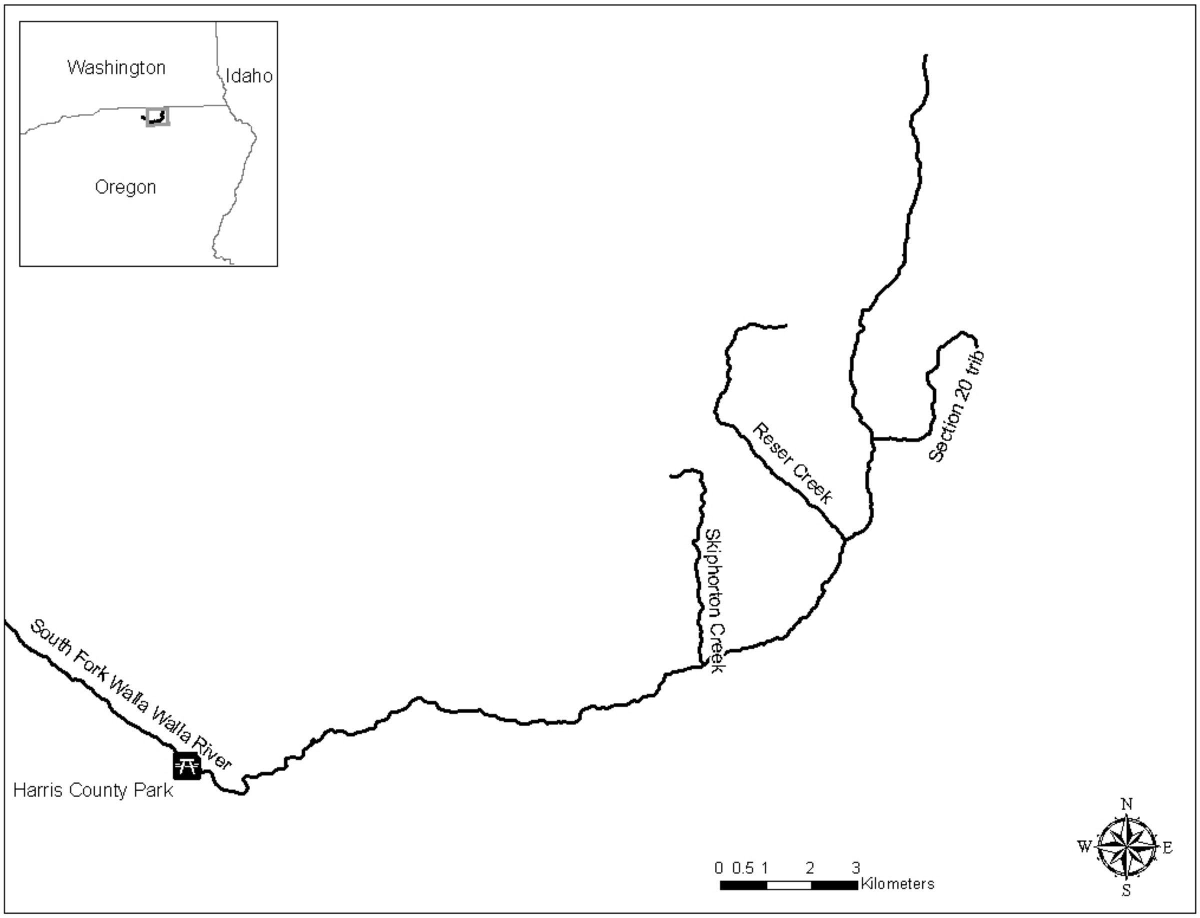

Figure 4.1. Map of the South Fork Walla Walla River which is located in Northeast Oregon.

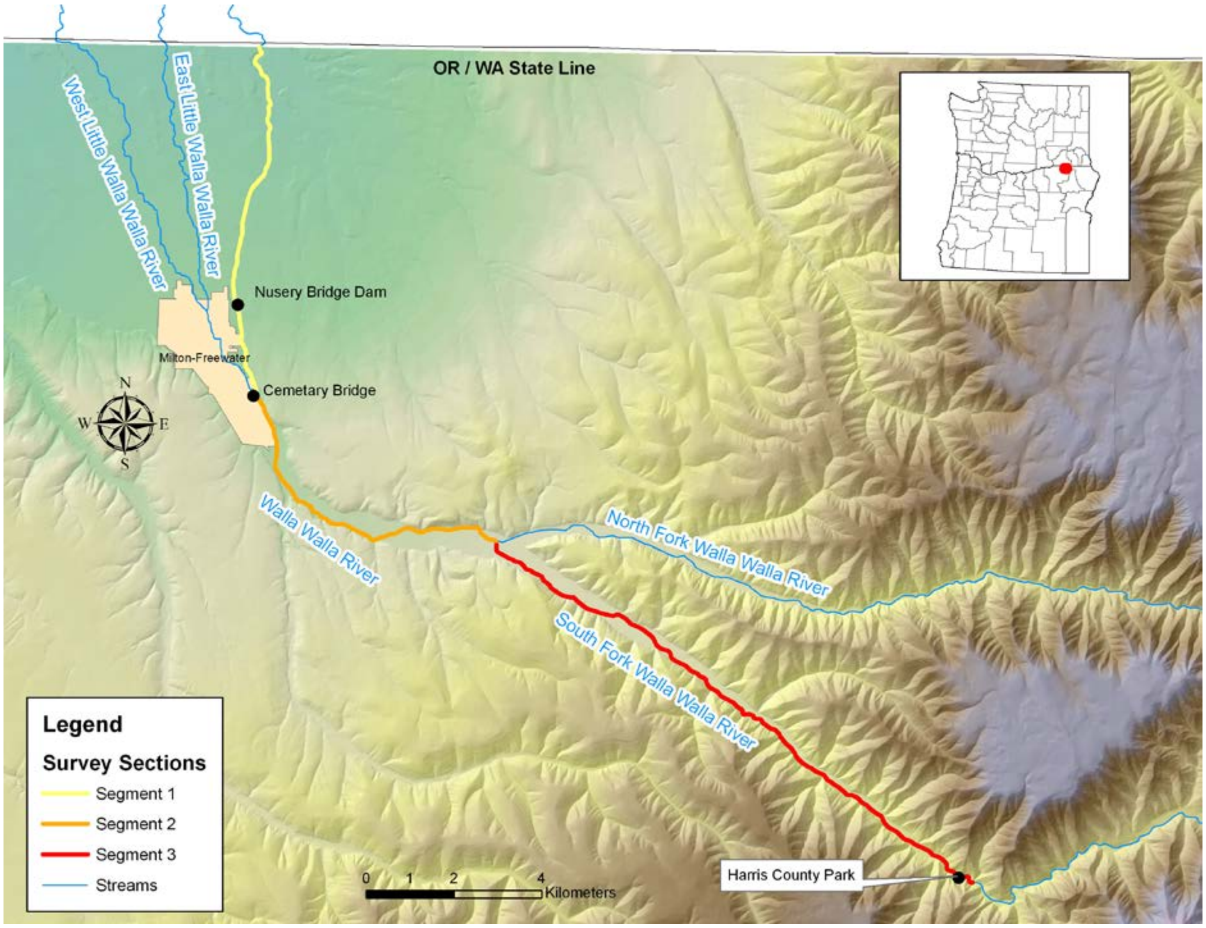

Figure 4.2. Map of the study area depicting 30 kilometers of the South Fork and mainstem Walla Walla Rivers divided into three segments.

Table 4.1. Substrate types and particle sizes used to classify dominant substrates for spawning bull trout.

Substrate Type	Particle size (cm)
Sand	<0.65
Pebble	0.65 – 2.54
Small Gravel	2.55 – 5.08
Large Gravel	5.09 – 7.62
Cobble	7.63 – 15.24
Boulder	>15.24

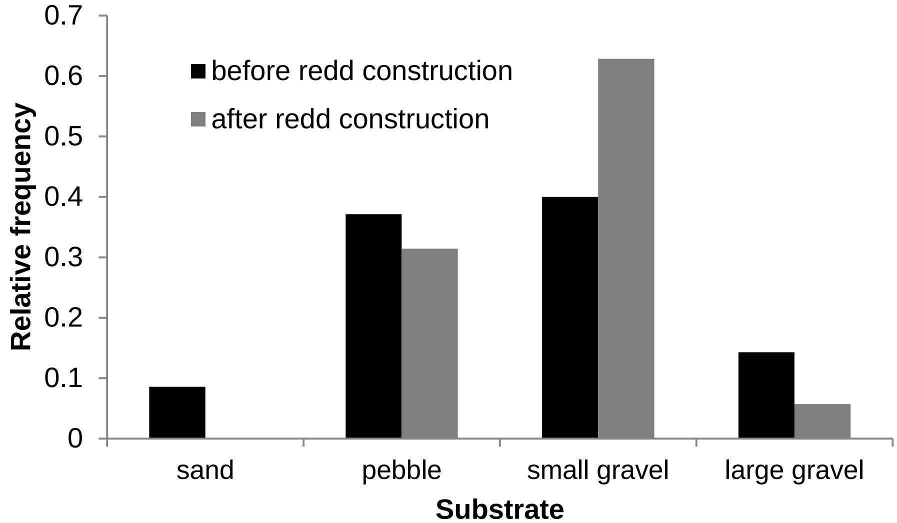

Figure 4.3. Relative frequency of substrate types before and after redd construction in the South Fork Walla Walla River.

Table 4.2. Mean, standard deviation, and min-max values (parentheses) at microhabitat use and non-use sites for spawning bull trout in the South Fork Walla Walla River used for model development.

Redd size and habitat status	Depth (m)	Nose velocity (m/s)	Mean column velocity (m/s)	n
Small				
Use	0.26 ± 0.10 (0.15 - 0.49)	0.12 ± 0.09 (0.01 - 0.29)	0.15 ± 0.14 (0.01 - 0.38)	15
non-use	0.32 ± 0.16 (0.06 - 0.70)	0.24 ± 0.26 (0.01 - 0.77)	0.51 ± 0.33 (0.01 - 1.05)	15
Medium				
Use	0.27 ± 0.12 (0.06 - 0.73)	0.13 ± 0.11 (0.00 - 0.51)	0.24 ± 0.18 (0.00 - 0.83)	175
non-use	0.34 ± 0.12 (0.03 - 0.98)	0.27 ± 0.23 (0.00 - 1.29)	0.58 ± 0.34 (0.00 - 1.63)	175
Large				
Use	0.32 ± 0.13 (0.09 - 0.58)	0.14 ± 0.13 (0.00 - 0.58)	0.27 ± 0.18 (0.00 - 0.86)	79
non-use	0.35 ± 0.17 (0.06 - 0.88)	0.273 ± .237 (0.00 - 1.42)	0.59 ± 0.32 (0.00 - 1.25)	79

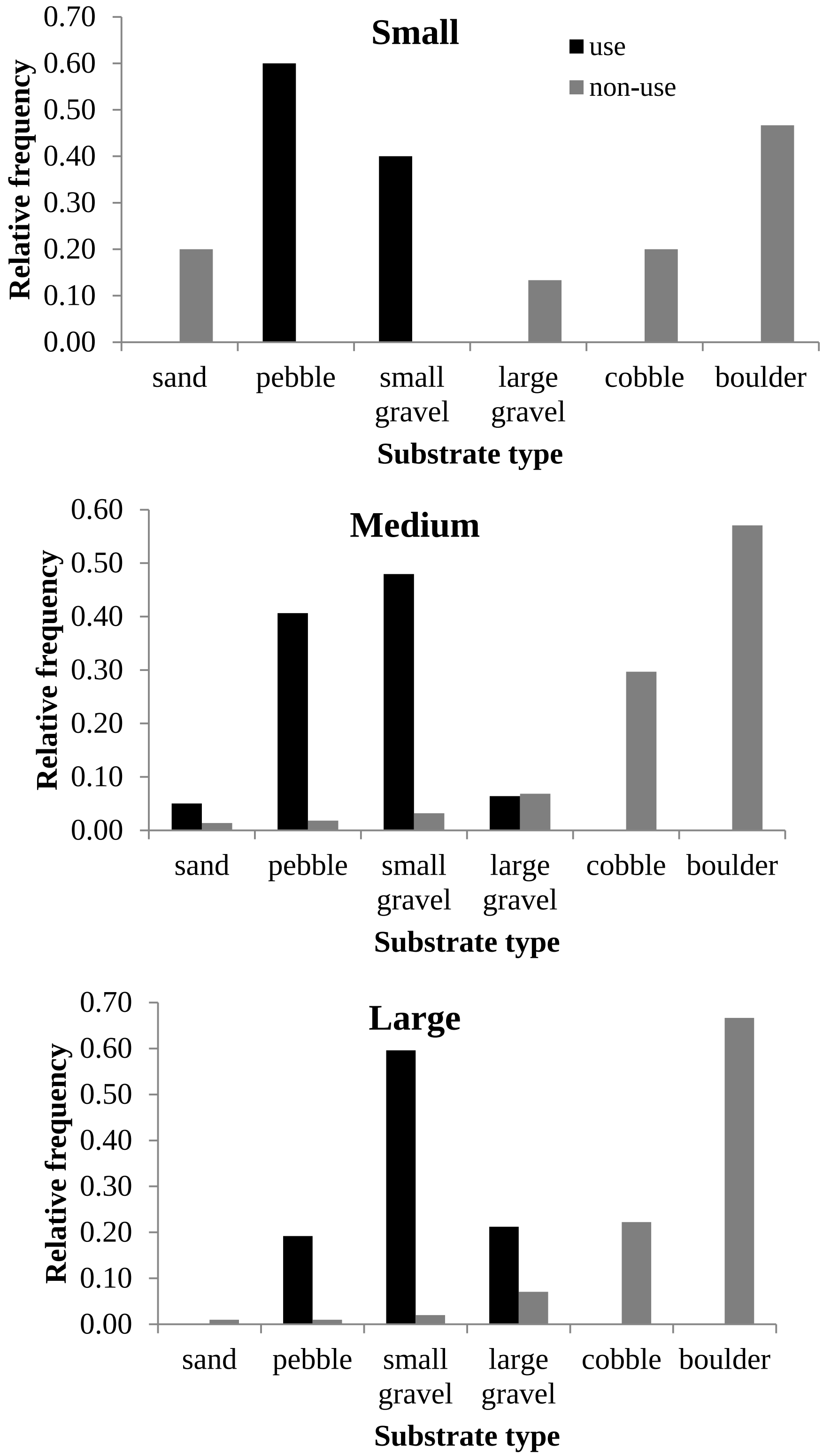

Figure 4.4. Relative frequency of substrate size classes at small, medium and large bull trout redd locations and at sites that were not used for spawning.

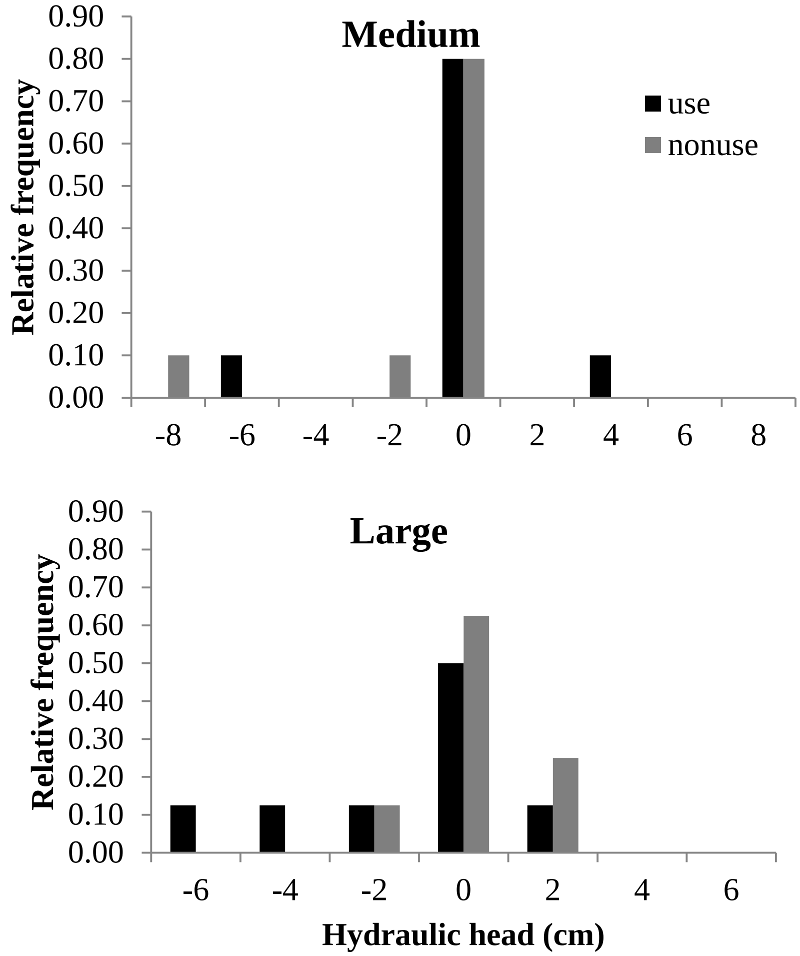

Figure 4.5. The relative frequency of hydraulic head measured at medium (0.5-1.5m) and large (>1.5m) bull trout redds and nonuse points in the South Fork Walla Walla River.

Table 4.3. Akaike Information Criterion (AIC) values, delta AIC values, and AIC weights for logistic regression models of substrate class (Sub.), mean column velocity (Vel.), and depth (Dep.) for the small redd size class.

Model	AIC	Δ AIC	AIC wt.
Sub.	12.0	0.0	0.53
Sub.+Vel.	14.0	2.0	0.20
Sub.+Dep.	14.0	2.0	0.20
Sub.+Vel.+Dep.	16.0	4.0	0.07
Vel.	31.3	19.3	0.00
Vel.+Dep.	32.1	20.1	0.00
Dep.	44.0	32.0	0.00

Table 4.4. Akaike Information Criterion (AIC) values, delta AIC values, and AIC weights for logistic regression models of substrate class (Sub.), mean column velocity (Vel.), and depth (Dep.) for the medium redd size class.

Model	AIC	Δ AIC	AIC wt.
Sub.+Vel.+Dep.	120.0	0.0	0.87
Sub.+Dep.	123.9	3.9	0.12
Sub.+Vel.	131.0	11.0	0.00
Sub.	131.8	11.8	0.00
Vel.	370.2	250.2	0.00
Vel.+Dep.	371.1	251.1	0.00
Dep.	474.4	354.4	0.00

Table 4.5. Akaike Information Criterion (AIC) values, delta AIC values, and AIC weights for logistic regression models of substrate class (Sub.), mean column velocity (Vel.), and depth (Dep.) for the large redd size class.

Model	AIC	Δ AIC	AIC wt.
Sub.+Vel.	51.7	0.0	0.73
Sub.+Vel.+Dep.	53.7	2.0	0.27
Sub.	63.1	11.4	0.00
Sub.+Dep.	64.8	13.1	0.00
Vel.	172.9	121.2	0.00
Vel.+Dep.	174.5	122.8	0.00
Dep.	221.1	169.4	0.00

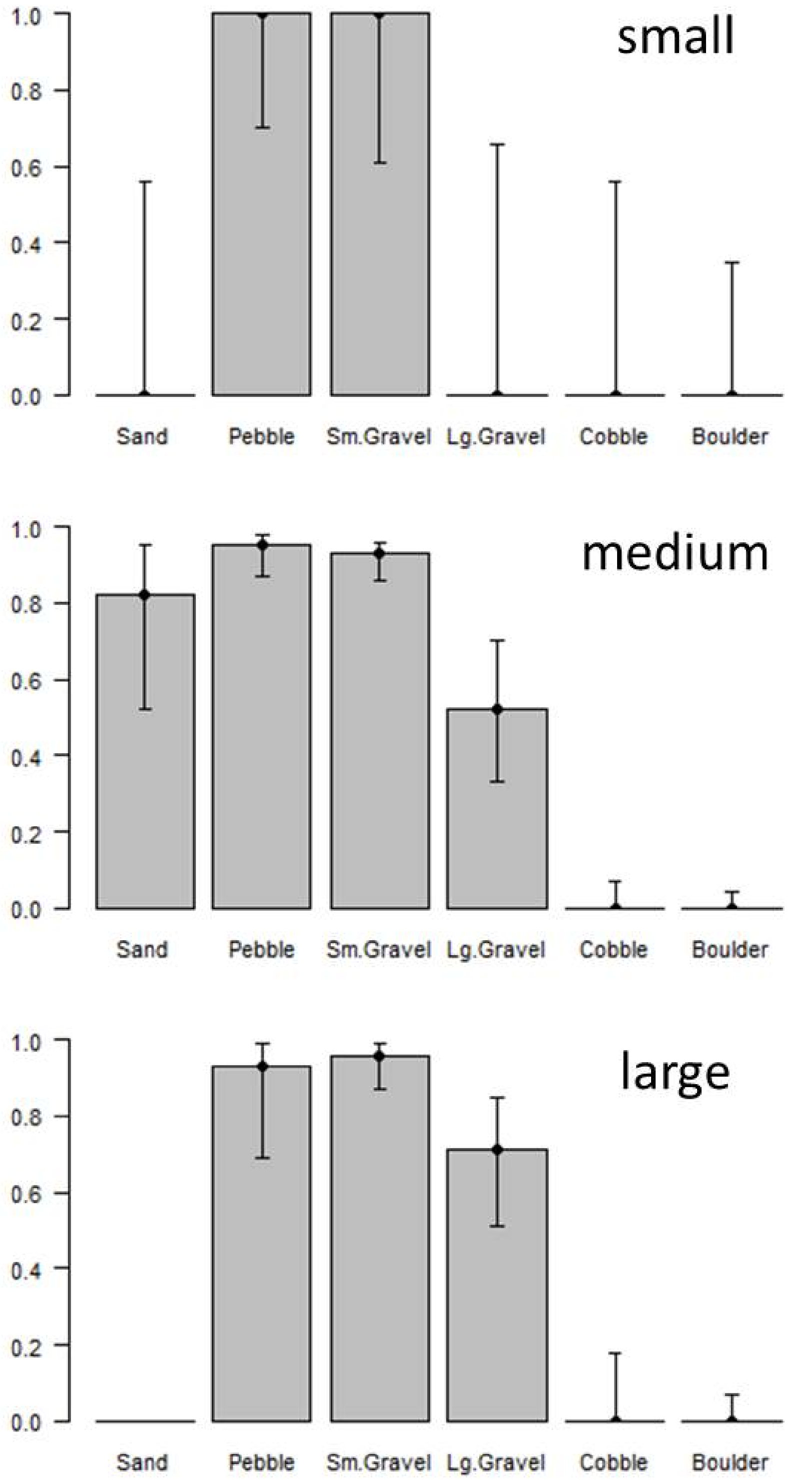

Figure 4.6. Model averaged predictions of the relative probability of spawning habitat use for each of the six substrate size classes across the small, medium, and large redd size classes.

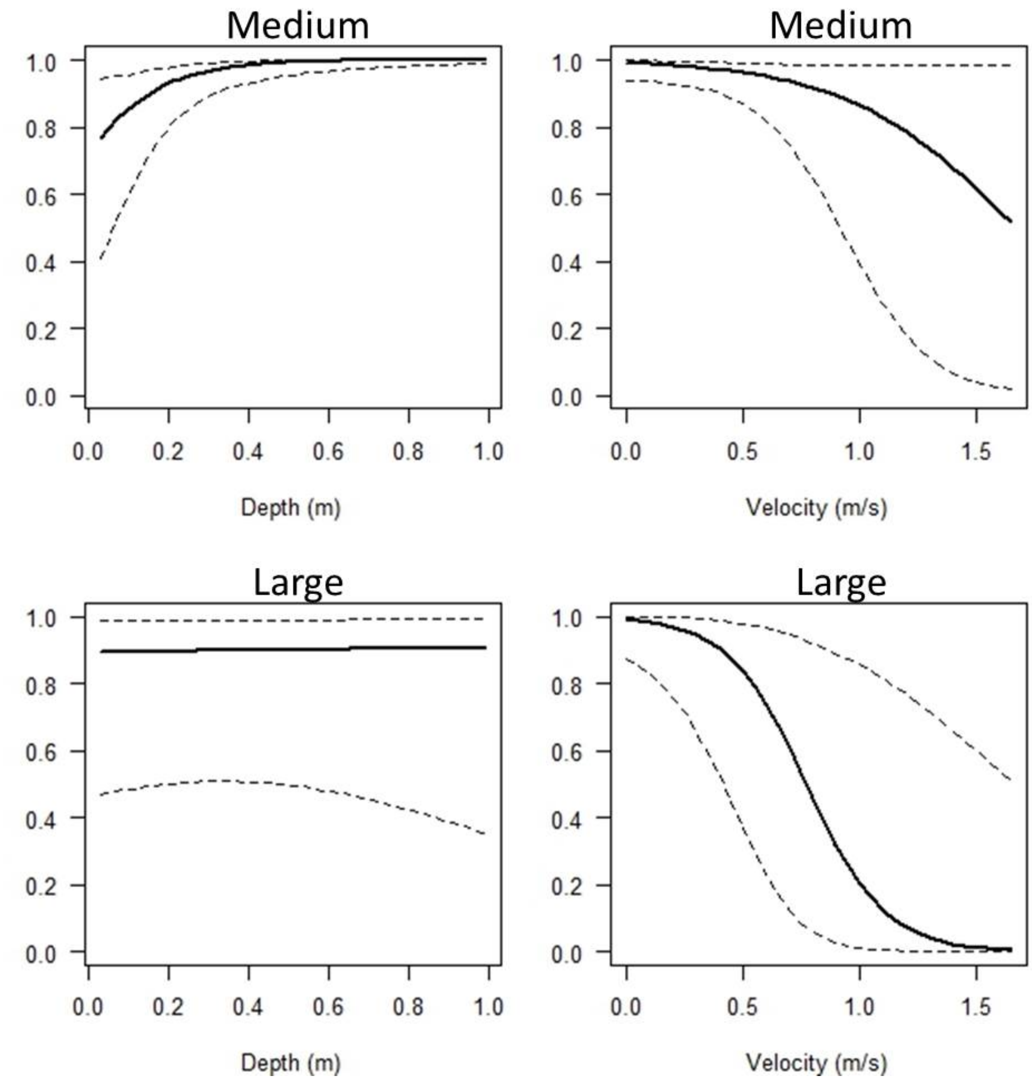

Figure 4.7. Model averaged predictions of the relative probability of spawning habitat use versus water depth (left column) and mean column velocity (right column) for redds in the medium size class (top row) and in the large size class (bottom row). The dashed lines represent 95% confidence intervals.

Table 4.6. Estimates of the number of degrees of heating that occurred per five river kilometers (rkm) distance downstream in the lower Walla Walla River, August-November 2004 and July-November 2005.

Period	Heating per 5 rkm
Jul 2005	2.1
Aug 2004	2.0
Aug 2005	1.9
Sep 2004	1.2
Sep 2005	1.4
Oct 2004	1.2
Oct 2005	0.9
Nov 2004	0.4
Nov 2005	0.5

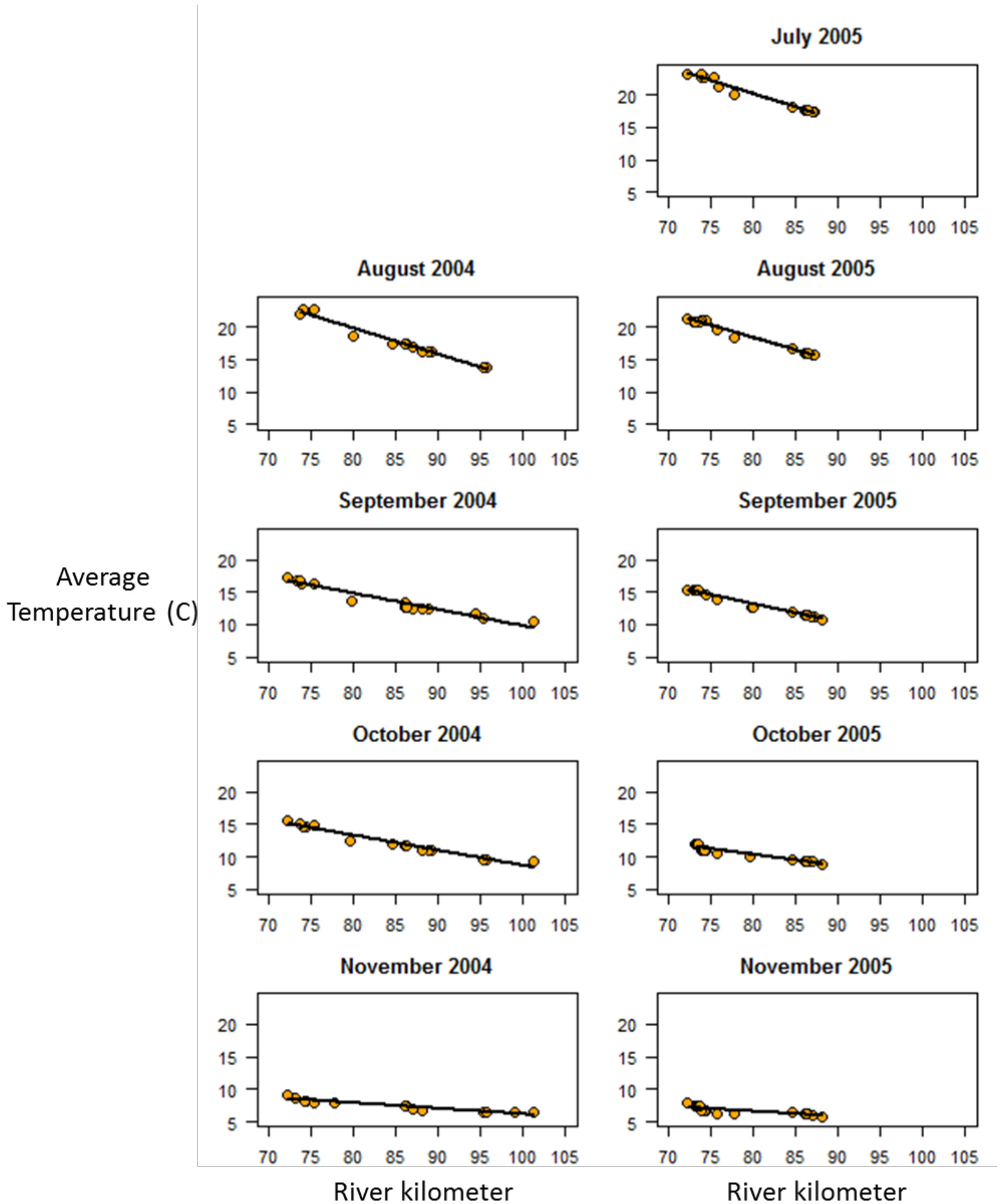

Figure 4.8. Average water temperatures versus river kilometer in the lower Walla Walla River during August-November 2004 (left column) and July-November 2005 (right column). Lines indicate linear association between water temperature and river kilometer.

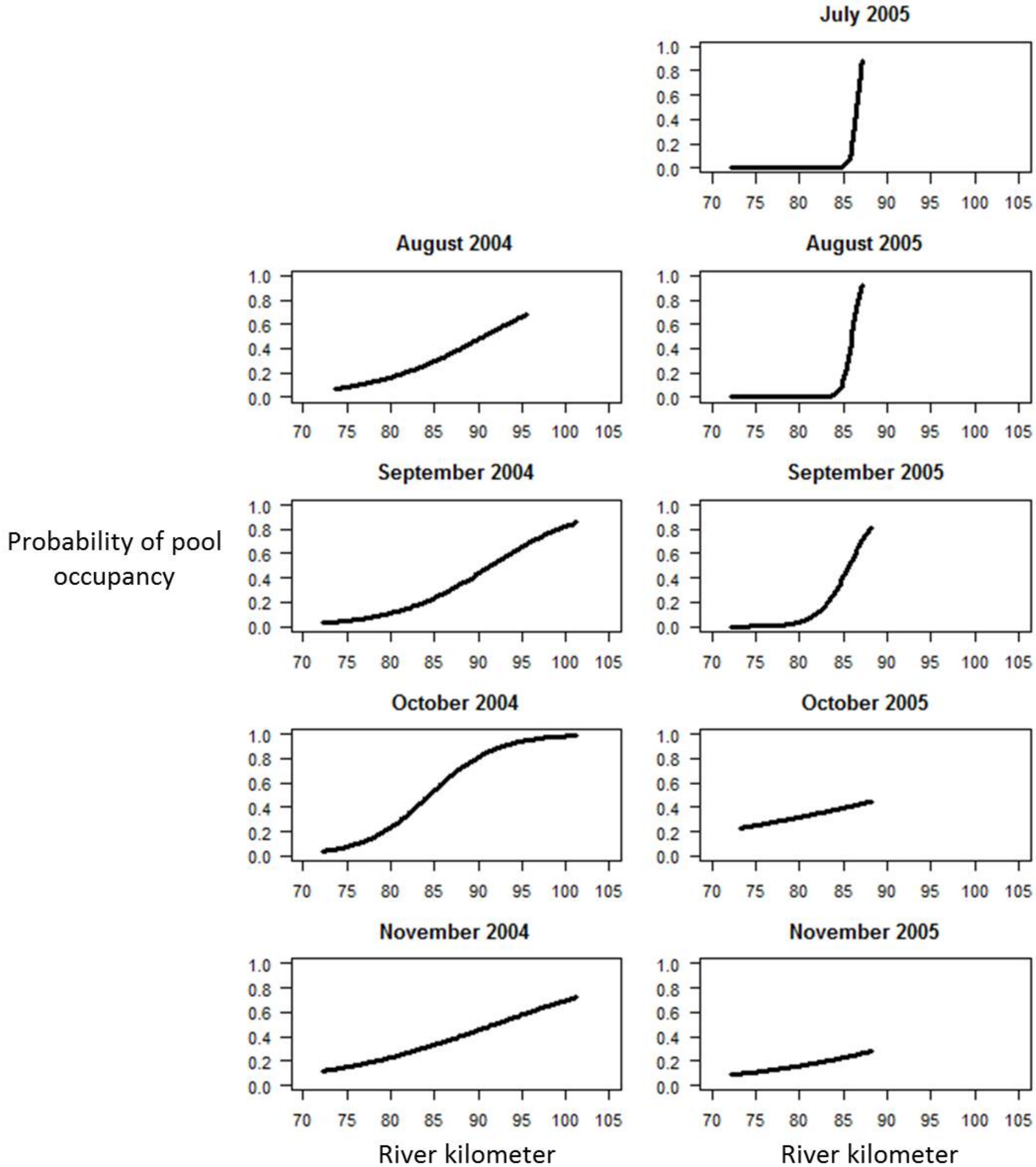

Figure 4.9. Probability of pool occupancy versus river kilometer in the lower Walla Walla River during August-November 2004 (left column) and July-November 2005 (right column).

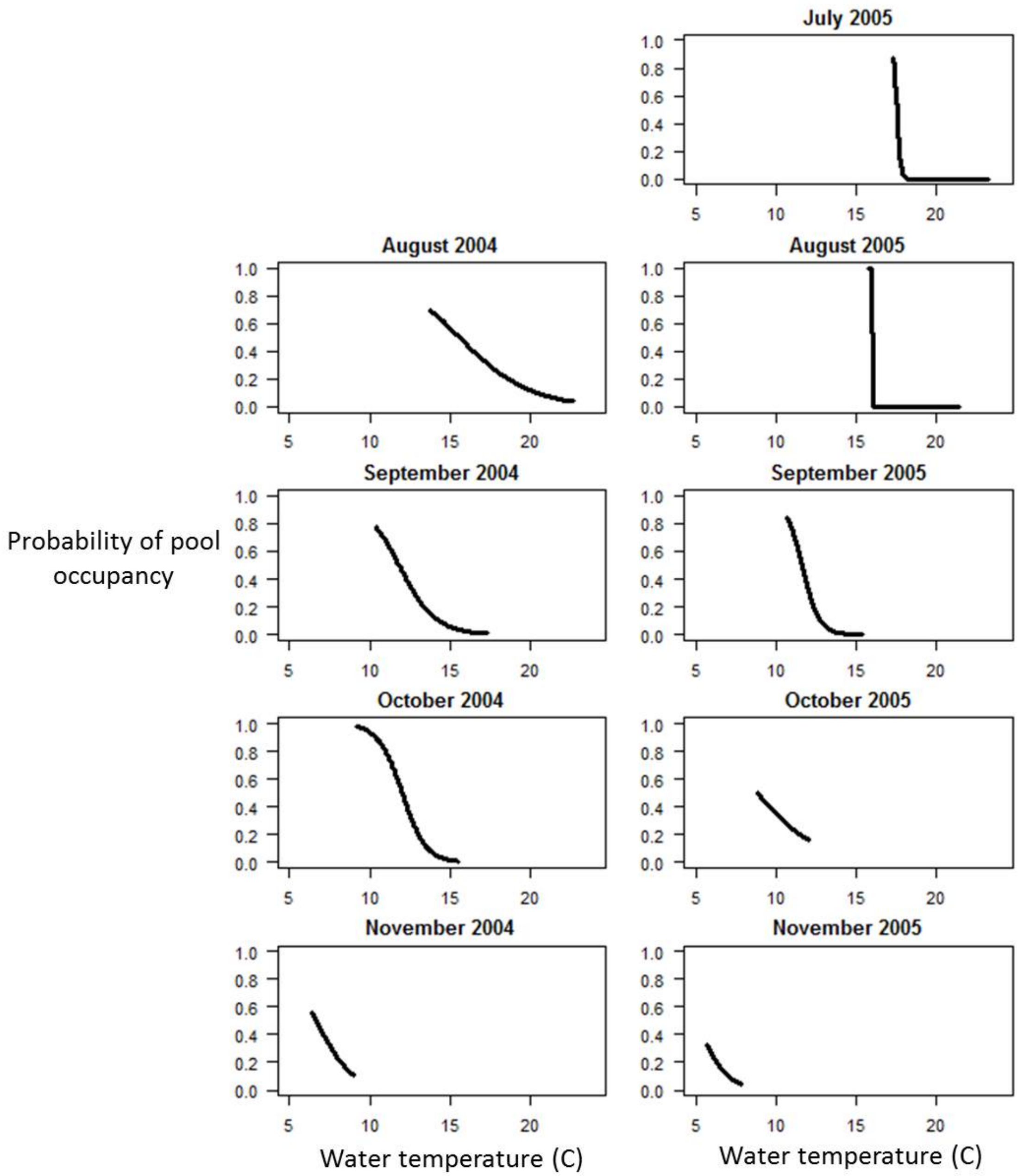

Figure 4.10. Probability of pool occupancy versus average water temperature in the lower Walla Walla River during August-November 2004 (left column) and July-November 2005 (right column).

Chapter 5 : Growth of Bull Trout from the South Fork Walla Walla River: an Assessment of Individual Variability and Differences between Life-history Forms

authored by

Julianne Harris
Courtney Newlon
Ryan Koch
Steven Haeseker

U.S. Fish and Wildlife Service

Introduction

Evaluating demographic variability both within a population and across a species' range is vital for effective conservation and management. Accurate and precise estimates of demographic parameters such as individual growth improve our understanding of basic ecology as well as provide inputs for modeling population change under different management scenarios (Haddon 2001). However, it is not only important to estimate expected values for demographic parameters, but also to evaluate variability among individuals within a population or species (Pilling et al. 2002; Johnston and Post 2009; Marco-Rius 2013; Lloyd-Jones 2014). This is especially important for species of conservation value that exhibit large variation in life-history and thus also in their demographic rates, such as bull trout *Salvelinus confluentus* (Brenkman et al. 2007; Al-Chokhachy and Budy 2008; Johnston and Post 2009).

Bull trout is a salmonid found in streams in the northwestern United States and Canada that demonstrates variation in migration patterns and demographic rates both within and among populations (Rieman and Dunham 2000; Al-Chokhachy and Budy 2008; Tyre et al. 2011). Bull trout life histories are classified as stream resident, fluvial (e.g., Al-Chokhachy and Budy 2008), adfluvial (e.g., Johnston and Post 2009), and anadromous (e.g., Brenkman et al. 2007). While residents permanently remain in their natal streams, migrants (i.e., fluvial, adfluvial, and anadromous) emigrate as young and return as adults (Mogen and Kaeding 2005). Migratory individuals have been observed to grow to larger sizes than residents (Mochnacz et al. 2013) and as a result are likely more fecund (Johnston and Post 2009). Within a system, migratory and resident forms of bull trout have been observed together and such life-history variability is considered essential for population persistence (Homel et al. 2008; Watry and Scarnecchia 2008; Paragamian and Walters 2011; Tyre et al. 2011).

Bull trout populations historically declined due to multiple compounding anthropogenic factors which vary by basin and include habitat degradation and fragmentation, overfishing, and the introduction of non-native species (Fraley and Shepard 1989; Rieman and McIntyre 1995; Buktenica et al. 2013). The U.S. Fish and Wildlife Service (FWS) listed Columbia River bull trout populations as threatened on the Endangered Species Act (ESA) in 1998 and all other populations in the United States followed in 1999; they are ecologically important and many populations are in need of recovery efforts (USFWS 2012). Evaluation of variability in population demographic parameters such as growth among individuals, life stages, and life-history forms would improve our understanding of basic biology, identify differences between populations, and provide information for population modeling to aid in recovery and management. Specifically, information on growth rates and variability can be important for stage-based population viability modeling (USFWS 2012).

Individual variability in growth is commonly examined using either back-calculated length-at-age or changes in length over time. Each approach has pros and cons. Back-calculating length-at-age from an ageing structure (i.e., otolith, scale, fin ray, etc.) is efficient since the life-long growth pattern of a fish can be examined upon collection (Pilling et al. 2002). However, this method is only appropriate when a structure can be collected and used successful to estimate age (i.e., age validation; Beamish and McFarlane 1983), and growth of the structure must be correlated with growth of the fish in length (Pilling et al. 2002; Alós et al. 2009). Modeling individual growth by changes in length over time is also informative and does not necessitate a successful ageing structure, but does require that individuals be marked and subsequently recaptured after time at large in the natural environment, which can require considerable effort. Also, marking and capture procedures must not impact growth.

We incorporated data on change-in-length from a PIT tag mark-recapture study with back-calculated length-at-age from otoliths to estimate parameters, examine individual variability, and identify patterns in growth for bull trout that spawn in the South Fork Walla Walla River (SFWWR) in Northeast Oregon. The SRWWR is a tributary to the Walla Walla River (WWR) which flows into the Columbia River in Washington (Figure 5.1). It has a fluvial population of bull trout that includes both residents and migrants (Al-Chokhachy and Budy 2008; Homel et al. 2008). Simultaneous movement information allowed us to differentiate migratory and resident PIT tagged individuals and back-calculation of length-at-age allowed us to better evaluate growth patterns and to examine length-at-age. Objectives were to determine if growth varied between migratory and resident components, to evaluate individual variability and patterns in growth, and to estimate von Bertalanffy growth parameters for this population of bull trout.

Previously, the Utah Cooperative Fish and Wildlife Research Unit at Utah State University (USU) evaluated growth for bull trout in the SFWWR (Al-Chokhachy and Budy 2008; Budy et al. 2011). Although researchers did not examine individual variability or differences by life-history form, they did use multiple sampling methods. Budy et al. (2011) used mark-recapture data to produce estimates of average growth in both length and weight by size class and found that annual growth in length generally decreased with fish length, but that annual growth in weight generally increased with fish length. Average growth in length for resident bull trout was as high as approximately 70 mm total length (TL) per year. Average growth in weight was as high as around 180 grams per year. They also used a power function to estimate length-at-age from otolith data: $TL = 88.43*(\text{age in years})^{0.826}$. Al-Chokhachy and Budy (2008) used information on total length (in m) at age (in years) from otoliths to produce a von Bertalanffy growth curve: $TL= 2.308*(1\text{-}EXP^{-0.00254*(time+0.462)})$. Differences between the von Bertalanffy curve fit by Al-Chokhachy and Budy (2008) and the curve generated from otolith data in this study could be related to differences in ageing-techniques, analysis methods, and the specific otoliths included.

Methods

PIT-tagging and recapture

Bull trout were PIT-tagged and recaptured in the SFWWR between Harris Park and Reser Creek, June-August 2002-2011, by USU (Figure 5.1). Sampling periods occurred when migratory individuals were present for spawning (Al-Chokhachy and Budy 2008). This long term project had many objectives and more detailed sampling methods can be found in Budy et al. (2003) and Al-Chokhachy and Budy (2008). Fish were collected by multiple methods including snorkeling to move fish into trap nets, electrofishing to a seine net, and angling. At capture, each fish was anesthetized with MS-222 (tricaine methanesulfonate), measured for either fork length (FL, in mm) or TL (in mm; which was later converted to FL; Budy et al. 2011), and scanned for a PIT tag. If no PIT tag was detected, a 12 mm or a 23 mm (usually) PIT tag was placed in a small (3-7 mm) incision in the body cavity on the ventral side of the fish anterior to the pelvic fin. After tagging, the individual was placed in a flow-through recovery tank until equilibrium was restored and then released in slow-water habitat near the capture location.

Additional bull trout were tagged and recaptured by the FWS year-round, 2007-2011, by angling in the lower SFWWR below Harris Park and in the mainstem of the WWR from the mouth of the SFWWR to the mouth of the WWR (Figure 5.1). For this effort, most bull trout were tagged in the WWR between river kilometers 74 and 76, immediately south of the Washington state line (Figure 5.1). Each captured bull trout was anesthetized with MS-222, measured for FL (in mm), and scanned for the presence of a PIT tag. For each untagged bull trout, a 23 mm PIT tag was inserted into a 3-4 mm abdominal incision. Individuals were released into nearby sheltered areas after equilibrium was restored.

Although all bull trout tagged in the WWR would be considered “migratory”, those first collected in the SFWWR would be considered a mix of migrants and residents, since both would be collected by sampling in the area during the spawning period. Individuals tagged in the SFWWR were considered “presumed migratory” if they passed a PIT tag antenna located at Harris Park (Figure 5.1) and were considered “presumed resident” if they did not, as done by Al-Chokhachy and Budy (2008) and Homel et al. (2008). All recaptures made within 14 days of tagging were eliminated from analysis; some fish recaptured soon after tagging were not re-measured and this would also reduce the short-term impacts of handling and tagging on results.

Otolith collection and preparation

Up to 10 bull trout each year (2002-2011) in the SFWWR were measured and sacrificed by USU for the collection of otoliths to assess age and growth. Since otoliths must be lethally collected, sample sizes were small for ESA-listed bull trout and otoliths have not been formally validated to estimate age; however, when compared to other potential structures, they are considered accurate and precise (Zymonas and McMahon 2009). Otoliths were mounted in epoxy and sanded to produce a cross section that included the core. On three separate occasions, the section of each otolith was examined for annulus count under 16-20X magnification and the distance of each annulus (i.e., the location of closely spaced circuli, as done in Zymonas and McMahon 2009) from the core was measured using a Leica digital image analysis system. For each occasion, annulus count and distance measurements were recorded along a trajectory selected as the clearest on that examination. If the same age was assigned each time the otolith was examined, the otolith was included in analyses. If not, the otolith was examined and assigned an age once more. If three of the four age assignments were the same, the otolith was included and the one alternate age was dropped. All otoliths not assigned the same age in three out of a possible four reads were excluded from analysis. Back calculation was based on the measured distance from the core to each annulus using the direct proportion method, since otoliths can be present at the time of hatch (Klumb et al. 2001). Back calculation was completed using measurements from each time each otolith was examined to evaluate measurement error (i.e., error in the measured estimate of FL-at-age) separately from process error (i.e., lack of fit to the selected growth model).

Growth analyses

We first assessed growth by change-in-length over time from mark-recapture data and back-calculated length-at-age from otoliths separately, and then estimated final growth parameters using both approaches in an integrated model. We described bull trout growth using the von Bertalanffy model which can estimate three growth parameters: k (growth rate coefficient), L_∞ (asymptotic length) and t_0 (hypothetical age at which length is zero; Quinn and Deriso 1999; Haddon 2001). The von Bertalanffy model assumes that the rate of growth declines linearly with increasing size and is commonly used for describing fish growth (Smith et al. 1997; Quinn and Deriso 1999; Haddon 2001). We used a hierarchical approach to assess individual variability in growth parameters and differences between life-history forms (Alós et al. 2009; Zhang et al. 2009; Windsland et al. 2013; Tang et al. 2014). All models were evaluated with Bayesian methods using OpenBUGS software (v. 3.1.2). Model priors are in Table 5.1; priors were selected to be fairly uninformative in a similar manner to previous studies (Zhang et al. 2009; Windsland et al. 2013; Tang et al. 2014). Models were run with two chains and a burn-in period of 50,000 after which convergence was reach as assessed by examining history plots

(Spiegelhalter et al. 2003; Kéry 2010). We saved an additional 50,000 iterations using a thinning rate of 50, which reduced autocorrelation and produced stable parameters as identified by history and density plots.

Fabens (1965) transformed the standard von Bertalanffy model which expresses mean length as a function of age, for use with mark-recapture data (i.e., change in length over time). Assumptions of the Fabens (1965) method are that expected values of L_∞ and k are the same for all individuals. However, when individual variability is high, estimates can be substantially biased (Sainsbury 1980; Smith et al. 1997; Wang 1998; Eveson et al. 2007). For our mark-recapture data we used a hierarchical extension to the von Bertalanffy model developed by Zhang et al. (2009) to incorporate individual variability when length of an individual (i) is measured at capture and then after time-at-large in the natural environment (j):

$$\hat{L}_{i,j} = L_{\infty,i} * (1\text{-}\exp(-k_i * (A_i + t_{i,j})))$$

where $\hat{L}_{i,j}$ is the expected length of fish i at time j, $L_{\infty,i}$ is the estimated asymptotic length of fish i, k_i is the estimated growth rate coefficient for fish i, A_i is the estimated age (in years) at tagging minus t_0 for fish i, and $t_{i,j}$ is the period at large for fish i between tagging and time j. Each measured length ($L_{i,j}$) comes from a normal distribution with mean $\hat{L}_{i,j}$ and an estimated standard deviation (σ), which represents both measurement error (i.e., length measurement errors) and process error (i.e., lack of model fit). Each individual's estimated L_∞ (i.e., each $L_{\infty,i}$) is assumed to be a random sample from a population-level normal distribution with mean UL_∞ and population standard deviation σ_{L_∞} representing variability in L_∞ among individuals. Similarly, all k_i are assumed to be random samples from a normal distribution with mean Uk and standard deviation σ_k. Comparable hierarchical approaches have been used previously to assess individual variability in growth (Windsland et al. 2013; Tang et al. 2014).

Using our mark-recapture data, we evaluated differences in growth by life-history form and individual variability in growth. Specifically, von Bertalanffy models were run assuming that: 1) L_∞ and k were the same for each individual (i.e., one non-hierarchical model using the Fabens method); 2) growth parameters differed between residents and migrants (i.e., two non-hierarchical models, one for residents, the other for migrants); 3) either or both growth parameters showed individual variability (i.e., $L_{\infty,i}$ and k_i as random effects); and, 4) growth parameters for residents and migrants differed, but also showed individual variability (i.e., $L_{\infty,i}$ and k_i as random effects from different distributions for residents and migrants). Similar to Zhang et al. (2009) and Tang et al. (2014), we used the Deviance Information Criterion (DIC) to quantify model fit and complexity (i.e., estimated number of model parameters). Comparable to the more common Akaike Information Criterion, DIC is an information theoretic approach to select between candidate models and the model with the lowest score (i.e., appropriate tradeoff between fit and the number of parameters) is selected; however, DIC is more commonly used in Bayesian analyses focused on estimating random effects, since assessing model complexity can be difficult in hierarchical models (Askey et al. 2007; Zhang et al. 2009; Tang et al. 2014).

As the age of marked individuals was unknown, no direct estimates of t_0 could be produced. Gould (1987) observed that bull trout were an average of approximately 14 mm FL when hatching was "nearly complete". Using 14 mm as the expected length at age-0, we estimated a hypothetical t_0 using the following:

$$t_0 = \frac{Log_e(1 - \frac{14}{UL_\infty})}{Uk}$$

where UL_∞ and Uk were from the model with the lowest DIC score. We used the hypothetical estimate of t_0 to estimate age-at-tagging for migrant and resident bull trout.

Environmental variability likely impacts bull trout growth (Selong et al. 2001; Johnston and Post 2009). To examine potential impacts of annual environmental variability on growth, we calculated means (with 95% credible intervals) of L_∞ values by year-at-large for residents. Since most residents were sampled in the summer, we considered the year-at-large to be from one summer (June - August) to the next summer. We did not include migrants since they were collected year round. We restricted analysis to individuals at large for just one year.

We also estimated growth parameters using back-calculated FL-at-age from otoliths. For otolith data, we used the standard von Bertalanffy growth model adapted for individual variability in L_∞, k, and t_0 (Pilling et al. 2002; Alós et al. 2009):

$$\hat{L}_{i,j} = L_{\infty,i} * (1\text{-exp}(-k_i * (t_j - t_{0,i})))$$

where $L_{\infty,i}$ and k_i and their associated standard deviations were estimated in the same manner as for mark-recapture data. Each individual's t_0 (i.e.,$t_{0,i}$) was estimated from a normal distribution with population mean Ut_0 and population standard deviation σ_{t_0}. Different from mark-recapture models, measurements of length (L_{ijk}) for each individual (i) at each year interval (j) from each of the three back-calculations (k) were drawn from normal distributions with mean estimated length-at-age ($\widehat{mL}_{i,j}$) for that individual (i) at that time interval (j) and an estimated standard deviation (σ_B) to account for measurement error associated with back-calculation. Each $\widehat{mL}_{i,j}$ then also was drawn from a normal distribution with mean expected length ($\hat{L}_{i,j}$) and an estimated standard deviation (σ_P) to account for process error. Differentiating measurement error and process error allowed us to evaluate how well growth fit the von Bertalanffy model produced for each otolith. Assuming back-calculated length-at-age is appropriate, process error could be examined by evaluating non-overlapping 95% credible intervals between $\widehat{mL}_{i,j}$ and $\hat{L}_{i,j}$. Since included otoliths varied in age from 1-6, we also evaluated if mean length-at-age-1 varied (by 95% credible intervals) by collection age.

In addition to models developed for mark-recapture and otolith datasets, final growth parameters were estimated using an integrated model combining both data sources. Integrated models jointly analyze multiple independent data sets to produce parameter estimates; they can increase estimate precision, allow for examination of potential biases, and potentially estimate parameters that cannot be estimated using only one method (Abadi et al. 2010; Maunder and Punt 2013). Final growth parameter estimates were made using the mark-recapture model selected by DIC. The joint likelihood of independent datasets is the product of the individual likelihoods. In OpenBUGS, the joint likelihood can be defined implicitly from the individual likelihood models to estimate common parameters with appropriate variance (Rhodes et al. 2011; Kéry and Schaub 2012). Mark-recapture data on change in length over time was used to estimate UL_∞ and Uk and back-calculated length-at-age was used to estimate UL_∞, Uk, and t_0. Although we did detect individual variability in t_0 from otolith data, we did not model t_0 as a random effect in the integrated model that included both data sources, as posterior distributions of fit were poor. Parameter estimates from the integrated model were used to assess the extent of individual variability in growth as well as differences between life-history forms.

Results

After removing recaptures less than 14 days after tagging, there were a total of 253 individuals recaptured one to four times, 2002 to 2011. Most (88.5%) individuals were only recaptured once. Of the 253 recaptured individuals, 124 were considered "presumed resident" (i.e., tagged in the SFWWR and did not pass the Harris Park antenna; see Figure 5.1), 41 were considered "presumed migratory" (i.e., tagged in the SFWWR and did pass the Harris Park antenna at some point), and 88 were migratory (i.e., tagged in the WWR). Presumed residents were at-large for 26 to 1841 days for an average of 454 days and were collected at sizes of 91 to 523 mm FL. Presumed migrants were at-large for 126 to 1452 days for an average of 661 days and ranged from 92 to 620 mm FL. Migratory bull trout were at-large for 15 to 1134 days for an average of 173 days and were collected at sizes from 159 to 645 mm FL.

Change in FL between tagging and first recapture (i.e., growth) appeared to decline with FL at tagging after fish reached 200 mm FL (Figure 5.2). There was high variability in growth, likely as a result of individual variability and the seasonal period at-large between tagging and first recapture. Growth rates were higher and more variable for migrants than for residents. For residents, growth was similar among the smallest tagged individuals (up to ~200 mm FL) followed by a decline, which could suggest either a different growth rate for young fish or an impact of the PIT tag on growth of small fish. For presumed migrants, growth rates started out similar to those of residents, but appeared to increase slightly as fish approached 200 mm FL. Only three bull trout tagged in the SFWWR between 200 and 400 mm FL were classified as "presumed migratory". Presumed migrants less than 200 mm FL had likely not left and those greater than 400 mm FL were likely returning to spawn. Migrants showed higher rates of growth, by size, as compared to residents or young presumed migrants. Presumed residents were modeled as "residents" and migrants as "migrants". Presumed migrants were removed from further growth analyses.

The model with the lowest DIC score included individual variability in L_∞ and k, but did not suggest that individual estimates of L_∞ and k for migrants and residents came from different distributions (Table 5.2). The 95% credible intervals on standard deviation estimates for both L_∞ and k were not close to overlapping zero, suggesting the need for individual variability in both parameters. Models with individual variability ranked more highly (i.e., had lower DIC scores) than those without, especially models with variability in L_∞. Models that did not include individual variability in either parameter had high (i.e., poor) DIC scores. In general, models that incorporated individual variability resulted in lower estimates of L_∞ and higher estimates of k, than models without individual variability. Models with differences between residents and migrants produced higher estimates of L_∞ and k for migrants than for residents, suggesting that migrants grow faster and attain larger sizes than residents. However, individual variability in terms of L_∞ and k for residents and migrants was estimated to be fairly similar in magnitude (Table 5.2). In the model with the lowest DIC score, estimates of $L_{\infty,i}$ showed substantial variability ranging from 207 to 690 mm FL. Variability in L_∞ could not be attributed to annual differences, as 95% credible intervals between mean values by year overlapped for all years (Figure 5.3). The mean L_∞ for migrants (median= 453, 95% credible intervals= 428-483) was 87 mm FL higher than the mean for residents (366, 342-393) and 95% credible intervals on estimates did not overlap. Similarly, individual estimates for k ranged from 0.31 to 1.18. The mean estimate of k for migrants (0.85, 0.69-1.04) was higher than that for residents (0.70, 0.55-0.88), although 95% credible intervals did overlap. Most bull trout were estimated to be young at tagging, with mean ages slightly higher for residents (1.7, 1.4-1.9) than for migrants (1.1, 1.0-

1.3). Estimated ages at tagging ranged from 0.4 to 3.1 years for residents and from 0.5 to 2.2 years for migrants.

A total of 36 otolith sections were assigned the same age in three out of a possible four reads. Included otoliths were from individuals that ranged from 97 to 544 mm FL and were assigned an age of 1-6. The 95% credible intervals for measurement error, σ_B, did not include zero, suggesting that there were errors associated with back-calculation; however, the mean estimate was 10.2 mm FL, which is relatively small compared to the estimated differences between annuli (Table 5.2). Generally, the estimated FL-at-age-1 increased with assigned age at collection (Figure 5.4).

Estimates of L_∞ from back-calculation of length-at-age from otoliths overlapped with those of tagged resident and migrant individuals, ranging from 462 to 956 mm FL. In contrast, median values for k were lower, ranging from 0.125 to 0.132. The estimate of UL_∞ by analysis of otolith data was higher than that from mark-recapture data and the estimate of Uk was lower and 95% credible intervals did not overlap (Table 5.3). Variability associated with UL_∞ (i.e., σ_{L_∞}) from otoliths was slightly higher than that from mark-recapture data, although 95% credible intervals overlapped. In contrast, very little individual variability was estimated for k with 95% credible intervals on σ_k including zero out to the third decimal place. The estimate of Ut_0 from otoliths was lower than those estimated from auxiliary information on size-at-hatch obtained from a laboratory study (14 mm FL; Gould 1987), resulting in a median age-0 length of 30 mm FL. A higher estimated length-at-age-0 could suggest the need for an intercept in back-calculation, although, t_0 does not always correspond to empirical estimates of length at hatch (Pardo et al. 2013) and 95% credible intervals included 14 mm FL. Some non-trivial individual variability was estimated for t_0 (Table 5.3).

Evaluation of 95% credible intervals of average FL-at-age ($\widehat{mL_{i,j}}$) and expected FL-at-age ($\hat{L}_{i,j}$) illustrated patterns in process error (Figure 5.5). All non-overlapping 95% credible intervals were from otoliths assigned an age of five (2 of 9 individuals) or six (3 of 6 individuals). For all individuals with non-overlapping 95% credible intervals, expected FL at age-4 was less than the average back-calculated FL value at age-4. In addition, for three out of five of these individuals, expected FL values at ages 2 or 3 were higher than back-calculated estimates at those ages, possibly suggesting higher growth between 2 and 4, than expected by the best-fit von Bertalanffy model for that individual. During these apparent higher-than-expected growth periods, individuals were estimated to range in size from 189 to 419 mm FL with mean growth rates estimated up to 0.31 (i.e., 114 mm FL in one year).

The integrated model combining change in length data from recapture of tagged residents and migrants with back-calculation of length-at-age from otoliths of individuals with unknown migratory status generally resulted in intermediate parameter estimates (Table 5.3). As expected, measurement error associated with back-calculation of length was unchanged. Error associated with model fit for recaptured residents and migrants, as well as process error for otoliths all increased slightly suggesting a decrease in fit from separate models, although 95% credible intervals did overlap from previous estimates, suggesting that the reduction in fit was not substantial. Estimates of UL_∞, $Uk,$ and their associated estimates of individual variability were intermediate between those originally estimated by separate models, although more variability was attributed to L_∞, as opposed to k (Table 5.3). Precision increased for some parameters and decreased for others as compared to mark-recapture data alone. The estimated mean age for migrants at tagging (1.7, 1.5 – 2.1) was lower than that for residents (2.6, 2.3 – 2.9), although estimated ages were higher for both in the combined model, ranging from 0.6 to 5.4 years for residents and 0.72 to 3.5 years for migrants. An increase in estimated age occurred since estimates L_∞ were higher and those for k were lower in the combined model as compared to the model including only mark-recapture data.

Examination of individual estimates of L_∞ and k produced from the integrated model indicated potential differences for residents and migrants (Figure 5.6). Although, distributions overlapped, migrants generally had higher individual estimates of both L_∞ and k than did residents (Figure 5.6). The mean estimate of L_∞ for migrants (559, 514-625) was 123 mm FL higher than that for residents (436, 405-491) and 95% credible intervals did not overlap. The mean estimate for k was also higher for migrants (0.44, 0.29-0.55), than for residents (0.36, 0.26-0.44), but 95% credible intervals did overlap. Estimated growth parameters from most otoliths generally resembled those of residents, although some older fish (5-6 years old), had L_∞ values similar to migrants, but had much lower estimates of k (Figure 5.6). Overall, the integrated model resulted in higher estimates of L_∞ and lower estimates of k for recaptured individuals and lower estimates of L_∞ and higher estimates of k for otoliths. The final growth curve suggested that the average bull trout would be expected to reach 200 mm FL between 2 and 3 years old and would reach 400 mm FL at around 6 years old. For migrants, reaching 400 mm FL would be expected to occur for the average individual around age 4, whereas the average resident would not be expected to reach 400 mm FL until about age 8 (Figure 5.7).

Discussion

We evaluated individual growth patterns of SFWWR bull trout by age and life-history form using two methods. Although results varied between approaches, they were fairly similar and the combination produced parameter estimates that were precise and appeared appropriate given ages, growth rates, and lengths observed for this population. In particular, annual length-frequency distributions in Budy et al. (2011), often demonstrated a peak at approximately 50 mm FL (possibly young hatched earlier that year) followed by a highly variable peak centered around 110 mm FL (possibly juveniles hatched the previous year) with no other discernible patterns for larger fish, but few fish observed over 600 mm FL. The integrated model resulted in estimated ages-at-tagging, expected lengths-at-ages, and variability that appeared generally reasonable given this apparent distribution. Bayesian analysis procedures in OpenBUGS (i.e., Markov-chain Monte Carlo simulation) allowed for easy estimation of parameters and associated variability from multiple component likelihoods with random effects. Similar to other studies employing a hierarchical von Bertalanffy growth model (Zhang et al. 2009; Windsland et al. 2011; Tang et al. 2014), long chains with large thinning rates were needed to obtain stable, relatively uncorrelated samples, likely due to the inherent correlation between L_∞ and k. Using multiple approaches resulted in a better understanding of growth patterns than either would have alone. The integrated modeling approach took advantage of these two data sources to produce appropriate parameter estimates; a similar approach would likely be highly productive for other rare or ESA-listed species for which data from any one source could be limited.

By evaluating growth of recaptured individuals we combined data on change-in-length with data on movement to examine differences in growth between resident and migratory bull trout in the SFWWR. Although the DIC selected model did not include life-history type, it was evident from plots of L_{∞_i} and k_i that differences in growth between residents and migrants exist. Larger sample sizes may have clarified differences. Recapture and detection of tagged individuals can elucidate movement, survival, and growth, as well as allow for examination of how one parameter might affect others. Long-term PIT tag programs offer the potential to identify environmental and life-history parameters that affect population persistence, although impacts of the tagging process and the tag itself cannot be ignored. Compared to growth assessment methods using age, errors in growth estimation associated with measuring time at-large and fish length would likely be relatively small (although see Bunch et al. 2013). In this study, seasonal growth patterns could increase apparent variability, especially for migratory fish which were captured year-round. Lloyd-Jones et al. (2014) suggested incorporating covariates, such as the impact of tagging and seasonality in growth modeling, but noted that such analyses would be difficult if tagged individuals were not recaptured on multiple occasions. It is also difficult to distinguish errors associated with field length measurements from those associated with lack of model fit (i.e., measurement errors vs. process errors), as well as any impact of tagging when most individuals are recaptured only once and tagging occurs over a variety of fish ages and years. Sigourney et al. (2012) developed a model to evaluate individual and temporal variability in growth, with process and measurement error, for a cohort of age-1 Atlantic salmon, *Salmo salar*, by recapturing most individuals at three regularly spaced seasonal intervals after tagging. Such an experimental design would be ideal for a mark-recapture study, but unlikely feasible for this bull trout population.

In contrast, errors in age assignment could bias growth modeled by back-calculation of length-at-age. For an ageing structure to be useful it must be both accurate and precise. Ages assigned by otoliths have been validated for accuracy for the long-lived arctic lake trout, *S. namaycush* (Campana et al. 2008), and high precision has been identified for bull trout and Dolly Varden, *S. malma* (Zymonas et al. 2009; Stolarski and Sutton 2013). To back-calculate age-at-length, the structure must also grow proportionally to somatic growth, as has been observed for a salmonid with comparable resident and migratory life-history forms (Aubin-Horth and Dodson 2002). Zymonas and McMahon (2009) did validate annulus formation and the ability to successfully back-calculate length-at-age for fin rays of young bull trout tagged and at-large for one year. They noted high agreement for all ages between fin rays and otoliths and suggested that either structure would likely provide reasonably accurate and precise age estimates for bull trout (Zymonas and McMahon 2009). Although some imprecision associated with back-calculation of length-at-age was detected in our results, growth patterns were still evident. Generally, the core was not difficult to identify on the otolith section; however, error could be based on the specific trajectory selected on each read. We did not evaluate differences between right and left otoliths, which might have increased measurement error. Also, older or migratory bull trout may be comparatively more difficult to age and thus more likely to be removed from analyses (Zymonas and McMahon 2009). Since otoliths must be lethally obtained and bull trout are an ESA-listed species, a proper validation study would not currently be appropriate. Similar to mark-recapture, otoliths could potentially elucidate migration patterns with age through microchemistry (Campana 1999), as examined for adfluvial bull trout by Downs et al. (2006) and anadromous bull trout by Brenkman et al. (2007).

The integrated model appeared to produce appropriate estimates; however, the two methods (i.e., mark-recapture and back-calculation) assessed growth slightly differently. Our mark-recapture data resulted in a lower estimate of UL_∞ and a higher estimate of Uk than back-calculated data from otoliths. Stewart et al. (2013) similarly estimated a slightly higher L_∞ and a lower k from size-at-age using otoliths, as compared to mark-recapture of Australian bonito, *Sarda australis*, although variability was also high and growth patterns were similar between the two methods as well as from an assessment of length frequency. Erhardt and Scarnecchia (2013) found slightly higher estimates of L_∞ for migratory bull trout in Idaho using mark-recapture methods as compared to fin rays and scales, although 95% confidence intervals overlapped and estimates of k were similar. There is often a negative relationship between L_∞ and k (seen only in our otolith data) and assuming that our sample of otoliths contained a similar mix of migrants and residents, the model using back-calculated length-at-age suggested that individuals take longer to reach larger sizes than suggested by models of mark recapture data. Errors in age assignment may be an issue, as the highest rates of growth (>150 mm FL/year) observed by mark recapture, were not detected by otoliths, although this may have been a function of sample size. Differences may also be a function of how each model deals with process error, which could play a role, since our results suggest that growth may not follow the von Bertalanffy model during all life stages.

For example, our results suggest that single values of UL_∞ and Uk may not fully describe life-time growth for all individuals. The von Bertalanfy model assumes a continuously declining rate of growth, but actually an increase in growth occurred for migratory individuals after emigration. Similarly, expected length differed from average back-calculated length for some bull trout in a pattern suggesting that growth rate increased between 2-3 and four years old (~189-419 mm FL), possibly suggesting that these individuals were migratory. Models incorporating a change in growth at a certain size or age have been developed (Alós et al. 2009; Armstrong and Brooks 2013), but would be difficult to implement with our mark-recapture data since most fish were only recaptured once and the migratory phase occurs over a range of sizes and time post-tagging (Bowerman and Budy 2012). Since most marked individuals were only recaptured once, variability in growth over different life stages may be illustrated by increased individual variability. For data from back-calculation, a change in growth at emigration may result in higher estimates of L_∞ and lower estimates of k for migratory individuals, explaining patterns for individuals that did not overlap with mark-recapture data (Figure 5.6).

It is not known with certainty if genetics, environmental factors, or both influence transition to a migratory life-history (Mogen and Kaeding 2005). Homel et al. (2008) did not detect genetic differences between presumed migratory and presumed resident bull trout in the SFWWR, thus, differential growth in early life may play a role. Bowerman and Budy (2012) observed juveniles emigrating from Skiphorton Creek, a tributary to the SFWWR, throughout the year and at almost all examined sizes (i.e., 80-170 mm TL), although the proportion to emigrate increased with length. Small (<200 mm FL) bull trout tagged in the SFWWR that became migratory initially exhibited growth similar to residents, but growth apparently increased as fish approached 200 mm FL, either because observed growth rates were a mix of those in the SFWWR and those after emigration or because individuals that experienced higher growth had a greater probability of becoming migratory. Few fish tagged at 200-400 mm FL in the SFWWR later appeared to exhibit migratory behavior, which could suggest that emigration occurs at less than 200 mm FL and few return before about 400 mm FL. Our results suggest that most outmigration could be expected at 1-3 years old and migrants appear to return to spawn at around 400 mm FL, often at age 4-5. Residents would not be expected to reach 400 mm FL until around 8-9 years old. It is unknown if individuals always emigrate after spawning; thus, it is unclear if individuals over 400 mm that appear resident are true residents or if they previously migrated. Continued examination would improve our understanding of factors affecting the migratory life-history of bull trout in the SFWWR and the potential need for additional growth parameters, especially for migrants. We suggest that growth parameters and expected length-at-age estimated for resident fish be applied to all bull trout that have not emigrated. After emigration, estimates for migratory fish would apply.

For bull trout, growth varies between populations and within populations and as a result of life-history form (Johnston and Post 2009; Erhardt and Scarnecchia 2013; Mochnacz et al. 2013). Small migratory bull trout collected in the WWR exhibited higher growth rates than those identified in other studies and fish greater than 400 mm FL seem comparatively rare (Mogen and Kaeding 2005; Parker et al. 2007; Johnston and Post 2009; Mochnacz et al. 2013). Von Bertalanffy estimates for the SFWWR population were more similar to those from a system in

Idaho (i.e., Erhardt and Scarnecchia 2013), than to more northern Canadian systems, where migratory fish reached older ages with higher estimates of L_∞ and lower estimates of k (Johnston and Post 2009; Mochnacz et al. 2013), suggesting possible latitudinal differences in growth in different environments. Potentially, a large food base in combination with higher water temperatures in the WWR may result in fast growth of migratory sub-adults, but environmental factors may negatively affect survival or migration efficiency, resulting in few large migrants returning to the SFWWR as mature adults either at maturation or afterwards. Differences in sampling protocols in the WWR and SFWWR could impact results, but differences in survival might also play a role, as suggested by Bowerman and Budy (2012). The estimated average age of residents was older than that of migrants and residents were generally at-large longer than migrants, also possibly indicating higher survival for residents than for migrants. Differential survival within and between systems could impact perceived differences in growth, since faster growing fish may survive in situations of low or variable survival (Rice et al. 1993). Although sample sizes were small, we did observe that the estimated back-calculated size at age-1 was higher for older individuals, as compared to younger individuals also suggesting that faster growing fish have higher survival, although this may also be a function of the otoliths considered readable and small sample sizes. Interestingly, Pinto et al. (2013) suggested that migration by larger adfluvial juvenile bull trout may increase their overall survival, with smaller juveniles benefiting by remaining in the shallower areas of spawning creeks; thus, individual growth may impact the life-history strategy resulting in the highest survival rate. A relationship between growth and survival, as well as how that relationship plays a role in the transition to a migratory life-history is likely impacted by multiple factors that require further study.

Growth patterns and individual variability could result from mechanisms other life-history form, such as a change in reproductive status or environmental variability. The onset of maturity may reduce somatic growth of bull trout (Johnston and Post 2009). Al-Chokhachy and Budy (2008) identified 200 mm TL bull trout that were mature in the SFWWR, but some individuals may not mature until they are older and larger, since length has been correlated with increased fecundity (Al-Chokhachy and Budy 2008; Johnston and Post 2009). Budy et al. (2011) found that annual growth in weight increased and became more variable as bull trout in the SFWWR increased in size, possibly suggesting that individuals allocate different amounts of energy towards growth and reproduction as they age. Differences between males and females could play a role in growth patterns and variability also, since males and females may not have similar energy allocation, maturity schedules, or reproductive behavior (Johnston and Post 2009; Nitychoruk et al. 2013). Fish density (i.e., due to limited food resources) and environmental conditions (Selong et al. 2001; Johnston and Post 2009) could also result in annual patterns in growth, since growth rates may increase when resources are more plentiful. Incorporating environmental covariates known to affect growth such as temperature (Selong et al. 2001) would potentially explain some of the observed patterns. If a large enough sample of older individuals had been collected for otoliths over at least a few years, examining patterns in residuals could possibly indicate impacts of annual environmental variability on growth. We did not detect any pattern in asymptotic length as a function of year-at-large for tagged residents, but individual variability might have masked such a relationship. An impact of a PIT tag on growth of small tagged bull trout cannot be ruled out either; however, Ostrand et al. (2012) did not detect differences in growth for bull trout of 100-150 mm FL tagged with either a 12 mm or 23 mm PIT tag, as compared to untagged controls, although their study was conducted in a laboratory, which may not be entirely representative of a wild population.

Regardless of the causes, there appears to be substantial variability in growth for SFWWR bull trout that needs to be accounted for in population modeling. Analysis of mark-recapture data suggested notable individual variability in both L_∞ and k whereas, otolith analysis alone only suggested considerable variability in L_∞. Eveson et al. (2007), Punt et al. (2009), and Zhang et al. (2009) all found that unbiased parameter estimates could be obtained by only incorporating individual variability in L_∞ and reasons for this require more study, but could be related to the relationship between L_∞ and k (Punt et al. 2009). In an attempt to not over-parameterize models, some authors elect to only consider variation in L_∞ (Windsland et al. 2011; Lloyd-Jones et al. 2014). The DIC selected model included individual variability in both parameters, but estimates of UL_∞ and Uk were similar to the model that only included individual variability in L_∞; thus, including individual variability just in L_∞ may be sufficient. Individual variability in our study may also have been inflated by lack-of-fit caused by observed growth patterns (i.e., increased growth at 200-400 mm FL, possibly just for migrants) and by seasonal growth patterns (especially for migrants). However, it is possible that strict classification as “migrant” or “resident” should not be made, but rather that there is a gradient of growth, resulting in truly individual patterns possibly based on some combination of genetics, movement, and habitat selection. It has been suggested that variability in bull trout life-history has adaptive advantages for population persistence and is ecologically important for the inhabited ecosystems in terms of nutrient cycling (Homel et al. 2008). Ignoring individual variability in growth can lead to biased parameter estimates (Smith et al. 1997; Sainsbury 1980; Everson et al. 2007) and since growth is inherently linked to other demographic rates, such as spawning frequency, fecundity, and survival (Pilling et al. 2002; Al-Chokhachy and Budy 2008; Johnston and Post 2009; Marco-Rius 2013), understanding individual patterns is important for evaluating and modeling population persistence for this ESA-listed species.

Literature Cited

Abadi, F., O. Gimenez, R. Arlettaz, and M. Schaub. 2010. An assessment of integrated population models: bias, accuracy, and violation of the assumptions of independence. Ecology 91:7-14.

Al-Chokhachy, R., and P. Budy. 2008. Demographic characteristics, population structure, and vital rates of a fluvial population of bull trout in Oregon. Transactions of the American Fisheries Society 137:1709-1722.

Alós, J., M. Palmer, S. Balle, A. M. Grau, and B. Morales-Nin. 2009. Individual growth pattern and variability in *Serranus scriba*: a Bayesian analysis. ICES Journal of Marine Sciences 67:502-512.

Armstrong, D. P., and R. J. Brooks. 2013. Application of hierarchical biphasic growth models to long-term data for snapping turtles. Ecological Modelling 250:119-125.

Askey, P. J., J. R. Post, E. A. Parkinson, E. Rivot, A. J. Paul, P. A. Biro. 2007. Estimation of gillnet efficiency and selectivity across multiple sampling units: A hierarchical Bayesian analysis using mark-recapture data. Fisheries Research 83:162-174.

Aubin-Horth, N., and J.J. Dodson. 2002. Impact of differential energy allocation in Atlantic salmon (*Salmo salar*) precocious males on otolith-somatic size proportionality: a longitudinal approach. Canadian Journal of Fisheries and Aquatic Sciences 59:1575-1583.

Beamish, R. J., and G. A. McFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Transactions of the American Fisheries Society 112:735-743.

Bowerman, T., and P. Budy. 2012. Incorporating movement patterns to improve survival estimates for juvenile bull trout. North American Journal of Fisheries Management 32:1123-1136

Brenkman, S. J., S. C. Corbett, E. C. Volk. 2007. Use of radiotelemtry to determine age-specific migratory patterns of anadromous bull trout in the Hoh River, Washington. Transactions of the American Fisheries Society 136:1-11.

Budy, P., R. Al-Chokhachy, and G. P. Thiede. 2003. Bull trout population assessment and life-history characteristics in association with habitat quality and land use in the Walla Walla River Basin: a template for recovery planning. Annual Progress Report for 2002. USGS Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan, Utah.

Budy, P., D. Epstein, T. Bowerman, and G. P. Thiede. 2011. Bull trout population assessment in northeastern Oregon: a template for recovery planning. Progress Report for 2011. USGS Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan, Utah.

Buktenica, M. W., D. K. Hering, S. F. Girdner, B. D. Mahoney, and B. D. Rosenlund. 2013. Eradication of non-native brook trout with electrofishing and Antimycin-A and the response of a remnant bull trout population. North American Journal of Fisheries Management 33:117-129.

Bunch, A. J., C. J. Walters, L. G. Coggins, Jr. 2013. Measurement error in fish lengths: evaluation and management implications. Fisheries 38(7):320-326.

Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188:263-297.

Campana, S. E., J. M. Casselman, and C. M. Jones. 2008. Bomb radiocarbon chronologies in the Arctic, with implications for the age validation of lake trout (*Salvelinus namaycush*) and other Arctic species. Canadian Journal of Fisheries and Aquatic Sciences 65:733-743.

Downs, C. C., D. Horan, E. Morgan-Harris, and R. Jakubowski. 2006. Spawning demographics and juvenile dispersal of an adfluvial bull trout population in Trestle Creek, Idaho. North American Journal of Fisheries Management 26:190-200.

Erhardt, J. M., and D. L. Scarnecchia. 2013. Precision and accuracy of age and growth estimates based on fin rays, scales, and mark-recapture information for migratory bull trout. Northwest Science 97(4):307-316.

Eveson, J. P., T. Polacheck, and G. M. Laslett. 2007. Consequences of assuming an incorrect error structure in von Bertalanffy growth models: a simulation study. Canadian Journal of Fisheries and Aquatic Sciences 64:602-617.

Fabens, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265-289.

Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology, and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake River system, Montana. Northwest Science 63(4):133-143.

Gould, W. R. 1987. Features in the early development of bull trout (*Salvelinus confluentus*). Northwestern Science 61(4):264-268

Haddon, M. 2001. Modelling and quantitative methods in fisheries. Chapman and Hall/CRC, Boca Raton, Florida. 136 pp.

Homel, K., P. Budy, M. E. Pfrender, T. A. Whitesel, and K. Mock. 2008. Evaluating genetic structure among resident and migratory forms of bull trout (*Salvelinus confluentus*) in Northeast Oregon. Ecology of Freshwater Fish 17:465-474.

Johnston, F. D., and J. R. Post. 2009. Density-dependent life-history compensation of an iteroparous salmonid. Ecological Applications 19(2):449-467.

Kéry M. (2010) Introduction to WinBugs for Ecologists. Burlington, MA: Elsevier Inc., 302 pp.

Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Waltham, MA: Elsevier Inc., 533pp.

Klumb, R. A., M. A. Bozek, R. V. Frie. 2001. Validation of three back-calculation models by using multiple oxytetracycline marks formed in the otoliths and scales of bluegill x green sunfish hybrids. Canadian Journal of Fisheries and aquatic Sciences 58:352-364.

Lloyd-Jones, L. R., Y. Wang, W. J. Nash. 2014. Generalised growth models for aquatic species with an application to blacklip abalone (*Haliotis rubra*). Ecological Modelling 272:311-322.

Marco-Rius, F., P. Caballero, P. Morán, C. Garcia de Leaniz. 2013. Mixed-effects modeling of scale growth profiles predicts the occurrence of early and late fish migrants. PLoS One 8(4):e61744.

Maunder, M. N., and A. E. Punt. 2013. A review of integrated analysis in fisheries stock assessment. Fisheries Research 142:61-74.

Mochnacz, N. J., R. Bajno, J. D. Reist, G. Low, and J. A. Babaluk. 2013. Distribution and biology of bull trout (*Salvelinus confluentus*) in the Mackenzie Valley, Northwest Territories, with notes on sympatry with Dolly Varden (*Salvelinus malma*). Arctic 66(1):79-93.

Mogen, J. T., and L. R. Kaeding. 2005. Identification and characterization of migratory and nonmigratory bull trout in the St. Mary River Drainage, Montana. Transactions of the American Fisheries Society 134:841-852.

Nitychoruk, J. M., L. F. G. Gutowsky, P. M. Harrison, T. J. Hossie, M. Power, and S. J. Cooke. 2013. Sexual and seasonal dimorphism in adult adfluvial bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences 91:480-488.

Ostrand, K. G., G. B. Zydlewski, W. L. Gale, and J. D. Zydlewski. 2012. Long term retention, survival, growth, and physiological indicators of juvenile salmonids marked with passive integrated transponder tags. In J. R. McKenzie, B. Parsons, A. C. Seitz, R. K. Kopf, M. G. Mesa, and Q. Phelps, editors. Advances in Fish Tagging and Marking Technology. American Fisheries Society, Symposium 76, Bethesda, Maryland.

Paragamian, V. L., and J. P. Walters. 2011. Bull trout (*Salvelinus confluentus*) movement in a transboundary river. Journal of Freshwater Ecology 26(1):65-76.

Pardo, S. A., A. B. Cooper, and N. K. Dulvy. 2013. Avoiding fishy growth curves. Methods in Ecology and Evolution 4:353-360.

Parker, B. R., D. W. Schindler, F. M. Wilhelm, and D. B. Donald. 2007. Bull trout population responses to reductions in angler effort and retention limits. North American Journal of Fisheries Management 27:848-859.

Pilling, G. M., G. P. Kirkwood, S. G. Walker. 2002. An improved method for estimating individual growth variability in fish, and the correlation between von Bertalanffy growth parameters. Canadian Journal of Fisheries and Aquatic Sciences 59:424-432.

Pinto, M. C., J. R. Post, A. J. Paul, F. D. Johnston, C. J. Mushens, and J. D. Stelfox. 2013. Lateral and longitudinal juvenile bull trout in response to upstream migration of spawning adults. Transactions of the American Fisheries Society 142:1590-1601.

Punt, A. E., R. Buckworth, C. M. Dichmont, and Y. Ye. 2009. Performance of methods for estimating size-transition matrices using tag-recapture data. Marine and Freshwater Research 60:168-182.

Quinn, T. J., and R. B. Deriso. 1999. Quantitative Fish Dynamics. Oxford University Press, New York. 560 pp.

Rice, J. A., T. J. Miller, K. A. Rose, L. B. Crowder, E. A. Marschall, A. S. Trebitz, and D. L. DeAngelis. 1993. Growth rate variation and larval survival: inference form an individual-based size-dependent predation model. Canadian Journal of Fisheries and Aquatic Sciences 50:133-142

Rieman, B. E., and J. B. Dunham. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. Ecology of Freshwater Fish 9:51-64.

Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124:285-296.

Rhodes, J. R., C. F. Ng, D. L. de Villiers, H. J. Preece, C. A. McAlpine, and H. P. Possingham. 2011. Using integrated population modelling to quantify the implications of multiple threatening processes for a rapidly declining population. Biological Conservation 144:1081-1088.

Sainsbury, K. J. 1980. Effects of individual variability on the von Bertalanffy growth equation. Canadian Journal of Fisheries and Aquatic Sciences 37:241-247.

Selong, J. H., T. E. McMahon, A. V. Zale, F. T. Barrows. 2001. Effects of temperature on growth and survival of bull trout, with application of an improved model for determining thermal tolerances in fishes. Transactions of the American Fisheries Society 130:1026-1037.

Sigourney, D. B., S. B. Munch, B. H. Letcher. 2012. Combining a Bayesian nonparametric method with a hierarchical framework to estimate individual and temporal variation in growth. Ecological Modelling 247:125-134.

Smith, E. B., F. M. Williams, and C. R. Fisher. 1997. Effects of intrapopulation variability on von Bertalanffy growth parameter estimates from equal mark-recapture intervals. Canadian Journal of Fisheries and Aquatic Sciences 54:2025-2032.

Spiegelhalter, D. J., A. Thomas, N. G. Best, W. and D. Lunn. 2003. WinBUGS User Manual. Version 1.4, January 2003.

Stewart, J. D., W. D. Robbins, K. Rowling, A. Hegarty, and A. Gould. 2013. A multifaceted approach to modeling growth of the Australian bonito, *Sarda australis* (Family Scombridae), with some observations on it reproductive biology. Marine and Freshwater Research 64:671-678.

Stolarski, J. T., and T. M. Sutton. 2013. Precision analysis of three aging structures for amphidromous Dolly Varden from Alaskan Arctic Rivers. North American Journal of Fisheries Management 33:732-740.

Tang, M., Y. Jia, and J. W. Jones. 2014. A hierarchical Bayesian approach for estimating freshwater mussel growth based on tag-recapture data. Fisheries Research 149:24-32.

Tyre, A. J., J. T. Peterson, S. J. Converse, T. Bogich, D. Miller, M. Post van der Burg, C. Thomas, R. Thompson, J. Wood, D. C. Brewer, M. C. Runge. 2011. Adaptive management of bull trout populations in the Lemhi Basin. Journal of Fish and Wildlife Management 2(2):262-281.

U.S. Fish and Wildlife Service (USFWS). 2012. Bull Trout Recovery: Monitoring and Evaluation Guidance, Volume II. Draft Report prepared for the U.S. Fish and Wildlife Service by the Bull Trout Recovery and Monitoring Technical Group (RMEG). Portland, Oregon. 126pp.

Wang, Y. 1998. An improved Fabens method for estimation of growth parameters in the von Bertalanffy model with individual asymptotes. Canadian Journal of Fisheries and Aquatic Sciences 55:397-400.

Watry, C. B., and D. L. Scarnecchia. 2008. Adfluvial and fluvial life history variations and migratory patterns of a relict charr, *Salvelinus confluentus*, stock in west-central Idaho, USA. Ecology of Freshwater fish 17:231-243.

Windsland, K., and C. Hvingel, E. M. Nilssen, and J. H. Sundet. 2013. Evaluation of von Bertalanffy growth curves for the introduced red king crab (*Paralithodes camtschaticus*) in Norwegian waters. Fisheries Research 145:15-21.

Zhang, Z. J. Lessard, and A. Campbell. 2009. Use of Bayesian hierarchical models to estimate northern abalone, *Haliotis kamtschatkana*, growth patterns from tag-recapture data. Fisheries Research 95:289-295.

Zymonas, N. D., and T. E. McMahon. 2009. Comparison of pelvic fin rays, scales, and otoliths for estimating age and growth of bull trout, *Salvelinus confluentus*. Fisheries Ecology and Management 16:15-164.

Table 5.1. Prior distributions for parameters used to model growth of bull trout that spawn in the SFWWR. Data were from change in length over time identified by mark-recapture and back-calculation of length-at-age from otoliths. Length was measured in mm fork length and time in years. For models in which any of the growth parameters were considered fixed effects (i.e., L_∞, k, or t_0), priors were from the same distribution as when they were random effects (i.e., UL_∞, Uk, or Ut_0).

Parameter name	Symbolic name	Prior distribution
Population asymptotic length	UL_∞	~normal(600,10^4)
Population variability in asymptotic length	σ_{L_∞}	~uniform(0,300)
Population growth coefficient	Uk	~beta(1,1)
Population variability in growth coefficient	σ_k	~uniform(0,0.5)
Age at tagging minus t_0 for each individual	A_i	~gamma(s,r); s and r ~Uniform (0,100)
Population theoretical length when age is zero	Ut_0	~normal(0,10^3)
Population variability in length when age is zero	σ_{t_0}	~uniform(0,100)
Measurement/process error from resident and migrant data	σ_R and σ_M	~uniform(0,100)
Measurement and process error from back-calculation	σ_B and σ_P	~uniform(0,100)

Table 5.2. Growth parameter estimates (and 95% credible intervals) ordered by deviance information criterion (DIC) score. Models assumed that asymptotic length (L_∞, in mm FL) and the growth coefficient (k, in years) were the same for each individual (L_∞, k), that they differed between residents and migrants, that they varied by individual (UL_∞, Uk or both), or that they varied by life-history form and individual.

Model	L_∞	σ_{L_∞}	k	σ_k	DIC	ΔDIC
UL_∞, Uk	403 (377 – 431)	95 (82 – 110)	0.77 (0.62 – 0.95)	0.28 (0.19 – 0.39)	1194	0
Resident: UL_∞, Uk Migrant: UL_∞, Uk	431 (391 – 488) 551 (492 – 626)	71 (48 – 92) 73 (46 – 96)	0.35 (0.25 – 0.47) 0.55 (0.42 – 0.70)	0.11 (0.06 – 0.18) 0.06 (0.00 – 0.13)	2726	1532
Resident: UL_∞, k Migrant: UL_∞, k	510 (389 – 669) 544 (490 – 620)	84 (14 – 112) 79 (61 – 100)	0.21 (0.13 – 0.41) 0.55 (0.42 – 0.69)		3071	1877
UL_∞, k	392 (370 – 417)	110 (99 – 124)	0.73 (0.61 – 0.86)		3187	1993
Resident: L_∞, Uk Migrant: L_∞, Uk	541 (502 – 622) 681 (653 – 727)		0.20 (0.15 – 0.24) 0.35 (0.31 – 0.40)	0.05 (0.02 – 0.09) 0.07 (0.05 – 0.10)	3655	2461
L_∞, Uk	666 (643 – 715)		0.25 (0.20 – 0.28)	0.10 (0.07 – 0.12)	3780	2586
Resident: L_∞, k Migrant: L_∞, k	600 (404 – 796) 695 (660 – 745)		0.12 (0.11 – 0.14) 0.33 (0.29 – 0.38)		4064	2870
L_∞, k	809 (709 – 936)		0.11 (0.09 – 0.13)		4468	3274

Table 5.3. Parameter estimates (with 95% credible intervals) from von Bertalanffy growth models for the SFWWR population of bull trout as assessed by of change-in-length for tagged individuals (DIC selected model), back-calculated length-at-age from otoliths, and an integrated model including both approaches. UL_{∞} = population asymptotic fork length (in mm), Uk = population growth coefficient (in years), Ut_0 = theoretical population fork length when age is zero (in mm), $\sigma_{L_{\infty}}$= standard deviation on asymptotic fork length (in mm), σ_k = standard deviation on the growth coefficient, σ_{t_0} = standard deviation on the theoretical population fork length when age is zero, σ_R = measurement error and lack of model fit for residents, σ_M = measurement error and lack of model fit for migrants, σ_P = process error for otolith data, and σ_B = back-calculation measurement error for otolith data. "NA" = no estimate.

Parameter	Mark Recapture (n = 124 R, 88 M)	Otoliths (n = 36)	Combined (n = 289)
UL_{∞}	403 (377 – 431)	639 (545 – 766)	479 (443 – 536)
$\sigma_{L_{\infty}}$	95 (82 – 110)	130 (95 – 182)	120 (102 – 143)
Uk	0.77 (0.62 – 0.95)	0.13 (0.10-0.16)	0.38 (0.27 – 0.47)
σ_k	0.28 (0.19 – 0.39)	0.01 (0.00 – 0.02)	0.12 (0.06 – 0.18)
Ut_0 or t_0	-0.05 (-0.05 – -0.04)	-0.37 (-0.54 – -0.22)	0.04 (-0.08 – 0.16)
σ_{t_0}	NA	0.20 (0.10 – 0.32)	NA
σ	σ_R = 9.5 (6.9 – 13.1)	σ_P = 9.7 (7.6 – 12.4)	σ_R = 10.1 (7.2 – 14.3)
	σ_M = 5.3 (4.2 – 6.9)	σ_B = 10.2 (9.4 – 11.2)	σ_M = 6.7 (5.0 – 12.3)
			σ_P = 12.4 (9.7 – 16.0)
			σ_B = 10.2 (9.4 – 11.2)

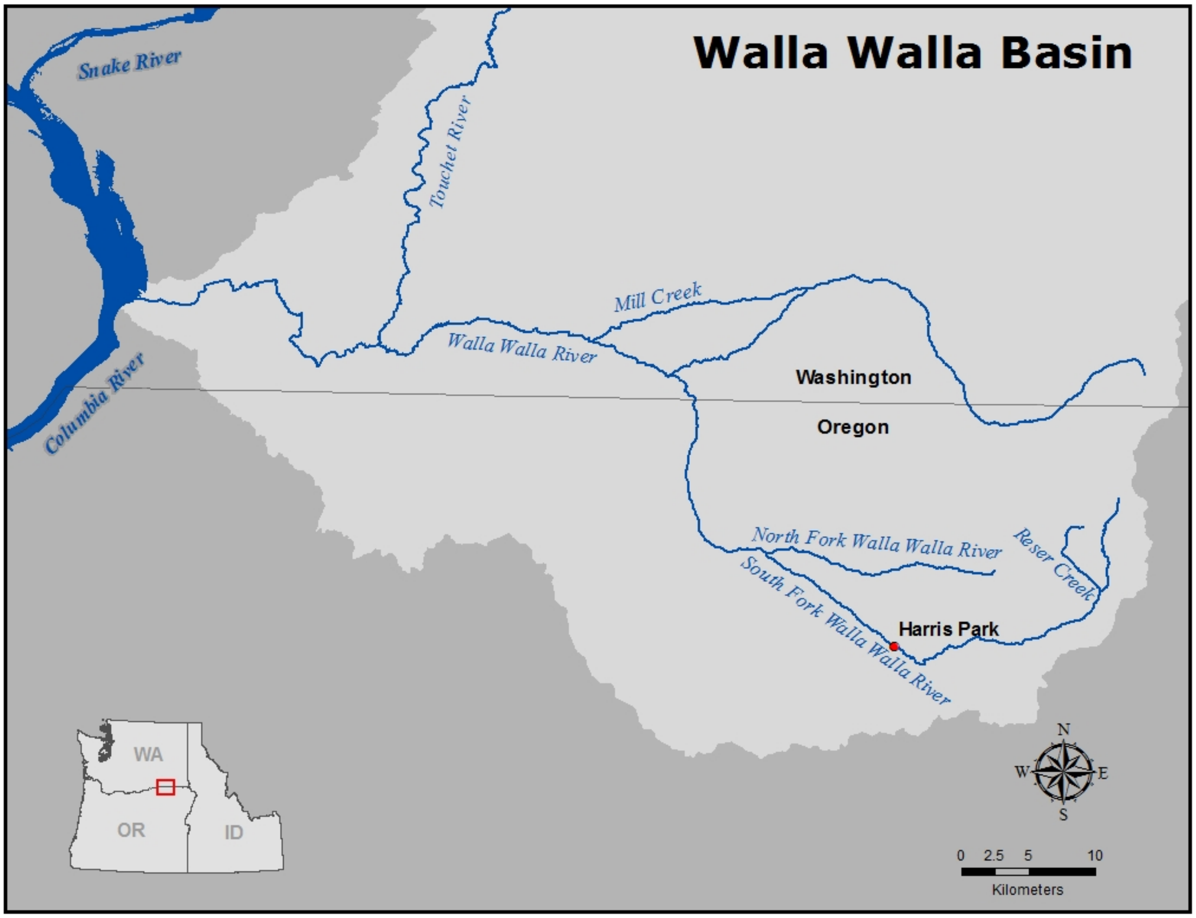

Figure 5.1. Map of the Walla Walla Basin in Washington and Oregon, with tagging, recapture, and detection sites indicated. The PIT antenna at Harris Park (red dot) indicates the break between "presumed resident" and "presumed migratory" life-histories for bull trout that spawn in the SFWWR.

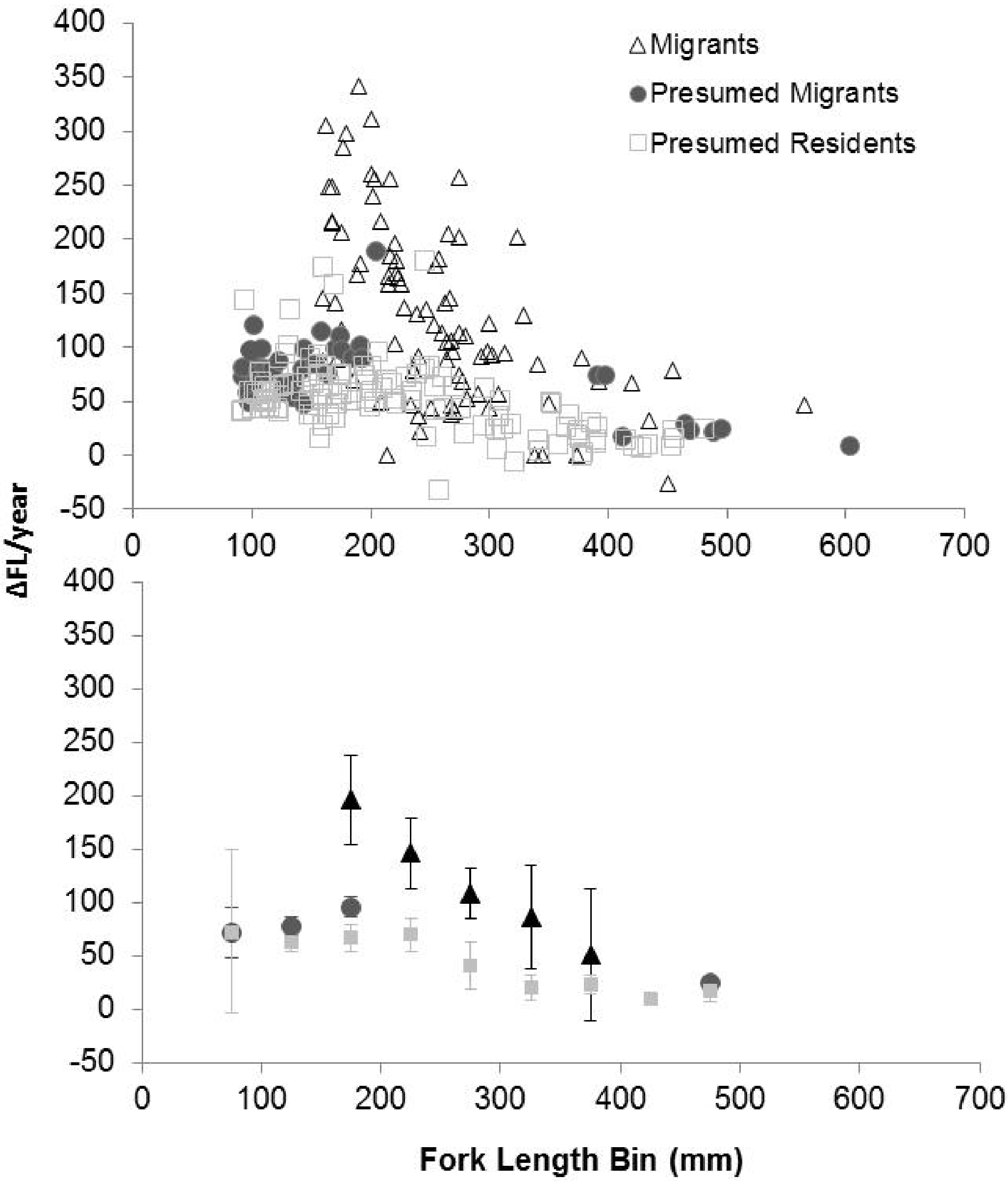

Figure 5.2. Change in fork length (in mm) per year between tagging and first recapture by fork length at tagging for individuals (upper panel) and 50-mm length bin means (with 95% credible intervals, lower panel). Means (with 95% credible intervals) for length bins with less than 3 individuals were not estimated. Note: individuals were at-large for different periods of time (15-1841 days) which could add seasonal variability.

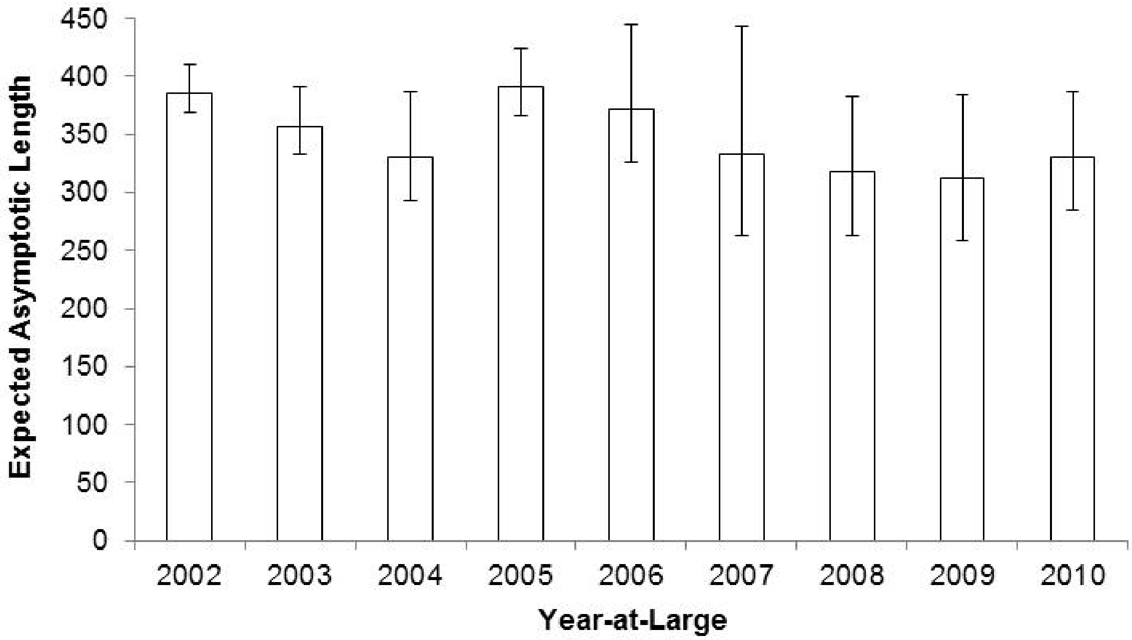

Figure 5.3. Average (with 95% credible intervals) estimated asymptotic length (i.e., average $L_{\infty,i}$) for residents, for the year the individual was at-large. Only individuals at-large for just one year, assessed as summer (June to August) to summer, were included.

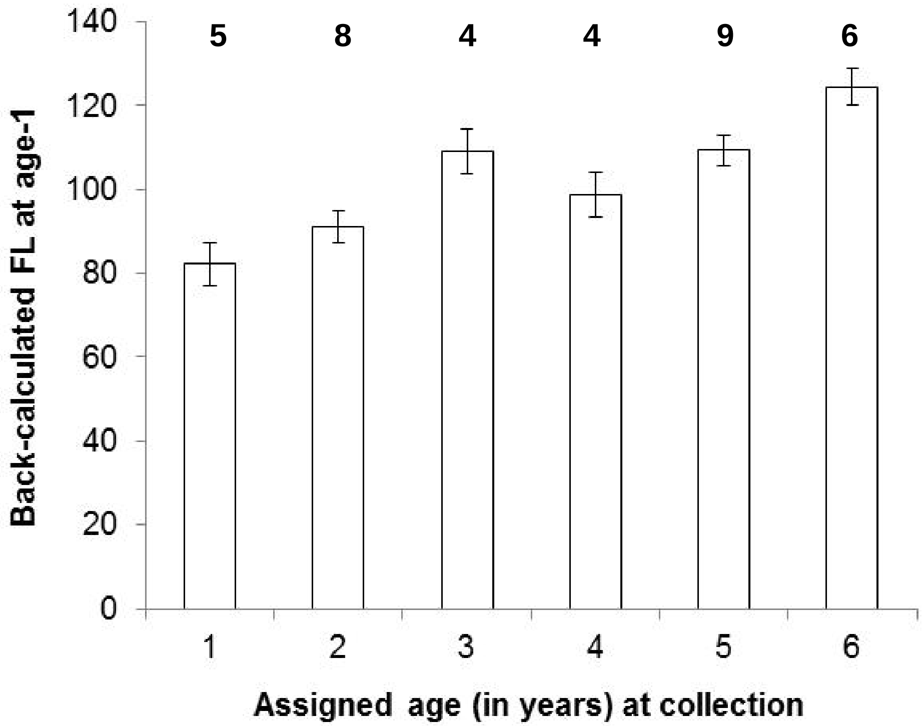

Figure 5.4. Average back-calculated fork length-at-age-1 (with 95% credible intervals) as assessed by otoliths, by age at the time of collection. The number at the top of each bar indicates the sample size for that bar.

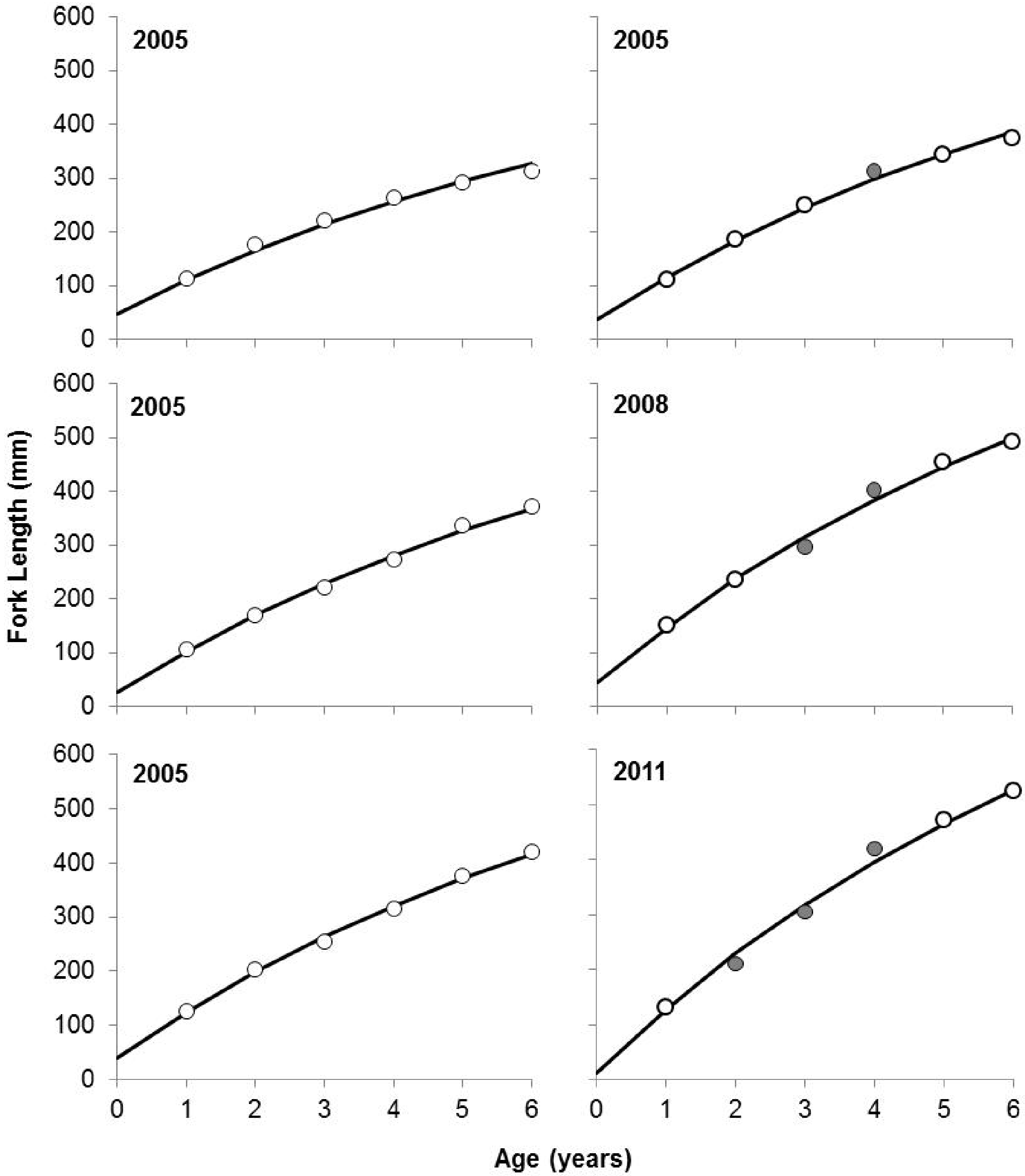

Figure 5.5. Expected fork length-at-age (line) and average back-calculated fork length-at-age (circles) from each individual estimated as age-6 in the year of collection (shown in the top left of each panel). Grey filled circles represent points at which 95% credible intervals for the fish's expected length based on the von Bertalanffy growth model did not overlap with its actual average fork length-at-age, as estimated from measurements on the otolith; white circles represent points at which 95% credible intervals did overlap. Patterns were similar for fish estimated as age-5 (not shown).

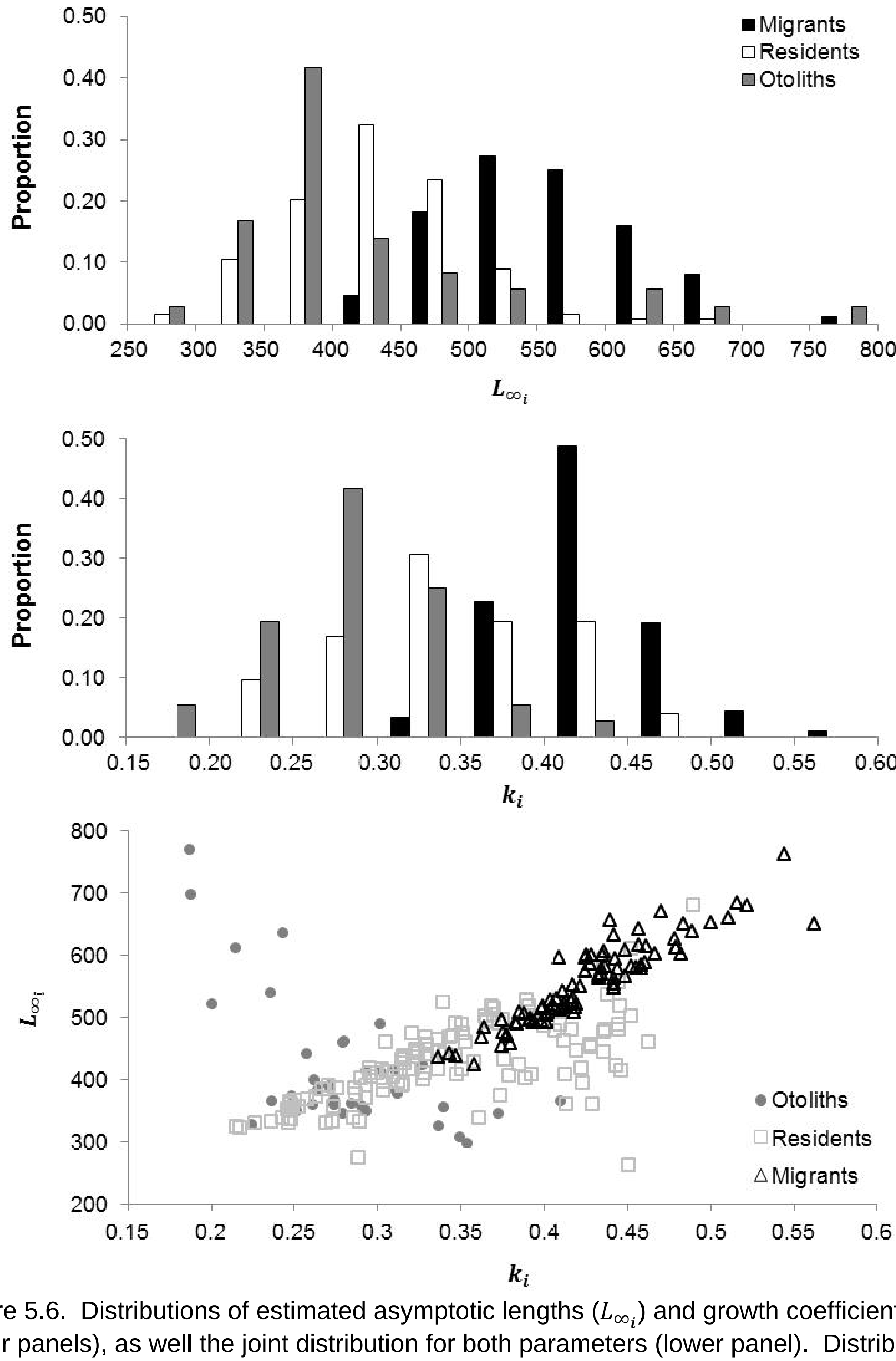

Figure 5.6. Distributions of estimated asymptotic lengths (L_{∞_i}) and growth coefficients (k_i; upper panels), as well the joint distribution for both parameters (lower panel). Distributions are individual estimates from the integrated model including data from both change-in-length from mark-recapture and back-calculation of length-at-age from otoliths.

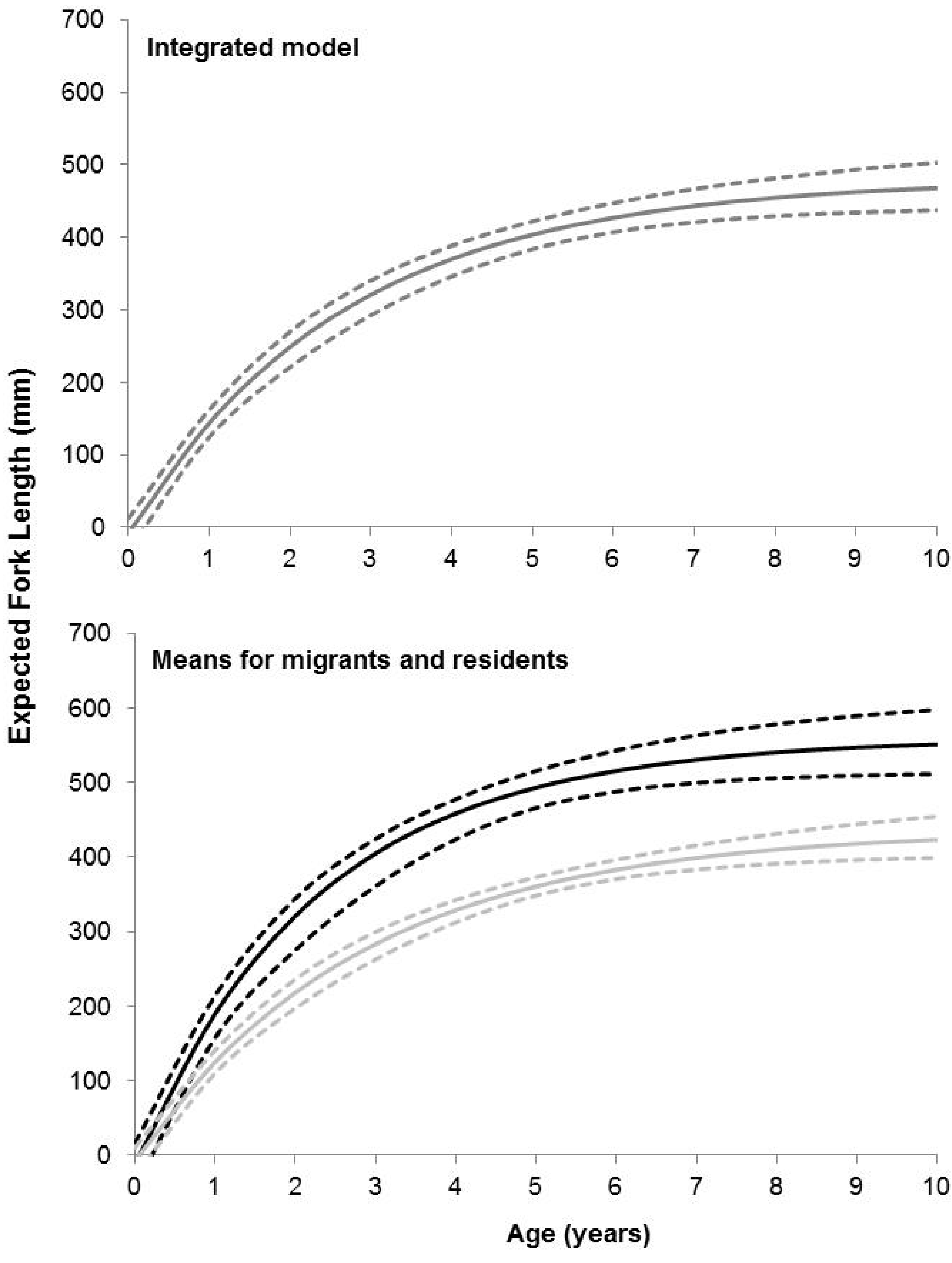

Figure 5.7. Growth curves produced by data on change of length over time from mark-recapture and back-calculation of length-at-age from otoliths. Curves were generated using population-level estimates for growth parameters (upper panel), as well as generated by mean growth parameters (lower panel) calculated for residents (light grey) and migrants (black). Solid lines indicate median estimates and dashed lines indicate 95% credible intervals on estimates.

Chapter 6 : Characterizing Bull Trout Movement Patterns in the Walla Walla River

authored by

Courtney Newlon
Howard Schaller

U.S. Fish and Wildlife Service

Introduction

Bull trout, *Salvelinus confluentus*, require large, connected habitats to persist and are therefore highly susceptible to riverscape disturbances as a result of human land practices and water use (Dunham and Rieman 1999). Generally, juvenile bull trout rear 1-3 years in headwater tributaries before moving downstream to larger rivers, lakes or the ocean (Fraley and Shepard 1989; Swanberg 1997). Bull trout express multiple life-history types within the same population (Northcote 1997; Jonsson and Jonsson 2001; Homel et al. 2008). Non-migratory (i.e., resident) adults spawn, rear, and live their entire life cycle in headwater streams. Fish that migrate benefit from feeding in multiple highly productive habitat types (i.e., larger and warmer water bodies) resulting in increased growth rates and higher fecundity than fish that remain in cold, lower productive headwater areas; thus migrants could provide a greater recovery benefit to the metapopulation of the Walla Walla River (WWR) Core Area. Further, in a spatial context, migratory individuals spread the risk for the population, in case of localized catastrophic events. However, this portion of the population is also more likely to encounter degraded and altered habitats, reducing survival and resulting in reduced contribution to the overall persistence of this population (resiliency).

Long-distance migrations can result in individuals dispersing into other populations or habitats, therefore increasing genetic exchange between populations (Cooper and Mangel 1999). It is important for managers to understand the potential range of movement patterns that a population can exhibit within a single river system since movement distances and timing can vary considerably between bull trout in the same river system. If altered conditions occur during important bull trout movement periods (e.g., during a pre-spawn migration), then there is potential to further limit connectivity. This diminished connectivity limits the ability of full life-history expression (representation), dispersal from one local population to another within a metapopulation (resiliency), or certain strategies may be eliminated. To effectively manage a species, we need to determine the limiting factors, movement behavior and spatial bottlenecks in the migration corridor for all life stages.

Connectivity can influence the occurrence and persistence of local bull trout populations through dispersal from surrounding populations (Rieman and McIntyre 1993). Patterns of occurrence have been associated with the estimated size of habitat patches and the relative isolation of patches (i.e., the distance to the nearest occupied patch; Rieman and McIntyre 1995; Dunham and Rieman 1999). Rieman and Allendorf (2001) concluded that few local bull trout populations are large enough to maintain genetic variation indefinitely without gene flow from other sources. Genetic analyses have similarly shown patterns of "isolation by distance", which suggest gene flow is higher among local populations in close proximity to one another (Costello et al. 2003; Whiteley et al. 2003). Other work has shown that populations of bull trout or related species isolated behind impassable barriers face increased risks of local extinction (Morita and Yamamoto 2002), loss of genetic variation (Yamamoto et al. 2006), and accelerated genetic drift (Costello et al. 2003; Whiteley et al. 2006). In addition, connectivity may play a similarly important role in maintaining life histories. Physical barriers or other impediments in a migratory corridor could constrain or eliminate the migratory life-history expression resulting in increased risk of extinction for local populations and possibly metapopulations (Rieman and Dunham 2000).

The WWR is a highly altered and human influenced river consisting of dams, irrigation canals, leveed and channelized banks resulting in barriers that compromise connectivity (Figure 6.3, 3.4, and 3.5 of Chapter 3; Figure III-1 of Appendix III). These barriers and water withdrawals result in an altered flow-regime and increased water temperatures (Schmetterling 2003; Chapter 3). If altered conditions occur during important bull trout movement periods (i.e., during a pre-spawn migration), then there is potential to further limit connectivity.

Previously, Utah State University (USU) described the migration timing and associated environmental cues for juvenile and sub-adult bull trout that were tagged in the South Fork Walla Walla River (SFWWR) during 2002 - 2005. Homel and Budy (2008) found that within the headwaters, these life stages exhibited downstream migrations year round, occurred mostly at night, and the greatest movement activity occurred during August, however later analysis revealed that peak sub-adult outmigration occurred in the spring. Migration response to environmental cues was also modeled and results suggested minimum water temperature may influence migration timing. In 2009, USU described fish movement using individuals tagged from 2002 - 2007 for all PIT tag sites in the Walla Walla basin (Budy et al. 2010). They found that in the SFWWR, peak upstream movements occurred during summer and peak downstream movements occurred during late summer/early fall. Additionally, USU defined a type of behavior termed “combination”, which are individuals that remained above Harris Park PIA for more than one full year after tagging, but also migrated past Harris Park PIA at some point during their life cycle, exhibited what we termed combination behavior.

Since these initial studies, a considerable amount of effort has gone into developing a long-term movement dataset. Since 1998, more than 11,000 bull trout have been tagged with passive integrated transponders (PIT) tags in the Walla Walla basin (e.g., SFWWR, WWR, Mill Creek, and, Touchet River). For this analysis, we have summarized movement patterns of bull trout that were individually marked with PIT tags in either the SFWWR or mainstem WWR between 2002 and 2011. Both resident and migratory life-history forms occur within this basin and a genetic assessment of this population demonstrated interbreeding between the two forms (Homel et al. 2008). The two life-history forms are morphologically indistinguishable, although migratory adults tend to be larger than resident fish. Therefore, we did not differentiate between the two different forms in this analysis, but instead sought to describe the variation in movement exhibited by migratory individuals within the entire river system. To assess the timing, frequency, distance, and rate of fish movement, we combined information from active recaptures with detections from a network of passive instream PIT tag detection arrays (PIA) (Figure I-1 of Appendix I). We use the term “recapture” to refer to both active captures and passive detections of previously marked fish. This description of fish movement will help to characterize the connectivity of the populations of the WWR in conjunction with the Chapter 3 habitat condition information.

We summarized data from fish that were tagged and subsequently recaptured at least once during the study period (2002 - 2011). A PIT tagged fish that was never recaptured may be subject to a number of different fates, including: 1) the tag was shed before the fish was detected, 2) the fish died before it was detected, 3) the tagged fish remained alive but was not physically recaptured in the WWR system and never moved past a PIA, or 4) the tagged fish remained alive and migrated past PIA without a detection. This last fate was possible because PIAs in the system did not have 100% detection efficiency, and several were broken or failed at numerous occasions throughout the study period (Appendix I). However, the probability of a tagged fish passing a PIA without being detected was increasingly less likely the greater the distance a fish moved in the system, since fish that moved more would be more likely to pass through more PIAs. Because considerably more recaptures occurred at PIAs than by active recapture (> 950 individual fish detected at least once at PIA, a little over 230 fish recaptured at least once by active stream sampling), the farther an individual fish moved in the system, the more likely it was to be detected. Therefore, this summary is focused on migratory fish rather than those that are less mobile (i.e., resident).

Methods

Identification of migrating bull trout. – Bull trout tagged in the South Fork Walla Walla River and detected and/or recaptured below Harris Park (rkm 97) were considered migratory. Walla Walla River tagged bull trout are of unknown natal stream origin, (i.e., presumably from SFWWR or Mill Creek), however, were classified as migratory because the species does not spawn in the lower or main stem river section.

Size designations. – Since 2002, USU has used a different size designation for population trend analyses; however, more recent unpublished results have yielded new size designations that more accurately describe this bull trout population. Bull trout life stage was determined using fork length at tagging and are designated: < 144 mm as juveniles, 144 – 290 mm as sub-adults, 291 – 406 mm as small adults and > 406 mm as large adults.

Fish sampling, marking, recapture, passive fish detection. – The same tagging population(s) (e.g., SFWWR, WWR) were used for different analysis throughout this report, therefore a condensed version of sampling, marking and detection methods are located in (Appendix II).

Movement timing

Movement timing was determined using SFWWR and WWR tagged bull trout. We summarized movement timing using PIT tag detection and recapture data from four PIAs located in the upper (Harris Park Bridge - rkm 97), middle (Nursery Bridge Dam- rkm 74 and Burlingame Dam - rkm 61) and lower (Oasis Road Bridge - rkm 10) river (Figure I-2, Appendix I). At each site the number of unique fish moving upstream and downstream by month was determined to identify movement timing throughout the year. To be considered an upstream movement, a fish needed to be detected at a downstream PIA prior to being detected at the PIA of interest, and vice versa for downstream moving fish. Individual fish were only counted once per month for each location. Movement timing was summarized by PIA site, for each year and then yearly summaries were then used to determine the movement timing for the entire population throughout the study duration (i.e., the grand mean). In addition, this information was converted to cumulative proportion and the associated 95% CI of upstream and downstream movements to determine how proportions of the migratory population use the river throughout the year.

Movement metrics

<u>South Fork Walla Walla River</u>

We used PIT tag detection and active recapture data from 2002 to 2011 to characterize bull trout movement patterns (e.g., direction, distance, duration and rate). Movement metrics were calculated for fish that were detected at least once after tagging. For SFWWR fish considered migratory, movement metrics were summarized by size designations at tagging and: 1) tag year and 2) migration year after tagging. For each fish, total distance traveled downstream and upstream and duration that it took to travel that distance were calculated for the life of the fish. This information was used to calculate rate of travel. For each metric; distance, duration, and rate summary statistics (i.e., sum, average, maximum, minimum, standard error and 95%

confidence intervals) were calculated for all size groups combined and for each individual size group.

Walla Walla River

We used PIT tag detection and active recapture data from 2004 to 2011 to characterize bull trout movement patterns (e.g., direction, distance, duration and rate). Movement metrics were calculated for fish that were detected at least once after tagging. For fish tagged in the WWR, movement metrics were summarized by size at tagging and tag year. For each fish, total distance, duration, and rate were calculated and organized by downstream and upstream movements. For each metric, summary statistics (i.e., sum, average, maximum, minimum, standard error and 95% confidence intervals) were calculated for each size group.

Columbia River

We used PIT tag detection and active recapture data from 2007 to 2012 to describe bull trout use of the Columbia River. This effort was part of a study funded by the Army Corp of Engineers and more detailed methods and results can be found in Barrows et al. (2014).

Results

Movement timing

Downstream movement in the headwaters at the Harris Park PIA followed a bimodal distribution, peaking in the spring and fall (Figure 6.1). Downstream movements occurred during all months, with peak movement in October and the least movement in February and March. The grand mean date for downstream movement was August 20, and ranged from July 13 (2010) to October 21 (2002). Upstream detections at Harris Park PIA occurred between May and September (Figure 6.1). The grand mean date for upstream movement was July 12, and ranged from June 16 (2005) to August 18 (2010) (Figure 6.2).

Downstream detections at the Nursery Bridge Dam PIA (rkm 74) reveal a bimodal distribution, with peak movement occurring in the late spring/early summer and again in the fall (Figure 6.3). Downstream movements occurred during all months, where peak movement occurred in November, and the least amount of detections occurred in March. The grand mean date for downstream movement was September 21, and ranged from June 21 (2004) to November 3 (2008) (Figure 6.4). Upstream detections at Nursery Bridge Dam PIA occurred between April and July (Figure 6.3). The grand mean date for upstream movement was June 10, and ranged from May 22 (2007) to June 25 (2008) (Figure 6.4).

Downstream movement in the middle river, at Burlingame Dam PIA (rkm 61) occurred primarily October to January and was the highest in November (Figure 6.5). Downstream movement detections were minimal from February through April and did not occur in August and September. The grand mean date for downstream movement was November 13, and ranged from October 8 (2007) to July 2 (2010) (Figure 6.6). Upstream detections at Burlingame Dam PIA occurred between April and July (Figure 6.5). The grand mean date for upstream movement was June 10 and ranged from April 16 (2007) to July 9 (2010) (Figure 6.6).

Downstream movement timing for bull trout in the lower river, at Oasis Road Bridge PIA (rkm 10) occurred between October and February (Figure 6.7). The grand mean date for downstream movement was December 7, and ranged from October 16 (2010) to February 26 (2011) (Figure 6.8). Upstream detections occurred between March and June (Figure 6.7). The grand mean date for upstream movement was April 29, and ranged from March 25 (2011) to June 8 (2009) (Figure 6.8).

We found similar downstream movement patterns between fish tagged as juveniles that migrated 2 years after tagging and sub-adults that migrated within the first year after tagging (Figure 6.9). This group moved downstream past Harris Park PIA throughout the year, however, in the lower PIA locations movement occurred during early spring, and late fall. This pattern was also observed between bull trout tagged as juveniles that migrated 3 years after tagging, sub-adults that migrated 2 years after tagging, and small adults that moved within 1 year of tagging (Figure 6.10). Similarly, this group moved past Harris Park Bridge PIA throughout the year, but movement peaked during the fall months. This group was documented moving farther downstream (e.g., Oasis Road Bridge PIA) and detections primarily occurred during the fall, winter and early spring.

Movement metrics

<u>South Fork Walla Walla River tagged fish</u>

We captured and PIT-tagged 4,763 bull trout in the SFWWR from 2002 through 2011 (Table 6.1). Bull trout captured in the SFWWR ranged in length from 66 to 693 mm and most were less than 300 mm (Figure 6.11). All bull trout tagged in the SFWWR and detected at the Harris Park Bridge PIA (rkm 97) or any detection or recapture site downstream were classified as migratory. During this study period, migratory bull trout comprised 11% of the total bull trout tagged. This suggests that the remaining 89% of the tagged bull trout were never detected or recaptured during the study period. Reasons for this include: 1) died 2) did not move 3) lost the PIT tag or 4) the fish moved but was not detected. Downstream movement metrics were calculated for 536 bull trout consisting of 211 juveniles, 229 sub-adults, 30 small adults and 66 large adults that were detected or recaptured at least once after tagging. Of these fish that migrated downstream below Harris Park Bridge PIA, only 18% (n=98) were detected making subsequent upstream movements.

Migration distance

We classified the total distance traveled by SFWWR tagged bull trout throughout their lifetime into downstream and upstream components. Bull trout tagged as juveniles (39%) and sub-adults (43%) comprised the majority of the sample size for downstream movements. All migrants exhibited an average downstream movement distance of 25 km (SD = 19.5) and ranged from 2 to 258 km (Table 6.3). Juvenile migrants exhibited an average movement distance of 29.3 km (SD = 29.2) and ranged from 6 to 107 km (Table 6.4). Sub-adult migrants exhibited an average distance of 21.7 km (SD = 15.8) and ranged from 2 to 104 km (Table 6.5). Small adult migrants exhibited an average distance of 47.1 km (SD = 51.7) and ranged from 1 to 258 km (Table 6.6). Large adult migrants exhibited an average movement distance of 19.4 km (SD = 13.6) and ranged from 2 to 99 km (Table 6.7).

All downstream migrants that moved in the first year after tagging exhibited an average movement distance of 21 km (SD = 19.8) and ranged from 1 to 258 km (Table 6.8). Juvenile migrants that moved downstream in the first year after tagging exhibited an average movement distance of 20.8 km (SD =13) and ranged from 7 to 103 km (Table 6.9). Sub-adult migrants that moved in the first year after tagging exhibited an average downstream movement distance of

18.9 km (SD = 13.7) and ranged from 2 to 94 km (Table 6.10). Small adult migrants that moved in the first year after tagging exhibited an average downstream movement distance of 34.8 km (SD = 54.4) and ranged from 1 to 258 km (Table 6.11). Large adult migrants that moved in the first year after tagging exhibited an average downstream movement distance of 22.4 km (SD = 17.5) and ranged from 2 to 99 km (Table 6.12). All downstream migrants that moved in the second or greater year after tagging exhibited larger average downstream movement distances that ranged from 29 to 40 km.

The 98 migrants that were also documented making upstream movements, averaged a distance of 20.6 km (SD = 18) and ranged from 1.6 to 213 km (Table 6.3). Of these upstream migrants, fish tagged as large adults exhibited the shortest average upstream movement distance of 16.4 km (SD = 9.1) and fish tagged as small adults exhibited the longest average upstream distance of 32 km (SD = 30.2). The largest average upstream migration distance (23 km) was exhibited by fish that migrated downstream in the first year after tagging, and ranged from 1.6 to 213 km. Of these 1st year downstream migrants, fish marked as small adults exhibited the largest subsequent upstream migration distance of 40.3 km.

Bull trout tagged in the SFWWR during any year migrated downstream in the first, second, third, or fourth year after tagging (Table 6.4). However, only 18% of those migrants exhibited subsequent upstream migration behavior. When we examine all fish, 90% of bull trout that migrate downstream out of the headwaters do so in the first two years after tagging. The largest average upstream migration distance (23 km) was exhibited by fish that migrated downstream in the first year after tagging, and ranged from 1.6 to 213 km. Of these 1st year downstream migrants, fish marked as small adults exhibited the largest subsequent upstream migration distance of 40.3 km. Large adults that migrate after tagging all do so in the first two years, and 94% migrate in the first year after tagging.

Migration duration

We classified the total duration (number of days between detections or recapture) traveled by SFWWR tagged bull trout throughout their lifetime into downstream and upstream components. Downstream moving migrants exhibited an average duration of 326 days (SD = 232.5) and ranged from 1 to 1497 days (Table 6.3). The downstream juvenile migrants exhibited an average duration of 455 days (SD = 230.1) and ranged from 13 to 1497 days (Table 6.4). Sub-adult migrants exhibited an average downstream movement duration of 275 days (SD = 214.3) and ranged from 1 to 1341 days (Table 6.5). Small adult migrants exhibited average downstream movement duration of 266 days (SD = 208.3) and ranged from 4 to 798 days (Table 6.6). Large adult migrants exhibited an average downstream movement duration of 137 (SD = 105.5) and ranged from 1 to 599 days (Table 6.7).

All downstream migrants that moved in the first year after tagging exhibited an average movement duration of 130 days (SD = 202.2) and ranged between 1 and 784 days (Table 6.8). The juvenile migrants that moved in the first year after tagging exhibited an average duration of 266 days (SD = 79.5) and ranged from 13.9 and 504 days (Table 6.9). Sub-adult migrants that moved in the first year after tagging exhibited an average downstream movement duration of 194 days (SD = 158.9) and ranged from 4.5 to 784 days (Table 6.10). Small adult migrants that moved in the first year after tagging exhibited an average downstream movement duration of 190 days (SD = 182.4) and ranged from 4 to 682 days (Table 6.11). Large adult migrants that moved in the first year after tagging exhibited an average downstream movement duration of 130 days (SD = 132.5) and ranged from 1 to 599 days (Table 6.12). All of the downstream migrants that moved in the second or greater year after tagging exhibited much smaller average downstream movement durations that ranged from 1 to 74 days.

The 98 downstream migrants that completed upstream movements, averaged a total duration of 142.7 (SD = 201.5) and ranged from 2.5 to 1124 days (Table 6.3). Of these upstream migrants, fish tagged as juveniles exhibited the shortest average upstream migration duration of 62 days (SD = 47.3) and fish tagged as small adults exhibited the longest average upstream migration duration of 266.3 (SD = 240.1).

The largest average upstream duration was 130 days and ranged from 1 to 785 days, was exhibited by fish that migrated downstream in the first year after tagging. Of these 1st year downstream migrants, fish marked as small adults exhibited the largest subsequent upstream migration duration of 146 days.

Migration rate

We classified the rate (km/day) of movement traveled by SFWWR tagged bull trout into downstream and upstream components. Migrants traveling downstream exhibited an average rate of 1.4 km/day (SD = 3.4) and ranged from less than 0.1 to 39.1 km/day (Table 6.3). Juvenile migrants exhibited an average downstream movement rate of 1.4 km/day (SD = 3.4) and ranged from less than 0.1 to 39.1 km/day (Table 6.4). Sub-adults exhibited an average rate of 1.2 km/day (SD = 2.7) and ranged from less than 0.1 to 28.7 km/day (Table 5). Small adults averaged a downstream movement rate of 1.8 km/day (SD = 1.7) and ranged from less than 0.1 to 13.9 km/day (Table 6.6). Large adults exhibited a movement rate of 2.3 km/day (SD = 3) and ranged from less than 0.1 to 17.9 km/day (Table 6.7).

All of the downstream migrants that moved in the first year after tagging exhibited an average downstream movement rate of 1.54 km/day (SD = 3.2) and ranged from less than 0.1 to 26.9 km/day (Table 6.8). The downstream juvenile migrants that moved in the first year after tagging exhibited an average downstream movement rate of 1.88 km/day (SD = 4.4) and ranged from 0.03 to 26.9 km/day (Table 6.9). The downstream sub-adult migrants that moved in the first year after tagging exhibited an average downstream movement rate of 1 km/day (SD = 2.1) and ranged from 0.01 to 22.7 km/day (Table 6.10). The downstream small adult migrants that moved in the first year after tagging exhibited an average downstream movement rate 1.7 km/day (SD = 3.3) and ranged from 0.02 to 13.9 km/day (Table 6.11). The downstream large adult migrants that moved in the first year after tagging exhibited an average downstream movement rate of 2.42 km/day (SD = 3.4) and ranged from 0.01 to 17.9 km/day (Table 6.12). Downstream migrants that moved in the second or greater year after tagging exhibited a considerable slower average downstream movement rate than fish that moved in the first year of tagging.

The 98 migrants documented moving upstream, averaged a rate of less than 0.54 km/day (SD = 0.49) and ranged from less than 0.01 to 2.9 km/day (Table 6.3). Of these upstream migrants, fish tagged as juveniles exhibited the fastest average upstream migration rate of 0.76 km/day (SD = 1.3) and fish tagged as small adults exhibited the slowest average upstream migration rate of 0.43 km/day (SD = 0.27).

The fastest average upstream migration rate was 0.58 km/day (ranged from less than 0.01 to 2.9) and was exhibited by fish that migrated downstream in the second year after tagging. Of these 2nd year downstream migrants, fish marked as juveniles exhibited the fastest subsequent upstream migration rate of 1.94 km/day.

<u>Walla Walla River tagged fish</u>

We captured and PIT-tagged 926 bull trout in the WWR from 2004 through 2011 (Table 6.13). Bull trout captured ranged from 102 to 645 mm in length and the majority of fish captured were between 144 - 406 mm (Figure 6.12). All bull trout tagged in the WWR were classified as migratory and of unknown stream origin, presumably from SFWWR or Mill Creek. Of the original tagged fish, only 42% were detected or recaptured again during the study period. This suggests that the remaining tagged bull trout were never detected or recaptured during the study period. Similar to SFWWR tagged fish, the possible reasons include: 1) fish died 2) did not move 3) lost the PIT tag or 4) the fish moved but was not detected. Downstream movement metrics were calculated for 392 bull trout consisting of 10 juveniles, 266 sub-adults, 95 small adults and 21 large adults that were detected or recaptured at least once after tagging. Of the fish tagged as migrators, only 31% (n=120) that traveled downstream were also documented making subsequent upstream movements (juveniles-1; sub-adult-63; small adult-43; and large adult-13) (Table 6.14).

Migration distance

We classified the total distance traveled by WWR tagged bull trout throughout their lifetime into downstream and upstream components (Table 6.15). Bull trout tagged as sub-adults (68%) and small adults (24%) comprised the majority of the sample size for downstream movements. Migrants exhibited an average cumulative downstream movement distance of 23 km (SD = 25.2) ranging from 2 to 135 km (Table 6.16). Juvenile migrants exhibited an average downstream movement distance of 7 km (SD = 3.8) and ranged from 2 to 19 km (Table 6.17). Sub-adult migrants exhibited an average downstream movement distance of 24 km (SD = 24.8) and ranged from 2 to 135 km (Table 6.18). Small adult migrants exhibited an average downstream movement distance of 25 km (SD = 25.6) and ranged from 2 to 124 km (Table 6.19). Large adult migrants exhibited an average downstream movement distance of 30 km (SD = 26.8) and ranged from 2 to 17 km (Table 6.20).

The 120 migrants that made upstream movements averaged a distance of 39 km (SD = 24.2) where the minimum upstream distance traveled was 2 km and the maximum was 125 km (Table 6.15). Consistent with downstream movements, bull trout tagged as sub-adults (53%) and small adults (36%) comprised the majority of the sample size. The one juvenile migrant exhibited a movement distance of 13 km. Sub-adult migrants exhibited an average upstream movement distance of 35 km (SD = 22.1) and ranged from 2 to 121 km. Small adult migrants exhibited an average upstream movement distance of 41 km (SD = 25.2) and ranged from 2 to 122 km. Large adult migrants exhibited an average upstream movement distance of 62 km (SD = 23.9) and ranged from 38 to 125 km.

Migration duration

We classified the total duration (number of days between detections or recapture) traveled by WWR tagged bull trout throughout their lifetime into downstream and upstream components (Table 6.15). Downstream moving migrants exhibited an average duration of 74 days (SD = 88.6) and ranged from 1 to 494 days. Juvenile migrants exhibited an average movement duration of 18 days (SD = 24.4) and ranged from 1 to 70 days (Table 6.16). Sub-adults exhibited an average downstream movement duration of 81 days (SD = 79.3) and ranged from 1 to 448 days (Table 6.17). Small adults exhibited an average duration of 64 days (SD = 83.8) and ranged from 1 to 494 days (Table 6.18). Large adults exhibited an average downstream duration 121 days (SD = 141.8) and ranged from 1 to 717 days (Table 6.19).

The 120 migrants that completed upstream movements, averaged a total duration of 184 days (SD = 170.5) and ranged from 1 to 1390 days (Table 6.15). The juvenile migrant (n = 1) exhibited an upstream duration of 11 days. Sub-adults exhibited an average duration of 180 days (SD = 166.6) and ranged from 4 to 1390 days. Small adults exhibited an average upstream movement distance of 173 days (SD = 142.3) and ranged from 2 to 860 days. The large adults exhibited an average duration of 289 days (SD = 112.7) and ranged from 113 to 488 days.

Migration rate

We classified the rate (km/day) of movement traveled by tagged bull trout into downstream and upstream components. Migrants traveling downstream exhibited an average rate of 1.7 km/day (SD = 2.7) and ranged from 0.01 to 21.6 km/day (Table 6.15). The juvenile migrant exhibited an average downstream movement rate of 1.8 km/day (SD = 1) and ranged from less than 0.1 to 8 km/day (Table 6.16). Sub-adults exhibited an average rate of 1.4 km/day (SD = 2.3) and ranged from less than 0.1 to 21.6 km/day (Table 6.17). Small adults averaged a downstream movement rate of 2.1 km/day (SD = 2.6) and ranged from less than 0.1 to 18.7 km/day (Table 6.18). Large adults exhibited a movement rate of 3.6 km/day (SD = 4.2) and ranged from less than 0.2 to 19.8 km/day (Table 6.19).

The 120 migrants documented moving upstream, averaged a rate of less than 1 km/day (SD = 0.77) and ranged from less than 0.1 to 7 km/day (Table 6.15). Of these upstream migrants, fish tagged as sub-adults exhibited the fastest average upstream migration rate of 1.8 km/day (SD = 0) and fish tagged as large adults exhibited the slowest average upstream migration rate of 0.22 km/day (SD = 0).

Discussion

Large data sets monitoring a long time series are essential when attempting to understand the life-history of a long lived, slow maturing fish species that can travel large distances over its lifetime (Dunham et al. 2003). Bull trout typically reach sexual maturity between 4-7 years (Fraley and Shepard 1989) thus it is important for a movement study to encompass at least a full life cycle, to fully understand a population. Bull trout spawn in the fall and can migrate long distances (e.g., greater than 200 rkm) from lower river foraging habitats to the clean, cold headwaters of their natal stream to spawn; after spawning, they travel back downstream to continue to forage (Rieman and McIntyre 1993). Our study has been conducted on a large spatial scale (i.e., over 100+ km of stream monitored) and over a long time series (i.e., 10 years). From 2002 to 2011, we observed patterns in bull trout movement timing that coincide with seasonal spawning migrations and general outmigration consistent with prior analyses completed within the WWR (Budy et al. 2010) and other similar studies (Swanberg 1997). Our work corroborates with other studies that the majority of downstream movement occurs in the spring and fall (Jakober et al. 1998) and dependednt on basin location, upstream movement occurs primarily in the spring, summer and fall (Budy et al. 2010).

In general, the downstream movements made are a result of either a directed post-spawning movement (e.g., adults) or emigration out of the headwaters to rear (e.g., juveniles, sub-adults). Moreover, upstream movements are likely a result of either a directed spawning movement (e.g., adults) or to avoid warmer water temperatures that occur during the summer in the middle/lower river sections. Overall, tagging location did not appear to influence average downstream movement distance or rate, but did affect duration (i.e., SFWWR fish averaged 4 times greater duration). Generally, fish tagged in the lower river are larger and were tagged after moving downstream from the headwaters likely leading to less documentation of their movements. Largely, the year a fish was tagged within a group (e.g., size class, location) did not affect the distance, duration or rate. When there were differences between tag years, it was likely due to small sample size.

With the exception of fish tagged as adults, both downstream and upstream rates were similar, irrespective of tagging location or size at tagging. The directed downstream movements completed by adults are likely post spawning migrations to the larger, more productive waters of the lower river. Downstream movement distances (sum and maximum) increased significantly in the later years of the study, likely because of an overall increase in antenna locations and subsequently an increased probability of being detected and a significant increase in tagging of lower WWR fish starting in 2007.

There were notable differences in distance, duration and rate between the SFWWR fish that emigrated within 1, 2 or 3 years after tagging. Generally, the longer a fish waited to emigrate, the farther that fish moved downstream and the greater the likelihood that the fish was subsequently detected (i.e., duration). This is notable especially for fish tagged as juveniles and sub-adults, where downstream distances moved increased by more than 50% for each subsequent year of additional rearing in the SFWWR headwaters. This suggests that fish that are older and larger at emigration move farther downstream and appear to have higher survival. Also, fish that reared longer in the headwaters upstream gaining biomass before emigrating made greater average downstream movements and smaller average upstream movements. Therefore, when evaluating migration metrics we need to account for size at movement. Small sample sizes of fish detected migrating back upstream resulted in difficulty in making comparisons between these movement metrics. These results should help identify conditions that impede movement and examine how movement relates to survival rates for fish of similar size at migration. Moreover, it would be beneficial to use the growth analysis results (Chapter 5) to evaluate movement metrics for fish of potentially similar size (such as juveniles that move after the second year of marking and sub-adults that move after the first year of marking).

Generally, bull trout migrated downstream out of the headwaters at similar sizes regardless of size at tagging (i.e., surrogate for age at marking – cohort). That is, fish of similar sizes move at the same times of the year and go to similar areas downstream. Passive instream antenna detections show that lower river movements for both cohort groups were greatly diminished in the summer months when the water temperatures were warm at these downstream locations (Figures 6.9 and 6.10).

Chapter 3 assessed habitat conditions to determine if migration corridors are accessible (i.e., flow and water temperature) for passage during migration periods. Our tagging efforts and detection data show that migration corridors are accessible (at least during certain times of year), but also revealed the majority of migratory fish, never subsequently complete upstream movements. The low percentage of fish exhibiting subsequent upstream movement may suggest that conditions in the lower and middle river have substantial influence on survival of the migratory population. During downstream movements a fish may not be obstructed from movement (i.e., no low flow barriers for these smaller fish). The fish may move downstream but choose to cease movement as flow decreases and/or water temperatures increase. The lack of the ability to move upstream could limit a bull trout's full life-history expression and reduce reproductive success (Watry and Scarnecchia 2008). These limitations are likely due to a few mechanisms: 1) blocking access to spawning grounds 2) exposure to unsuitable river conditions (i.e., more susceptible to avian predators during low flows, decreased survival) and 3) exposure to increased water temperatures that reduce fecundity due to higher oxygen demands, therefore contributing to an overall decrease in energy put into egg production and development (Dunham et al. 2003). Regardless, these impacts could be detrimental to the overall persistence of this bull trout population.

During this study, we documented connectivity and evidence of dispersal between local populations within the WWR Core Area. For example, we documented a Mill Creek tagged fish in the SFWWR spawning grounds. A Touchet River tagged bull trout has been detected in Mill Creek and vice versa. However, no SFWWR or WWR tagged fish have been detected or recaptured in Mill Creek indicating potential upstream passage concerns. In addition, a WWR tagged fish was detected at Three Mile Falls Dam on the Umatilla River and a genetic analysis determined that 7 of the 8 bull trout captured at the ladder were from the WWR Core Area. There is also genetic evidence that some bull trout captured in the lower WWR were crosses between Mill Creek and SFWWR local populations (Small et al. 2012). Three WWR tagged bull trout have also been detected at the McNary Dam facility on the mainstem Columbia River (Barrows et al. 2014). Moreover, we have documented 81 PIT tagged bull trout that were able to complete downstream migrations into the Columbia River (presumably, detected at Oasis Road Bridge PIA), and 11 were subsequently detected returning to the WWR and two were detected in the SFWWR at the Harris Park Bridge and Bear Creek PIAs during the spawning season. Individuals tagged in the SFWWR, WWR, and Mill Creek have been detected at the Oasis Road Bridge PIA, suggesting with the exception of the Touchet River, a migratory component in all local populations of the WWR Core Area. Given the low proportion of marked fish, a larger number of unmarked fish in the WWR Core Area likely express this long-distance migration pattern and potential for dispersal.

There were some periods when PIA's were broken, not functioning properly, or did not monitor the entire stream width, which could have cause missed detections and overall may have resulted in misleading conclusions (Appendix I). For example, a missed detection could suggest a fish has moved upstream, when it actually moved downstream. In addition, PIA locations can impact not only detection probability but also movement metrics such as, distance, duration and rate, especially in the lower river where there are large distances between PIA sites. Though there are limitations when using PIT tags, this method allowed for a large number of fish to be tagged and monitored over the lifetime of the fish, with a relatively low amount of effort. In lieu of these limitations, we operated 6-10 PIA's and recapture locations which monitored a 97 km stretch of river for a ten year period. Furthermore, bull trout life-history traits have the potential to impact PIA detection probability. For example, fish that skip a spawning migration or decide to spend more time foraging in the lower WWR or the Columbia River could have limited detection probability, as compared to those that migrate only within areas of PIAs.

Poor habitat conditions (Chapter 3) may compromise the ability of WWR bull trout to migrate, rear or disperse. It is important to consider all life-history strategies (e.g., migratory, resident) when evaluating factors that limit population abundance and recovery plan actions. In particular, these movement results suggest that the migratory component of the population is primarily impacted by these unfavorable habitat conditions. Whether a bull trout decides to move or not is a function of the individual's life-history, the environmental conditions experienced by that individual and the condition of the migratory corridors; but ultimately the decision to move is a strategy to maximize lifetime reproductive effort (Bronmark et al. 2013). Because of the considerably higher fecundity associated with the migratory component of the population, these habitat impacts likely affect the resiliency of the WWR Core Area populations. Many other Columbia River bull trout populations exhibit similar life-history strategies (e.g., partially migratory population) and are faced with similar anthropogenic impacts to their habitat. These findings should be transferrable in managing rivers to promote range-wide species recovery of bull trout. While this is a coarse assessment of bull trout movement in the WWR, the next phase of our study is to evaluate if environmental conditions (e.g., stream flow, water temperature) influence these movement patterns.

Literature Cited

Barrows, M.G., R. Koch, D.R. Anglin and S.L. Haeseker. 2014. Use of the Mainstem Columbia River by Walla Walla Basin Bull Trout. 2012 Annual Report to the U.S. Army Corps of Engineers, Walla Walla District. Project BT-W-10-2.

Brönmark, C., K. Hulthén, A. Nilsson, C. Skov, L.A. Hansson, J. Brodersen, and B. Chapman. 2013. There and back again: migration in freshwater fishes. Canadian Journal of Zoology 91:1-13.

Budy, P., T. Bowerman, and G.P. Thiede. 2010. Bull trout population assessment in northeastern Oregon: a template for recovery planning. 2009 Annual Progress Report to US Fish and Wildlife Service. UTCFWRU 2010(3):1-48.

Cooper, A. B., and M. Mangel. 1999. The dangers of ignoring metapopulation structure for the conservation of salmonids. Fishery Bulletin (U.S.) 97:213-226.

Costello, A. B., T.E. Down, S.M. Pollard, C.J. Pacas, and E.B. Taylor. 2003. The influence of history and contemporary stream hydrology on the evolution of genetic diversity within species: an examination of microsatellite DNA variation in bull trout, *Salvelinus confluentus* (Pisces: Salmonidae). Evolution 57(2):328-344.

Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of habitat size, isolation, and human disturbance. Ecological Applications 9(2):642-655.

Dunham, J., B. Rieman, and G. Chandler. 2003. Influences of temperature and environmental variables on the distribution of bull trout within streams at the southern margin of its range. North American Journal of Fisheries Management 23(3):894-904.

Fraley, J. J., and B. B. Shepard. 1989. Life-history, ecology, and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Science 63:133-143.

Homel, K., and P. Budy. 2008. Temporal and spatial variability in the migration patterns of juvenile and subadult bull trout in northeastern Oregon. Transactions of the American Fisheries Society 137(3):869-880.

Homel, K., P. Budy, M. E. Pfrender, T. A. Whitesel and K. E. Mock. 2008. Evaluating genetic structure among resident and migratory forms of bull trout (*Salvelinus confluentus*) in Northeast Oregon. Ecology of Freshwater Fish 10:465-474.

Jakober, M. J., T. E. McMahon, R. F. Thurow, and C. G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society 127(2):223-235.

Jonsson, B., and N. Jonsson. 2001. Polymorphism and speciation in Arctic charr. Journal of Fish Biology 58:605-638.

Morita K., and S. Yamamoto. 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. Conservation Biology 16:1318–1323.

Mundy, P.R. 1982. Computation of migratory timing statistics for adult Chinook salmon in the Yukon River, Alaska, and their relevance to fisheries management. North American Journal of Fisheries Management 2(4):359-370.

Northcote, T. G. 1997. Potamodromy in Salmonidae: living and moving in the fast lane. North American Journal of Fisheries Management 17(4):1029-1045.

Rieman, B. E., and F. W. Allendorf. 2001. Effective population size and genetic conservation criteria for bull trout. North American Journal of Fisheries Management 21:330-338.

Rieman, B. E., and J. B. Dunham. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. Ecology of Freshwater Fish 9:51-64

Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service General Technical Report Int-302.

Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124(3):285-296.

Schmetterling, D.A. 2003. Reconnecting a fragmented river: movements of westslope cutthroat trout and bull trout after transport upstream of Milltown Dam, Montana. North American Journal of Fisheries Management 23(3):721-731.

Small, M.P., M. Barrows, and E. Martinez. 2012. Genetic assignments for migratory bull trout captured in the Walla Walla and Umatilla rivers: assessing connectivity through genetic analyses. WDFW Genetics Laboratory, Olympia, Washington.

Swanberg, T. R. 1997. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. Transactions of the American Fisheries Society 126(5):735-746.

Watry, C. B., and D. L. Scarnecchia. 2008. Adfluvial and fluvial life-history variations and migratory patterns of a relict char, *Salvelinus confluentus*, stock in west central Idaho, USA. Ecology of Freshwater Fish 17:231-243.

Whiteley, A. R., P. Spruell, B. E. Rieman, and F. W. Allendorf. 2006. Fine-scale genetic structure of bull trout at the southern distribution limit. Transactions of the American Fisheries Society 135:1238-1253.

Yamamoto, S., K. Maekawa, T. Tamate, I. Koizumi, K. Hasegawa, and H. Kubota. 2006. Genetic evaluation of translocation in artificially isolated populations of white-spotted charr (*Salvelinus leucomaenis*). Fisheries Research 78:352-358.

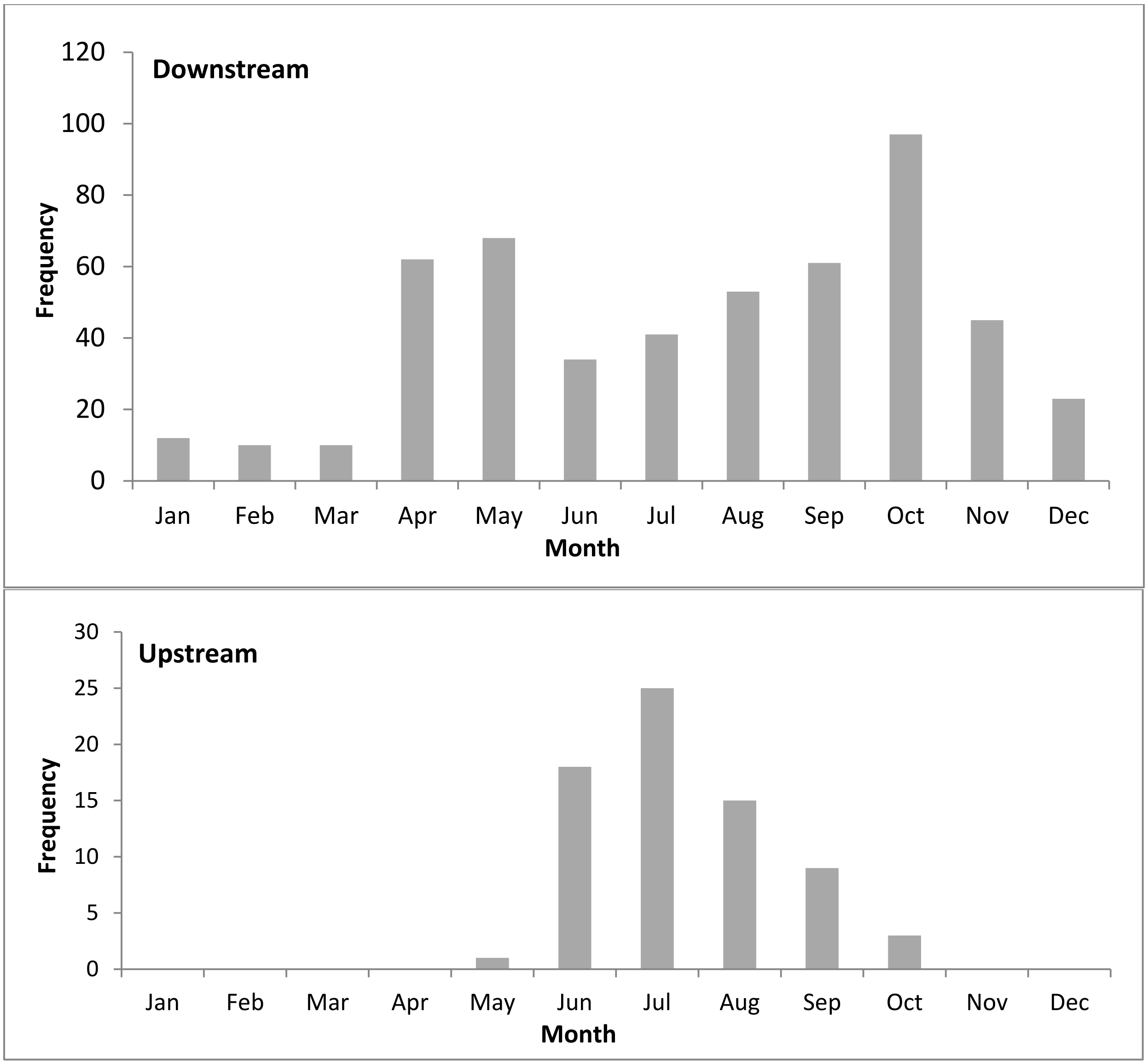

Figure 6.1. Number of unique monthly detections for bull trout detected at Harris Park Bridge PIA from 2002 – 2011.

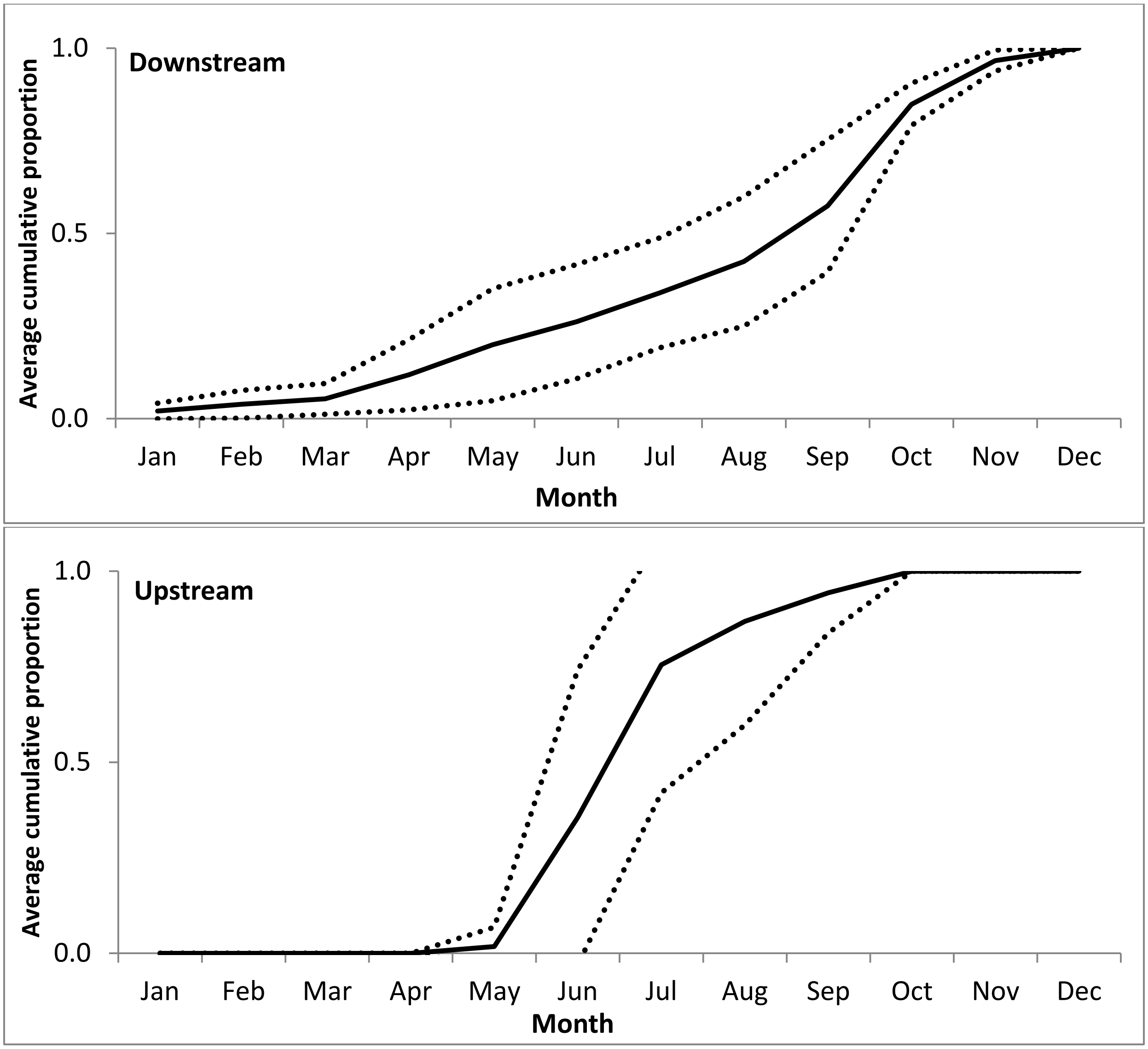

Figure 6.2. Average cumulative proportion of downstream and upstream PIT tag detections at the Harris Park Bridge PIA from 2002 – 2011. Dotted lines represent 95% CI.

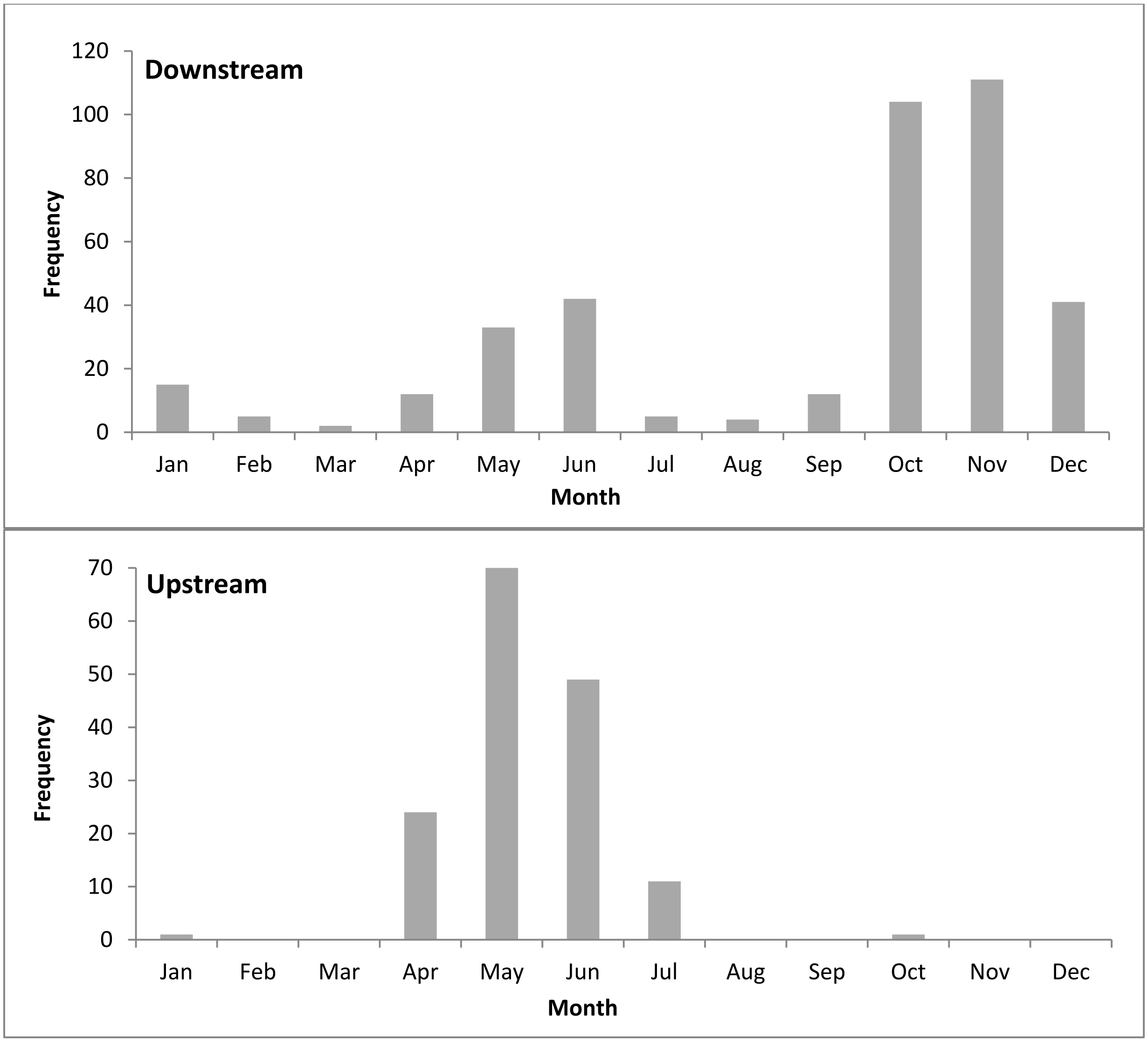

Figure 6.3. Number of unique monthly detections for bull trout detected at Nursery Bridge Dam PIA from 2003 – 2011.

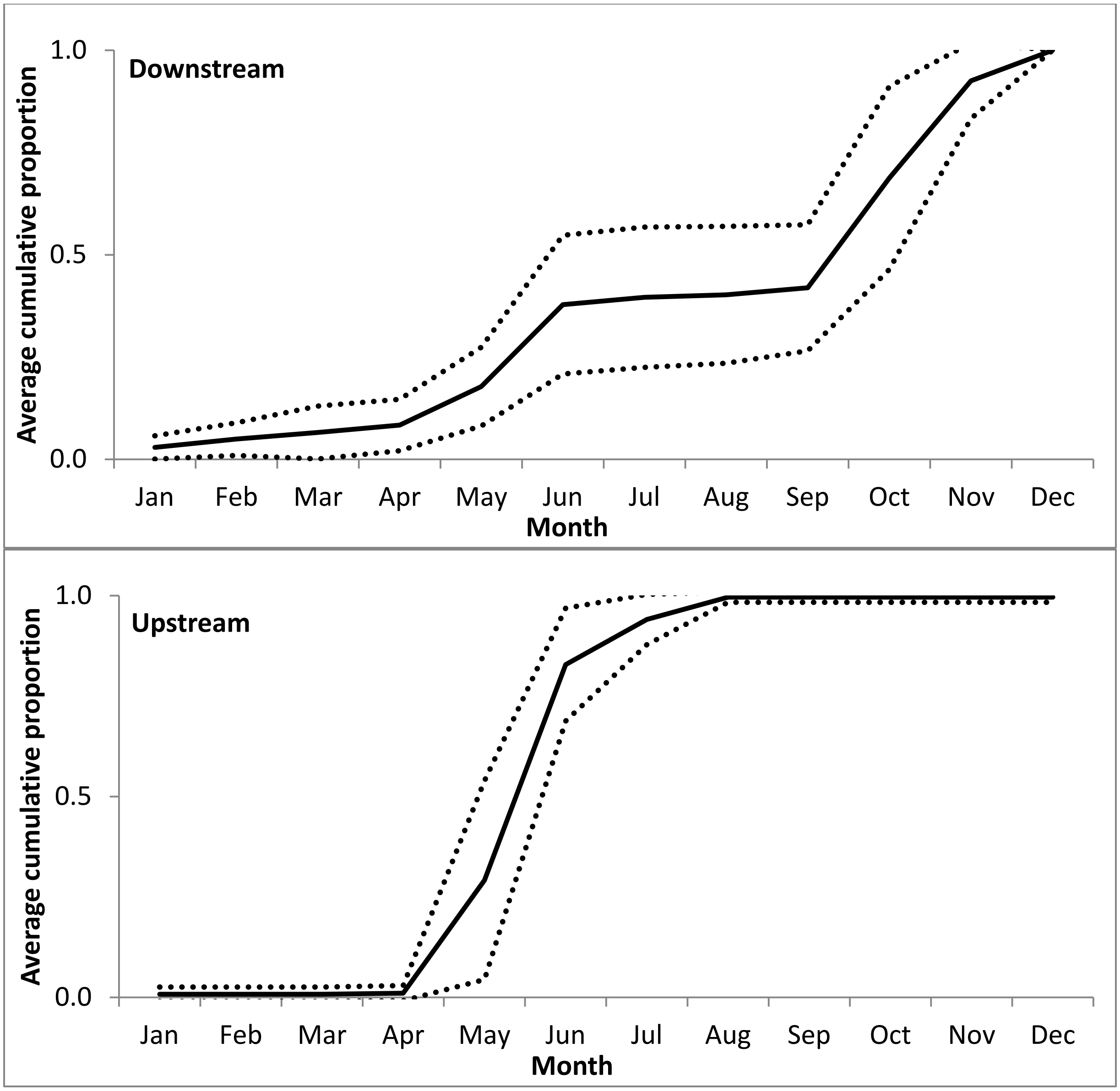

Figure 6.4. Average cumulative proportion of downstream and upstream detections at the Nursery Bridge Dam PIA from 2002 – 2011. Dotted lines represent 95% CI.

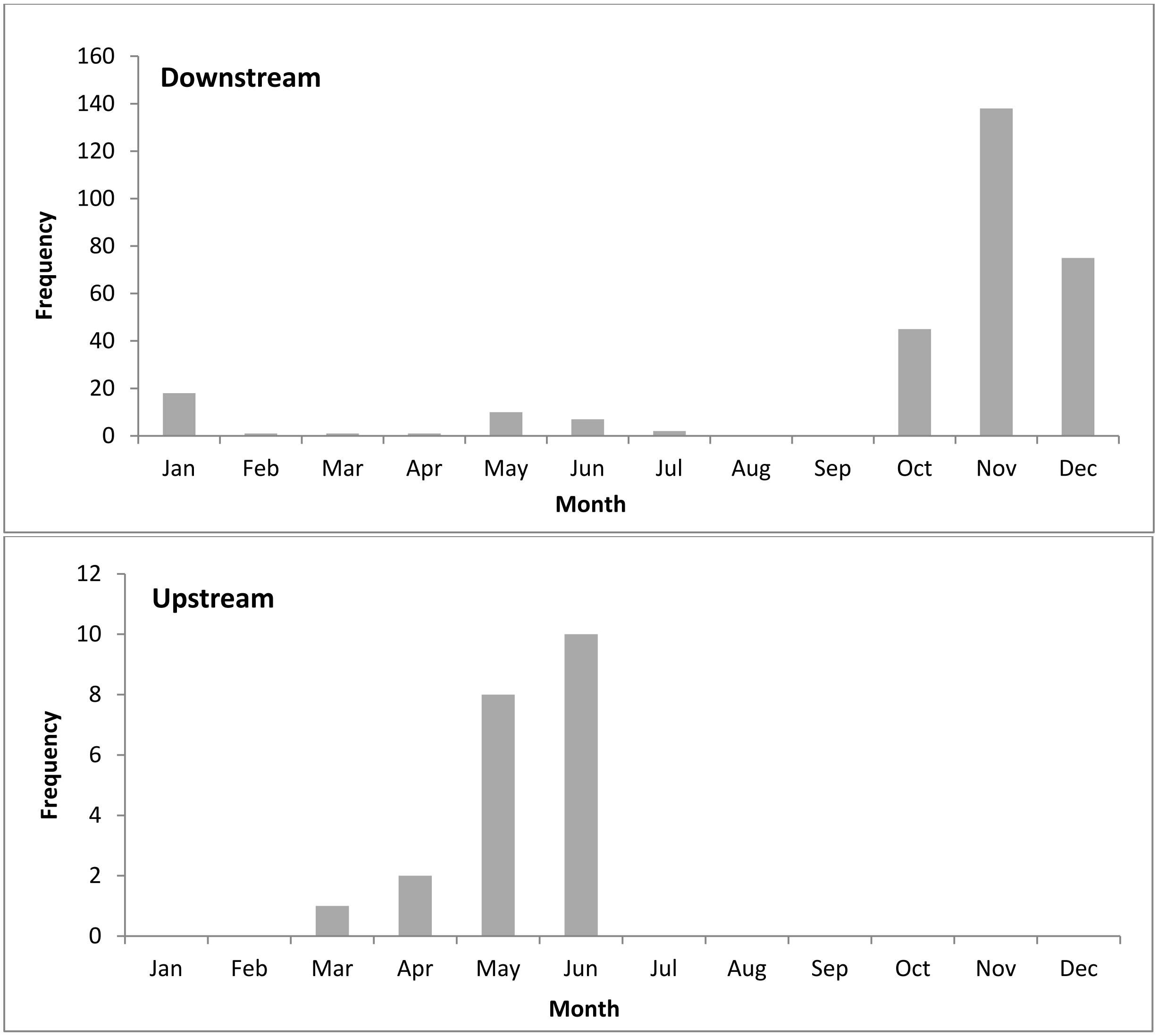

Figure 6.5. Number of unique monthly detections for bull trout detected at the Burlingame Dam PIA from 2007 – 2011.

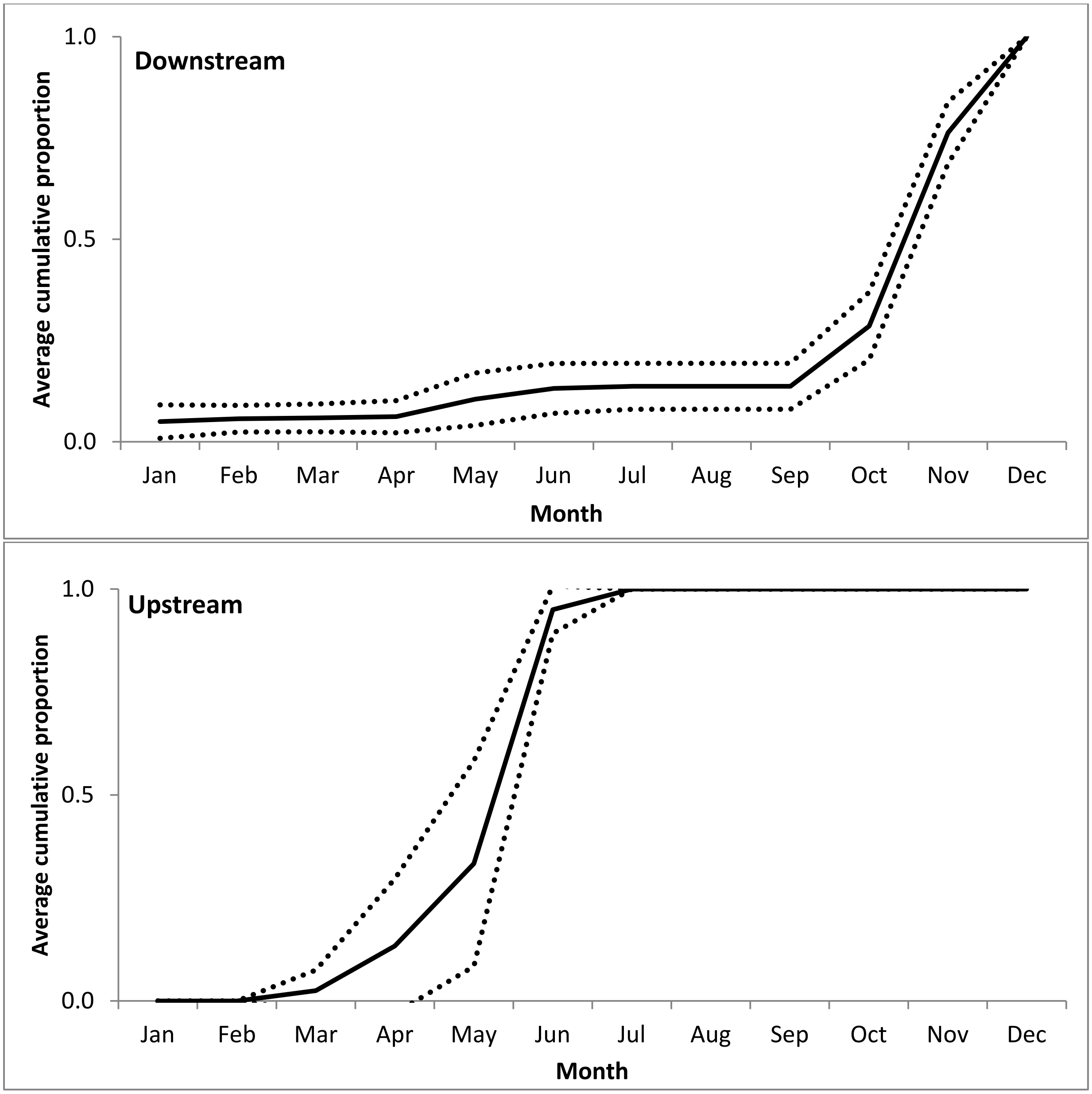

Figure 6.6. Average cumulative proportion for downstream and upstream detections at the Burlingame Dam PIA from 2007 – 2011. Dotted lines represent 95% CI.

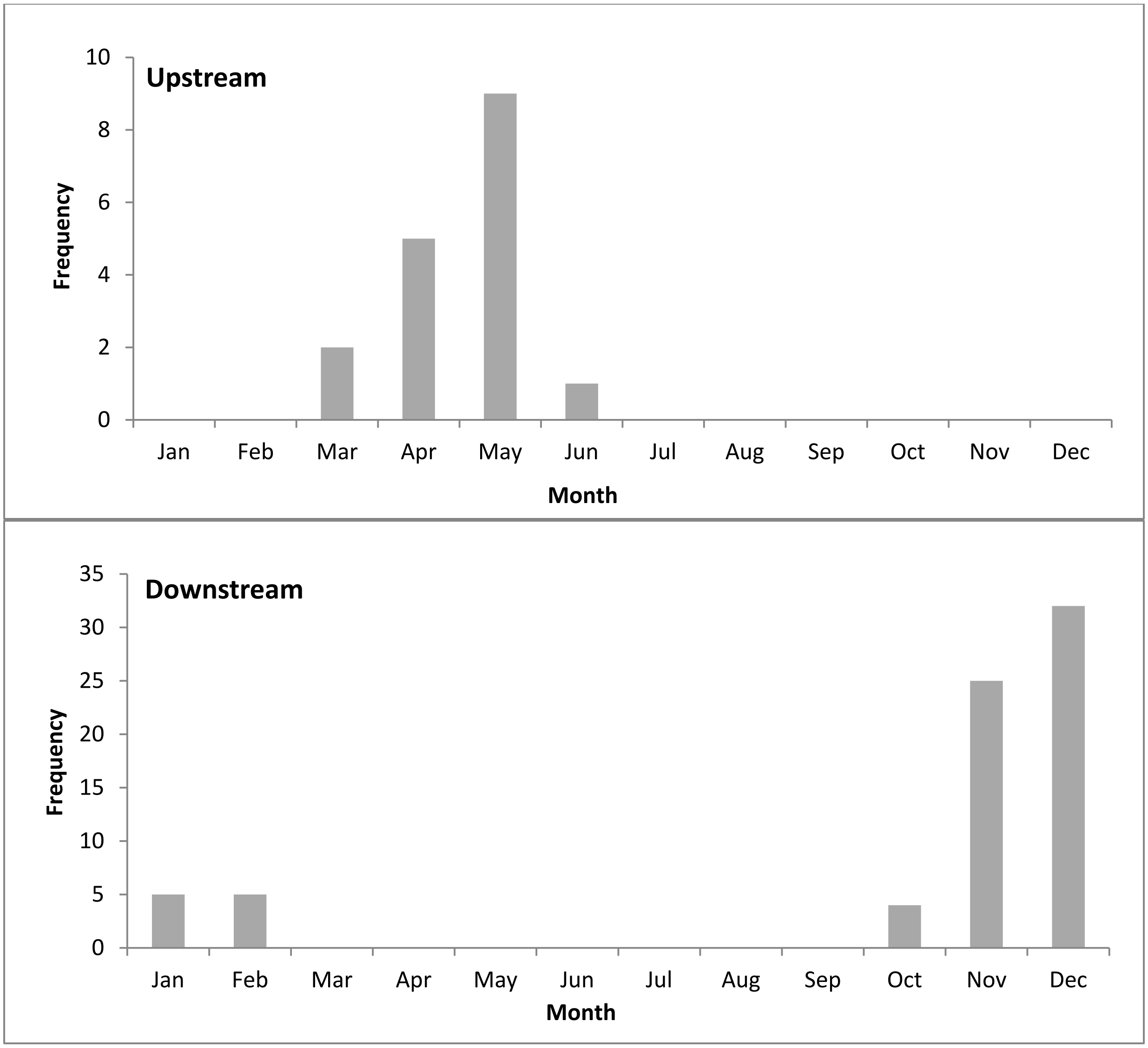

Figure 6.7. Number of unique monthly detections for bull trout detected at Oasis Road Bridge PIA from 2007–2011.

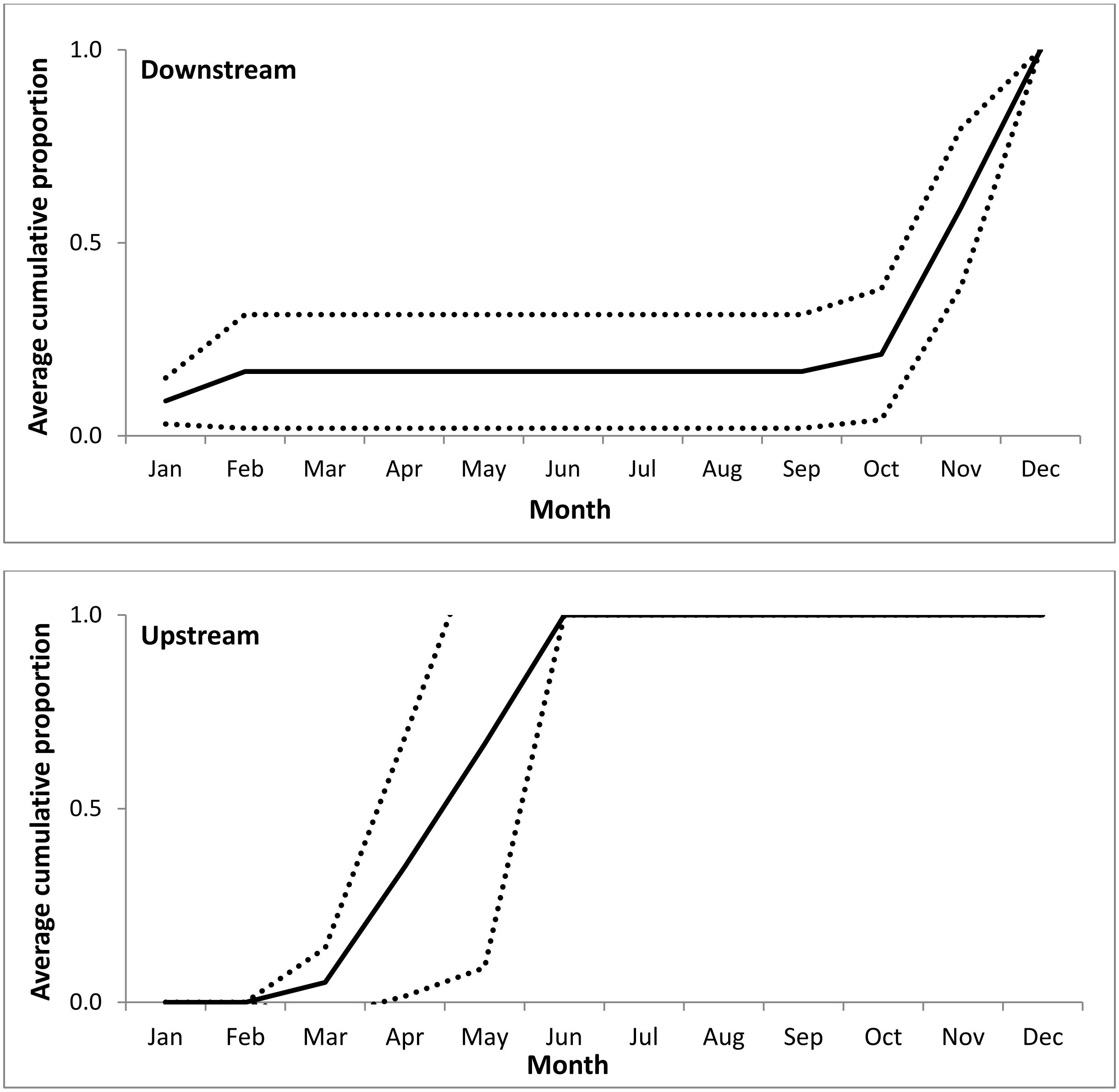

Figure 6.8. Average cumulative proportion for downstream and upstream detections at the Oasis Road Bridge PIA from 2007 – 2011. Dotted lines represent 95% CI.

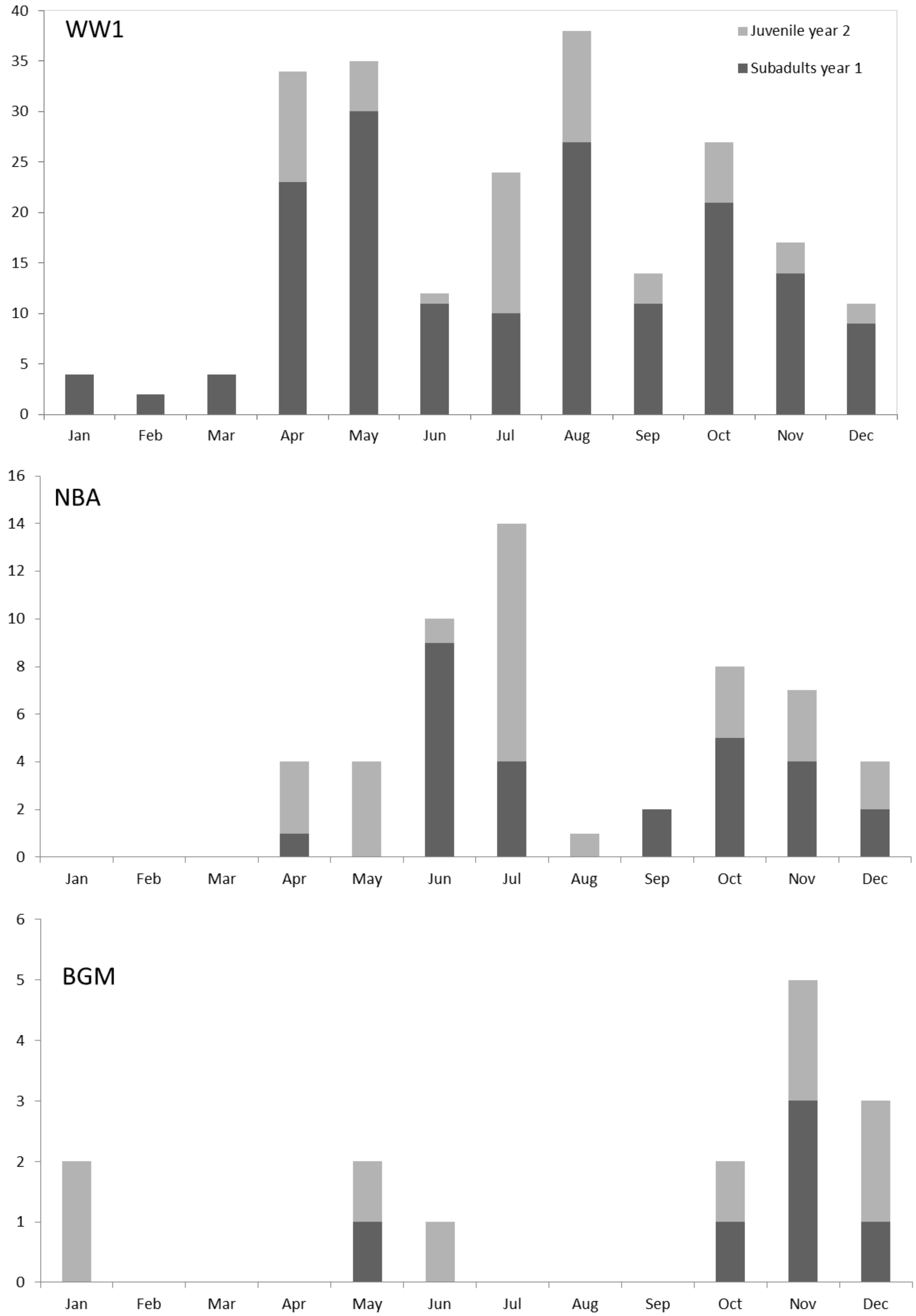

Figure 6.9. Downstream detections by month for sub-adult year 1 and juvenile year 2 combined for Harris Park Bridge (WW1), Nursery Bridge Dam (NBA) and Burlingame Dam (BGM) from 2002-2011.

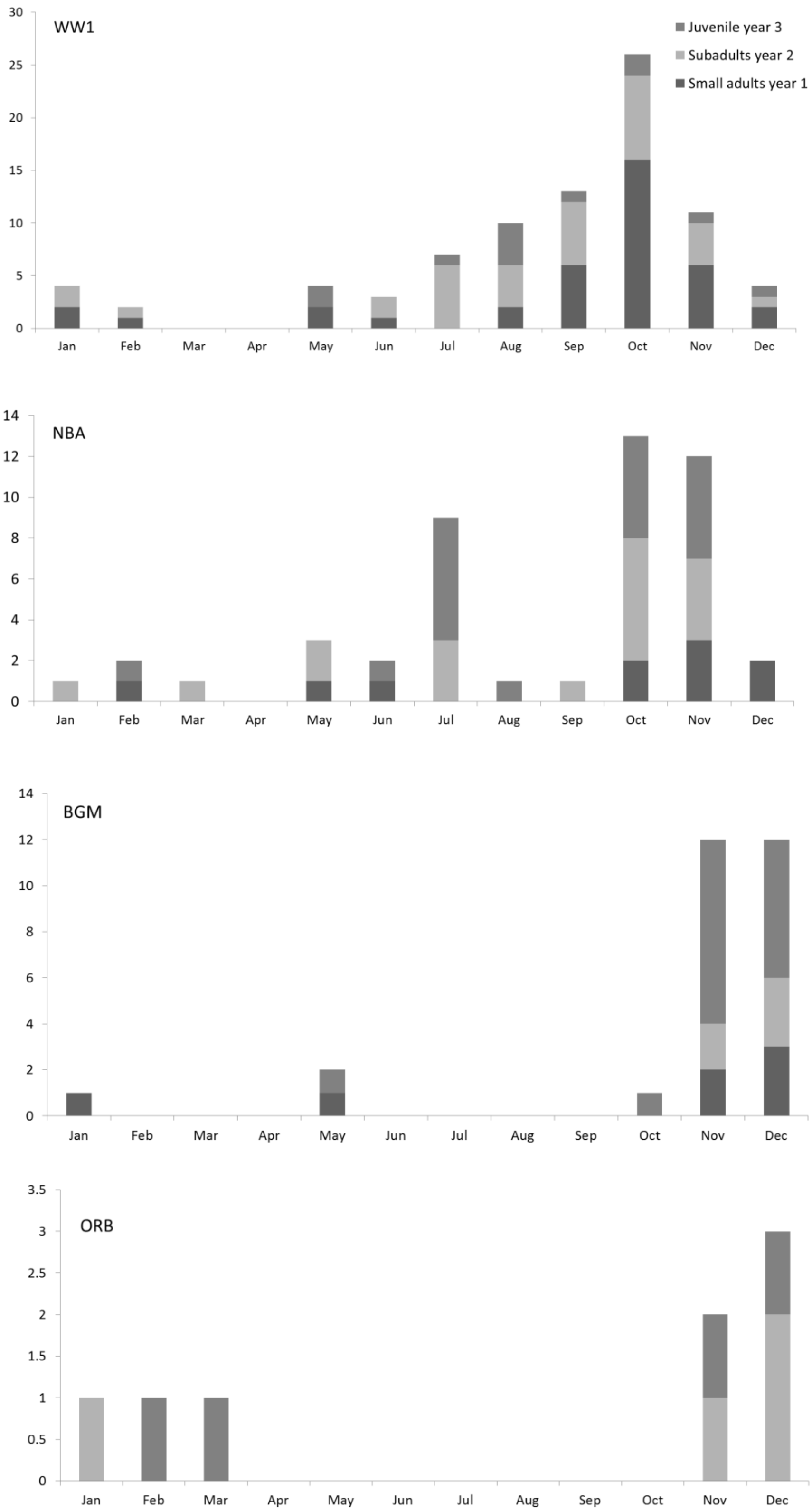

Figure 6.10. Downstream detections by month for small adults year 1, sub-adults year 2 and juvenile year 3 for Harris Park Bridge (WW1), Nursery Bridge Dam (NBA), Burlingame Dam (BGM) and Oasis Road Bridge (ORB) PIA's from 2002-2011.

Table 6.1. Total number of bull trout PIT tagged by USU in the SFWWR by year, 2002 – 2011.

Size class at tagging	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	Total
Juveniles	35	169	156	185	76	381	501	627	306	221	2657
Sub-adults	99	256	197	196	125	92	80	196	236	202	1679
Small Adults	50	51	36	22	20	7	13	11	20	19	249
Large Adults	27	46	23	21	8	5	7	13	18	10	178
	211	522	412	424	229	485	601	847	580	452	**4763**

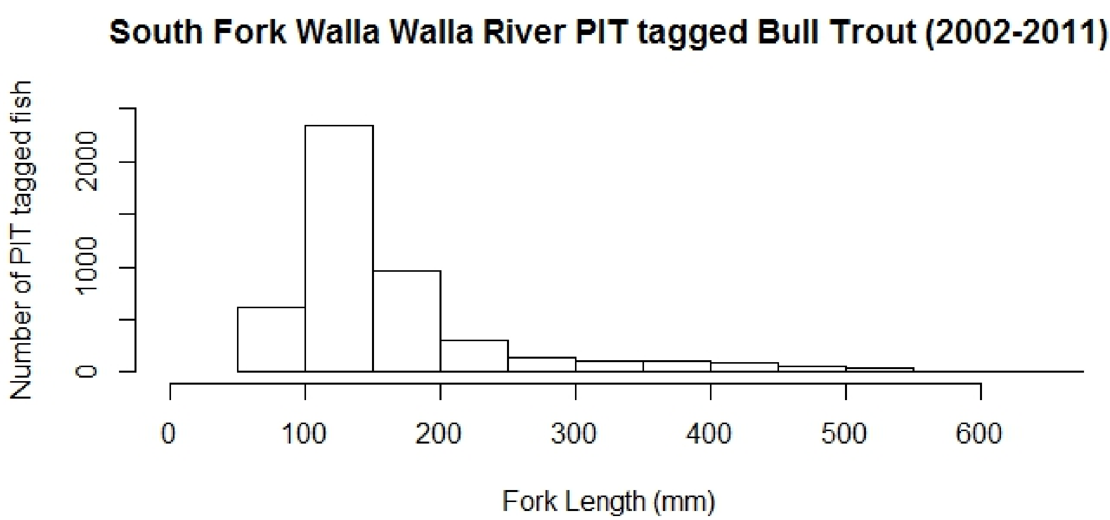

Figure 6.11. Length frequency distribution of bull trout PIT tagged in the SFWWR, 2002 – 2011.

Table 6.2. Number of bull trout PIT tagged in the SFWWR by size class. Number of migratory fish, % that migrated downstream, and % detected migrating upstream.

Size Class at Tagging (mm)	Tagged	Migratory	Downstream Movement (%)	Upstream Movement (%)
Juveniles (< 144)	2657	211	8%	5%
Sub-adults (144 - 290)	1679	229	14%	10%
Small Adults (291 - 406)	249	30	12%	63%
Large Adults (> 406)	178	66	37%	67%

Table 6.3. Movement metrics summarized by tag year for all bull trout tagged in the SFWWR that moved downstream of Harris Park Bridge (rkm 97) in 2002 – 2011.

Year Tagged	N	Downstream Distance (km)									Downstream Duration (days)								Downstream Rate (km/day)						
		Sum	Max	Min	Avg	Average (weighted)	SD	Weighted SD	SE	95% CI	Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Max	Min	Avg	Average (weighted)	SD	SE	95% CI
2002	26	-422.40	-54.20	-4.00	-16.25	-0.79	11.40	0.55	2.24	5.33	8078.26	797.58	1.80	310.70	15.07	234.10	45.91	109.48	4.78	0.01	0.78	0.04	1.37	0.27	0.64
2003	61	-1081.00	-52.20	-1.00	-17.72	-2.02	10.75	1.22	1.38	3.16	16963.61	1341.29	0.73	278.09	31.65	254.34	32.56	74.87	12.71	0.00	1.20	0.14	2.54	0.32	0.75
2004	41	-663.00	-44.00	-2.00	-16.17	-1.24	8.62	0.66	1.35	3.14	8446.04	1041.53	1.03	206.00	15.76	236.42	36.92	85.99	39.09	0.01	3.07	0.23	7.01	1.09	2.55
2005	52	-1595.60	-258.00	-3.00	-30.68	-2.98	37.91	3.68	5.26	12.14	16916.01	1119.32	6.46	325.31	31.56	246.70	34.21	79.01	28.69	0.01	1.80	0.17	5.13	0.71	1.64
2006	39	-860.60	-99.00	-2.00	-22.07	-1.61	19.22	1.40	3.08	7.18	9210.21	848.36	4.67	236.16	17.18	199.93	32.01	74.71	26.90	0.01	1.63	0.12	4.31	0.69	1.61
2007	49	-1607.00	-107.00	-5.00	-32.80	-3.00	24.89	2.28	3.56	8.23	23863.42	1497.95	5.48	487.01	44.52	352.75	50.39	116.60	4.26	0.02	0.68	0.06	1.09	0.16	0.36
2008	67	-1952.60	-103.00	-6.00	-29.58	-3.70	23.35	2.92	2.87	6.59	26526.06	985.63	15.32	401.91	50.24	261.29	32.16	73.80	12.19	0.02	0.92	0.11	1.91	0.23	0.54
2009	142	-3969.20	-104.00	-3.00	-27.95	-7.41	20.34	5.39	1.71	3.87	52580.41	886.21	9.58	370.28	98.10	205.72	17.26	39.11	28.03	0.01	1.71	0.45	3.95	0.33	0.75
2010	48	-1095.00	-56.00	-2.00	-22.81	-2.04	15.43	1.38	2.23	5.16	11111.82	507.12	15.54	231.50	20.73	172.41	24.89	57.62	17.94	0.01	1.05	0.09	2.77	0.40	0.93
2011	11	-210.60	-47.00	-3.00	-19.15	-0.39	14.89	0.31	4.49	11.82	713.38	126.09	3.99	64.85	1.33	39.59	11.94	31.44	2.16	0.04	0.79	0.02	0.80	0.24	0.63
Average	**536**	-1345.70	-92.44	-3.10	25.16	**-25.16**	18.68	19.78	-	-	17440.92	915.11	6.46	326.14	**326.14**	-	-	-	17.67	0.01	1.44	**1.44**	-	-	-

Year Tagged	N	Upstream Distance (km)									Upstream Duration (days)								Upstream Rate (km/day)						
		Sum	Max	Min	Avg	Average (weighted)	SD	Weighted SD	SE	95% CI	Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Max	Min	Avg	Average (weighted)	SD	SE	95% CI
2002	15	185.40	40.20	2.60	12.36	1.89	8.99	1.38	2.32	5.82	1012.74	409.89	8.84	67.52	10.33	105.56	27.26	68.40	1.65	0.03	0.64	0.10	0.56	0.14	0.36
2003	25	409.00	40.20	1.60	16.36	4.17	12.12	3.09	2.42	5.80	4130.70	1124.65	5.01	165.23	42.15	271.11	54.22	129.64	1.72	0.00	0.58	0.15	0.49	0.10	0.23
2004	13	143.80	31.60	1.60	11.06	1.47	8.85	1.17	2.46	6.29	1524.32	696.61	4.14	117.26	15.55	204.53	56.73	145.22	1.04	0.00	0.43	0.06	0.30	0.08	0.21
2005	8	489.20	213.40	8.60	61.15	4.99	66.20	5.40	23.40	66.50	1836.84	764.91	4.56	229.60	18.74	285.31	100.87	286.60	2.85	0.23	1.01	0.08	0.87	0.31	0.87
2006	5	86.00	54.60	5.60	17.20	0.88	20.95	1.07	9.37	32.75	204.93	101.97	10.87	40.99	2.09	35.68	15.96	55.78	0.85	0.16	0.49	0.03	0.31	0.14	0.49
2007	9	251.20	50.00	4.60	27.91	2.56	17.19	1.58	5.73	15.77	670.58	113.71	37.52	74.51	6.84	25.23	8.41	23.14	2.88	0.06	0.71	0.07	0.88	0.29	0.80
2008	11	238.20	90.60	2.00	21.65	2.43	25.39	2.85	7.65	20.16	2266.03	724.27	2.45	206.00	23.12	227.05	68.46	180.30	1.24	0.01	0.34	0.04	0.42	0.13	0.33
2009	8	183.00	46.00	2.00	22.88	1.87	16.74	1.37	5.92	16.82	2013.49	671.34	15.00	251.69	20.55	250.33	88.51	251.47	0.82	0.02	0.30	0.02	0.34	0.12	0.34
2010	3	23.40	11.20	3.60	7.80	0.24	3.86	0.12	2.23	13.84	273.92	138.52	32.37	91.31	2.80	54.04	31.20	193.60	0.11	0.08	0.09	0.00	0.02	0.01	0.07
2011	1	6.60	6.60	6.60	6.60	0.07	-	-	-	-	52.37	52.37	52.37	52.37	0.53	-	-	-	0.13	0.13	0.13	0.00	-	-	-
Average	**98**	201.58	58.44	3.88	20.57	**20.57**	-	**18.03**	-	-	1398.59	479.82	17.31	142.71	**142.71**	-	-	-	1.33	0.07	0.54	**0.54**	-	-	-

Table 6.4. Movement metrics summarized by tag year for bull trout tagged as juveniles in the SFWWR that moved downstream of Harris Park (rkm 97) in 2002 – 2011.

Year Tagged	N	Downstream Distance (km)								Downstream Duration (days)								Downstream Rate (km/day)						
		Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Max	Min	Avg	Average (weighted)	SD	SE	95% CI
2002	1	-11.00	-11.00	-11.00	-11.00	-0.05	-	-	-	178.35	178.35	178.35	178.35	0.85	-	-	-	0.09	0.09	0.09	0.00	-	-	-
2003	11	-216.20	-52.20	-10.00	-19.65	-1.02	11.95	3.60	9.49	4155.06	894.29	109.70	377.73	19.69	232.18	70.01	184.38	1.49	0.03	0.47	0.02	0.59	0.18	0.47
2004	4	-47.00	-17.00	-7.00	-11.75	-0.22	4.11	2.06	8.59	1705.28	1041.53	171.69	426.32	8.08	412.24	206.12	860.88	39.09	0.03	9.81	0.19	19.52	9.76	40.76
2005	10	-195.00	-50.00	-10.00	-19.50	-0.92	11.38	3.60	9.67	3929.77	688.60	13.39	392.98	18.62	190.77	60.33	161.98	23.95	0.04	3.23	0.15	7.33	2.32	6.22
2006	5	-158.00	-54.00	-16.00	-31.60	-0.75	19.17	8.57	29.96	2408.35	848.36	271.51	481.67	11.41	228.45	102.17	357.11	26.90	0.05	6.47	0.15	11.48	5.13	17.94
2007	30	-1177.20	-107.00	-8.60	-39.24	-5.58	25.93	4.74	11.19	19933.71	1497.95	121.57	664.46	94.47	320.51	58.52	138.33	3.35	0.02	0.35	0.05	0.82	0.15	0.36
2008	50	-1610.60	-103.00	-6.00	-32.21	-7.63	24.02	3.40	7.86	23490.60	985.63	104.31	469.81	111.33	240.67	34.04	78.70	12.19	0.03	0.78	0.19	2.00	0.28	0.65
2009	91	-2553.00	-103.00	-10.00	-28.05	-12.10	17.69	1.85	4.23	36668.00	886.21	18.16	402.95	173.78	211.35	22.16	50.50	20.43	0.02	1.63	0.70	3.64	0.38	0.87
2010	9	-212.00	-48.00	-10.00	-23.56	-1.00	12.80	4.27	11.74	3528.45	482.05	348.76	392.05	16.72	46.72	15.57	42.85	0.64	0.03	0.24	0.01	0.28	0.09	0.26
2011	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
(Avg)	**211**	-686.67	-60.58	-9.84	-24.06	**-29.29**	-	-	-	10666.40	833.66	148.60	420.70	**454.96**	-	-	-	14.24	0.04	2.56	**1.46**	-	-	-

Year Tagged	N	Downstream Distance (km)								Downstream Duration (days)								Upstream Rate (km/day)						
		Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Max	Min	Avg	Average (weighted)	SD	SE	95% CI
2002	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2003	1	40.20	40.20	40.20	40.20	3.65	-	-	-	62.69	62.69	62.69	62.69	5.70	-	-	-	0.96	0.96	0.96	0.09	-	-	-
2004	1	8.60	8.60	8.60	8.60	0.78	-	-	-	26.17	26.17	26.17	26.17	2.38	-	-	-	0.33	0.33	0.33	0.03	-	-	-
2005	1	13.00	13.00	13.00	13.00	1.18	-	-	-	4.56	4.56	4.56	4.56	0.41	-	-	-	2.85	2.85	2.85	0.26	-	-	-
2006	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2007	3	116.60	44.60	36.00	38.87	10.60	4.97	2.87	17.79	248.07	113.71	54.28	82.69	22.55	29.80	17.21	106.77	0.98	0.47	0.67	0.18	0.27	0.16	0.97
2008	4	59.60	31.60	2.00	14.90	5.42	12.28	6.14	25.65	329.09	158.66	2.45	82.27	29.92	71.97	35.98	150.28	0.82	0.08	0.51	0.18	0.37	0.19	0.78
2009	1	2.00	2.00	2.00	2.00	0.18	-	-	-	15.00	15.00	15.00	15.00	1.36	-	-	-	0.13	0.13	0.13	0.01	-	-	-
2010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2011	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Years (Avg)	**11**	40.00	23.33	16.97	19.59	**21.82**	-	-	-	114.26	63.46	27.53	45.56	**62.33**	-	-	-	1.01	0.80	0.91	**0.76**	-	-	-

Table 6.5. Movement metrics summarized by tag year for bull trout tagged as sub-adults in the SFWWR that moved downstream of Harris Park (rkm 97) in 2002 – 2011.

Year Tagged	N	Downstream Distance (km)								Downstream Duration (days)								Downstream Rate (km/day)						
		Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Max	Min	Avg	Average (weighted)	SD	SE	95% CI
2002	8	-123.20	-21.00	-5.00	-15.40	-0.54	5.89	2.08	5.92	3028.34	770.97	118.58	378.54	13.22	249.25	88.12	250.38	4.14	0.04	0.83	0.03	1.42	0.50	1.43
2003	30	-518.00	-41.80	-3.00	-17.27	-2.26	10.21	1.86	4.40	9107.47	1341.29	6.62	303.58	39.77	303.95	55.49	131.18	4.50	0.00	0.61	0.08	1.02	0.19	0.44
2004	25	-440.20	-44.00	-3.00	-17.61	-1.92	8.27	1.65	3.96	4941.99	743.80	1.07	197.68	21.58	227.85	45.57	108.96	22.72	0.02	2.50	0.27	4.66	0.93	2.23
2005	34	-839.20	-93.60	-3.00	-24.68	-3.66	17.66	3.03	7.11	10915.64	1119.32	6.46	321.05	47.67	264.20	45.31	106.40	28.69	0.01	1.49	0.22	4.91	0.84	1.98
2006	27	-572.80	-99.00	-3.00	-21.21	-2.50	19.79	3.81	9.06	6106.00	622.65	12.95	226.15	26.66	177.60	34.18	81.30	4.80	0.01	0.80	0.09	0.99	0.19	0.45
2007	15	-273.20	-53.00	-5.00	-18.21	-1.19	11.41	2.95	7.39	3712.79	662.54	5.48	247.52	16.21	175.41	45.29	113.66	3.68	0.02	1.09	0.07	1.15	0.30	0.75
2008	9	-114.00	-18.00	-10.00	-14.25	-0.56	2.92	1.03	2.93	2485.87	727.21	27.30	310.73	12.21	235.13	83.13	236.19	1.92	0.02	0.52	0.02	0.70	0.25	0.70
2009	47	-1291.40	-104.00	-3.00	-27.48	-5.64	25.27	3.69	8.54	15274.82	733.83	9.58	325.00	66.70	182.67	26.65	61.74	28.03	0.01	1.58	0.32	4.28	0.62	1.45
2010	28	-723.20	-56.00	-2.00	-25.83	-3.16	17.47	3.30	7.83	6857.93	507.12	15.54	244.93	29.95	176.01	33.26	78.95	5.26	0.01	0.40	0.05	0.98	0.19	0.44
2011	6	-77.00	-20.00	-3.00	-12.83	-0.34	6.74	2.75	8.70	344.27	98.49	8.56	57.38	1.50	37.73	15.40	48.72	1.99	0.04	0.57	0.01	0.74	0.30	0.96
Avg	**229**	-497.22	-55.04	-4.00	-19.48	**-21.77**	-	-	-	6277.51	732.72	21.21	261.26	**275.48**	-	-	-	10.57	0.02	1.04	**1.18**	-	-	-

Year Tagged	N	Upstream Distance (km)								Upstream Duration (days)								Upstream Rate (km/day)						
		Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Max	Min	Avg	Average (weighted)	SD	SE	95% CI
2002	1	8.60	8.60	8.60	8.60	0.36	-	-	-	69.30	69.30	69.30	69.30	2.89	-	-	-	0.12	0.12	0.12	0.01	-	-	-
2003	6	90.00	36.80	1.60	15.00	3.75	12.22	4.99	15.78	962.85	441.44	6.97	160.47	40.12	217.35	88.73	280.70	1.40	0.00	0.65	0.16	0.58	0.23	0.74
2004	4	18.80	8.60	1.60	4.70	0.78	3.45	1.73	7.21	1141.37	696.61	8.25	285.34	47.56	330.50	165.25	690.17	1.04	0.00	0.28	0.05	0.51	0.25	1.06
2005	3	84.80	44.60	8.60	28.27	3.53	18.23	10.53	65.31	136.30	93.75	13.28	45.43	5.68	42.60	24.60	152.62	1.69	0.36	0.90	0.11	0.70	0.40	2.49
2006	3	71.80	54.60	8.60	23.93	2.99	26.56	15.33	95.15	148.16	101.97	10.87	49.39	6.17	47.15	27.22	168.93	0.85	0.24	0.63	0.08	0.33	0.19	1.19
2007	2	58.60	50.00	8.60	29.30	2.44	29.27	20.70	526.85	121.29	77.38	43.91	60.64	5.05	23.67	16.74	425.93	2.88	0.11	1.50	0.12	1.96	1.39	35.26
2008	1	8.60	8.60	8.60	8.60	0.36	-	-	-	42.90	42.90	42.90	42.90	1.79	-	-	-	0.20	0.20	0.20	0.01	-	-	-
2009	4	104.60	46.00	2.00	26.15	4.36	18.64	9.32	38.93	377.45	141.75	28.07	94.36	15.73	47.72	23.86	99.64	0.82	0.02	0.51	0.09	0.38	0.19	0.80
2010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2011	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Avg	**24**	55.73	32.23	6.02	18.07	**18.58**	-	-	-	374.95	208.14	27.94	100.98	**124.98**	-	-	-	1.12	0.13	0.60	**0.62**	-	-	-

Table 6.6. Movement metrics summarized by tag year for bull trout tagged as small adults in the SFWWR that moved downstream of Harris Park (rkm 97) in 2002 – 2011.

Year Tagged	N	Downstream Distance (km)								Downstream Duration (days)								Downstream Rate (km/day)						
		Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Max	Min	Avg	Average (weighted)	SD	SE	95% CI
2002	5	-94.40	-54.20	-4.00	-18.88	-3.15	20.29	9.07	31.72	1839.11	797.58	12.71	367.82	61.30	324.11	144.95	506.65	0.68	0.01	0.28	0.05	0.29	0.13	0.46
2003	6	-101.00	-45.40	-1.00	-16.83	-3.37	16.19	6.61	20.90	1778.29	386.85	182.44	296.38	59.28	91.97	37.55	118.77	1.31	0.00	0.34	0.07	0.53	0.21	0.68
2004	3	-22.20	-17.20	-2.00	-7.40	-0.74	8.50	4.91	30.46	771.44	567.25	4.08	257.15	25.71	285.88	165.06	1024.23	6.69	0.01	2.23	0.22	3.86	2.23	13.81
2005	5	-424.00	-258.00	-11.00	-84.80	-14.13	99.63	44.55	155.73	1418.41	682.25	82.32	283.68	47.28	238.45	106.64	372.74	6.76	0.09	1.94	0.32	2.83	1.27	4.43
2006	2	-6.00	-4.00	-2.00	-3.00	-0.20	1.41	1.00	25.45	100.41	84.39	16.02	50.21	3.35	48.34	34.19	870.07	0.12	0.05	0.09	0.01	0.05	0.04	0.99
2007	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2008	4	-136.20	-90.60	-8.60	-34.05	-22.70	38.04	19.02	79.44	347.64	215.08	20.18	86.91	57.94	87.15	43.58	182.00	2.18	0.16	0.89	0.59	0.89	0.44	1.85
2009	1	-10.00	-10.00	-10.00	-10.00	-0.33	-	-	-	54.62	54.62	54.62	54.62	1.82	-	-	-	13.88	13.88	13.88	0.46	-	-	-
2010	1	-8.60	-8.60	-8.60	-8.60	-0.29	-	-	-	57.82	57.82	57.82	57.82	1.93	-	-	-	0.15	0.15	0.15	0.00	-	-	-
2011	3	-65.60	-47.00	-8.60	-21.87	-2.19	21.78	12.57	78.02	217.63	126.09	3.99	72.54	7.25	62.42	36.04	223.62	2.16	0.37	1.00	0.10	1.00	0.58	3.58
Avg	**30**	-96.44	-59.44	-6.20	-22.83	**-47.09**	-	-	-	731.71	330.21	48.24	169.68	**265.86**	-	-	-	3.77	1.64	2.31	**1.83**	-	-	-

Year Tagged	N	Upstream Distance (km)								Upstream Duration (days)								Upstream Rate (km/day)						
		Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Max	Min	Avg	Average (weighted)	SD	SE	95% CI
2002	3	60.00	40.20	2.60	20.00	3.16	18.96	10.94	67.91	82.13	38.72	12.91	27.38	4.32	13.19	7.61	47.24	1.40	0.09	0.96	0.15	0.75	0.43	2.70
2003	6	88.20	34.40	2.60	14.70	4.64	13.26	5.41	17.13	2218.58	1124.65	5.01	369.76	116.77	447.33	182.62	577.71	1.72	0.00	0.64	0.20	0.77	0.31	0.99
2004	1	13.20	13.20	13.20	13.20	0.69	-	-	-	26.13	26.13	26.13	26.13	1.38	-	-	-	0.68	0.68	0.68	0.04	-	-	-
2005	3	311.00	213.40	31.60	103.67	16.37	96.58	55.76	346.00	1280.63	764.91	44.39	426.88	67.40	362.31	209.18	1298.04	0.92	0.23	0.67	0.11	0.38	0.22	1.37
2006	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2007	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2008	3	101.20	90.60	4.60	33.73	5.33	49.25	28.44	176.46	590.21	405.41	63.93	196.74	31.06	182.95	105.62	655.43	1.24	0.01	0.45	0.07	0.69	0.40	2.46
2009	1	17.00	17.00	17.00	17.00	0.89	-	-	-	671.34	671.34	671.34	671.34	35.33	-	-	-	0.03	0.03	0.03	0.00	-	-	-
2010	1	11.20	11.20	11.20	11.20	0.59	-	-	-	138.52	138.52	138.52	138.52	7.29	-	-	-	0.08	0.08	0.08	-	-	-	-
2011	1	6.60	6.60	6.60	6.60	0.35	-	-	-	52.37	52.37	52.37	52.37	2.76	-	-	-	0.13	0.13	0.13	-	-	-	-
Avg	**19**	76.05	53.33	11.18	27.51	**32.02**	-	-	-	632.49	402.76	126.82	238.64	**266.31**	-	-	-	0.77	0.15	0.45	**0.57**	-	-	-

Table 6.7. Movement metrics summarized by tag year for bull trout tagged as large adults in the SFWWR that moved downstream of Harris Park (rkm 97) in 2002 – 2011.

Year Tagged	N	Downstream Distance (km)								Downstream Duration (days)								Downstream Rate (km/day)						
		Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Max	Min	Avg	Average (weighted)	SD	SE	95% CI
2002	12	-193.80	-36.20	-5.00	-16.15	-2.94	10.84	3.13	8.11	3032.46	598.90	1.80	252.71	45.95	191.64	55.32	143.45	4.78	0.03	1.01	0.18	1.65	0.48	1.23
2003	14	-245.80	-34.40	-8.60	-17.56	-3.72	9.27	2.48	6.27	1922.79	403.19	0.73	137.34	29.13	127.90	34.18	86.57	12.71	0.05	3.40	0.72	4.49	1.20	3.04
2004	9	-153.60	-31.60	-2.00	-17.07	-2.33	9.80	3.27	8.99	1027.33	226.97	1.03	114.15	15.57	67.89	22.63	62.27	8.35	0.01	1.92	0.26	2.89	0.96	2.65
2005	3	-137.40	-99.40	-19.00	-45.80	-2.08	46.42	26.80	166.30	652.19	539.22	48.47	217.40	9.88	278.82	160.98	998.93	0.39	0.29	0.33	0.01	0.06	0.03	0.20
2006	5	-123.80	-46.00	-8.60	-24.76	-1.88	16.98	7.59	26.54	595.45	242.93	4.67	119.09	9.02	107.19	47.93	167.55	3.88	0.09	1.90	0.14	1.73	0.77	2.71
2007	4	-156.60	-76.20	-8.60	-39.15	-	35.67	17.84	74.49	216.92	128.29	6.00	54.23	3.29	53.76	26.88	112.26	4.26	0.34	1.65	0.10	1.80	0.90	3.77
2008	4	-91.80	-34.40	-12.00	-22.95	-1.39	9.49	4.75	19.82	201.95	71.04	15.32	50.49	3.06	24.75	12.37	51.68	5.67	2.17	3.42	0.21	1.66	0.83	3.46
2009	3	-114.80	-47.60	-29.20	-38.27	-1.74	9.20	5.31	32.97	582.97	273.11	63.05	194.32	8.83	114.44	66.07	410.01	5.51	0.23	2.03	0.09	3.01	1.74	10.80
2010	10	-151.20	-36.00	-8.60	-15.12	-2.29	8.09	2.56	6.87	667.62	97.27	28.76	66.76	10.12	22.77	7.20	19.33	17.94	0.30	3.66	0.56	5.25	1.66	4.46
2011	2	-68.00	-47.00	-21.00	-34.00	-1.03	18.38	13.00	330.87	151.48	78.25	73.23	75.74	2.30	3.55	2.51	63.88	1.83	0.43	1.13	0.03	0.99	0.70	17.86
Avg	**66**	-143.68	-48.88	-12.26	-27.08	**-19.40**	17.41	8.67	68.13	905.12	265.92	24.31	128.22	**137.14**	99.27	43.61	211.59	6.53	0.39	2.04	**2.31**	2.35	0.93	5.02

Year Tagged	N	Upstream Distance (km)								Upstream Duration (days)								Upstream Rate (km/day)						
		Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Sum	Max	Min	Avg	Average (weighted)	SD	SE	95% CI	Max	Min	Avg	Average (weighted)	SD	SE	95% CI
2002	11	116.80	17.20	2.60	10.62	2.65	4.35	1.31	3.45	861.31	409.89	8.84	78.30	19.58	122.29	36.87	97.11	1.65	0.03	0.60	0.15	0.52	0.16	0.41
2003	12	190.60	37.20	5.60	15.88	4.33	10.87	3.14	8.14	886.58	454.27	8.80	73.88	20.15	122.68	35.41	91.83	1.00	0.09	0.47	0.13	0.27	0.08	0.20
2004	7	103.20	31.60	1.60	14.74	2.35	10.31	3.90	11.57	330.65	124.44	4.14	47.24	7.51	41.59	15.72	46.66	0.68	0.29	0.50	0.08	0.14	0.05	0.15
2005	1	80.40	80.40	80.40	80.40	1.83	-	-	-	415.35	415.35	415.35	415.35	9.44	-	-	-	0.55	0.55	0.55	0.01	-	-	-
2006	2	14.20	8.60	5.60	7.10	0.32	2.12	1.50	38.18	56.77	36.06	20.71	28.39	1.29	10.85	7.68	195.34	0.42	0.16	0.29	0.01	0.18	0.13	3.31
2007	4	76.00	34.20	4.60	19.00	1.73	16.09	8.05	33.60	301.22	100.10	37.52	75.31	6.85	26.88	13.44	56.14	0.84	0.06	0.34	0.03	0.35	0.17	0.73
2008	3	68.80	34.40	8.60	22.93	1.56	13.14	7.58	47.06	1303.83	724.27	113.26	434.61	29.63	306.74	177.09	1098.93	0.08	0.06	0.07	0.00	0.01	0.01	0.03
2009	2	59.40	42.20	17.20	29.70	1.35	17.68	12.50	318.15	949.70	498.24	451.46	474.85	21.58	33.08	23.39	595.32	0.12	0.06	0.09	0.00	0.04	0.03	0.77
2010	2	12.20	8.60	3.60	6.10	0.28	3.54	2.50	63.63	135.40	103.03	32.37	67.70	3.08	49.96	35.33	899.21	0.11	0.08	0.10	0.00	0.02	0.01	0.35
2011	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Avg	**44**	80.18	32.71	14.42	22.94	**16.40**	9.76	5.06	65.47	582.31	318.41	121.38	188.40	**119.11**	89.26	43.12	385.07	0.61	0.15	0.33	**0.43**	0.19	0.08	0.74

Table 6.8. Movement metrics summarized by emigration year after tagging for all bull trout tagged in the SFWWR that moved downstream of Harris Park (rkm 97) in 2002 – 2011.

Year Emigrated after tagging	N	Downstream Distance (km)							Downstream Duration (days)							Downstream Rate (km/day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
Year 1	346	-7262.80	-258.00	-1.00	-21.05	19.85	1.07	2.41	69753.51	784.46	0.73	202.18	145.51	7.83	17.64	26.90	0.00	1.54	3.23	0.17	0.39
Year 2	134	-3964.80	-104.00	-3.00	-29.59	20.64	1.78	4.04	60541.71	1006.5	21.58	451.80	164.26	14.19	32.17	28.69	0.01	1.26	4.21	0.36	0.82
Year 3	51	-2042.20	-107.00	-3.00	-40.04	27.18	3.81	8.80	39845.87	1341.29	1.07	781.29	226.73	31.75	73.37	39.09	0.00	1.36	5.55	0.78	1.80
Year 4	4	-148.20	-89.00	-8.60	-37.05	38.04	19.02	79.45	3907.63	1497.95	182.44	976.91	559.79	279.90	1169.00	0.49	0.01	0.15	0.23	0.12	0.48
Avg	**536**	-3354.50	-139.50	-3.90	-25.15	-	-	-	43512.18	1157.55	51.46	325.77	-	-	-	23.79	0.00	1.44	-	-	-

Year Emigrated after tagging	N	Upstream Distance (km)							Upstream Duration (days)							Upstream Rate (km/day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
Year 1	67	1538.40	213.40	1.60	22.96	29.74	3.63	8.33	9217.93	764.91	4.14	137.58	196.26	23.98	55.00	2.88	0.02	0.56	0.55	0.07	0.15
Year 2	19	321.80	54.60	1.60	16.94	15.99	3.67	8.97	2432.41	440.15	2.45	128.02	159.24	36.53	89.32	2.85	0.00	0.58	0.64	0.15	0.36
Year 3	10	114.00	40.20	2.60	11.40	10.43	3.30	8.86	1130.85	696.61	6.97	113.09	209.68	66.31	178.03	1.23	0.01	0.44	0.46	0.15	0.39
Year 4	2	41.60	36.00	5.60	20.80	21.50	15.20	386.87	1204.73	1124.65	80.08	602.37	738.62	522.29	13293.04	0.57	0.00	0.29	0.40	0.28	7.19
Avg	**98**	503.95	86.05	2.85	20.57	-	-	-	3496.48	756.58	23.41	142.71	-	-	-	1.88	0.01	0.54	-	-	-

Table 6.9. Movement metrics summarized by emigration year after tagging for bull trout tagged as juveniles in the SFWWR that moved downstream of Harris Park (rkm 97) in 2002 – 2011.

Year Emigrated after tagging	N	Downstream Distance (km)							Downstream Duration (days)							Downstream Rate (km/day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
Year 1	94	-1953.6	-103	-7	-20.78	13.03	1.34	3.06	25055.51	504.45	13.39	266.55	79.53	8.20	18.69	26.90	0.03	1.88	4.43	0.46	1.04
Year 2	78	-2268.2	-94	-6	-29.08	17.56	1.99	4.55	37718.69	1006.50	110.52	483.57	162.62	18.41	42.09	23.95	0.02	0.99	3.13	0.35	0.81
Year 3	37	-1827.2	-107	-16	-49.38	25.69	4.22	9.88	30617.50	1108.52	468.23	827.50	125.01	20.55	48.07	39.09	0.02	1.48	6.39	1.05	2.46
Year 4	2	-131	-89	-42	-65.50	33.23	23.50	598.11	2605.87	1497.95	1107.92	1302.94	275.79	195.02	4963.46	0.49	0.04	0.27	0.32	0.23	5.79
All Years (Avg)	**211**	-1545.00	-98.25	-17.75	-29.29	-	-	-	23999.39	1029.36	425.02	454.9648	-	-	-	22.61	0.03	1.46	-	-	-

Year Emigrated after tagging	N	Upstream Distance (km)							Upstream Duration (days)							Upstream Rate (km/day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
Year 1	1	2.00	2.00	2.00	2.00	-	-	-	15	15	15	15	-	-	-	0.13	0.13	0.13	-	-	-
Year 2	6	140.20	44.60	2.00	23.37	16.43	6.71	21.22	342.98	124.76	2.45	57.16	52.40	21.39	67.68	2.85	0.30	1.04	0.92	0.38	1.19
Year 3	3	61.80	40.20	8.60	20.60	17.12	9.88	61.32	247.52	158.66	26.17	82.51	68.43	39.51	245.17	0.96	0.08	0.46	0.46	0.26	1.63
Year 4	1	36.00	36.00	36.00	36.00	-	-	-	80.08	80.08	80.08	80.08	-	-	-	0.57	0.57	0.57	-	-	-
All Years (Avg)	**11**	60.00	30.70	12.15	21.818	-	-	-	171.40	94.63	30.93	62.33	-	-	-	1.13	0.27	0.756	-	-	-

Table 6.10. Movement metrics summarized by emigration year after tagging for bull trout tagged as sub-adults in the SFWWR that moved downstream of Harris Park Bridge(rkm 97) in 2002 – 2011.

Year Emigrated after tagging	N	Downstream Distance (km)							Downstream Duration (days)							Downstream Rate (km/day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
Year 1	166	-3129.00	-93.60	-2.00	-18.85	13.65	1.06	2.40	32238.84	784.46	4.46	194.21	158.96	12.34	27.91	22.72	0.01	1.00	2.06	0.16	0.36
Year 2	48	-1593.20	-104.00	-5.00	-33.19	25.05	3.62	8.37	20638.38	731.08	21.58	429.97	142.54	20.57	47.64	28.69	0.01	1.84	5.78	0.83	1.93
Year 3	12	-202.40	-38.00	-3.00	-16.87	10.55	3.04	7.89	8418.08	1341.29	1.07	701.51	338.63	97.75	253.49	8.04	0.00	1.16	2.46	0.71	1.84
Year 4	1	-8.60	-8.60	-8.60	-8.60	-	-	-	1119.32	1119.32	1119.32	1119.32	-	-	-	0.01	0.01	0.01	-	-	-
Year 6	1	-39.00	-39.00	-39.00	-39.00	-	-	-	360.50	360.50	360.50	360.50	-	-	-	1.77	1.77	1.77	-	-	-
All Years (Avg)	**228**	-994.44	-56.64	-11.52	-21.81	-	-	-	12555.02	867.33	301.39	275.3295	-	-	-	12.25	0.36	1.18	-	-	-

Year Emigrated after tagging	N	Upstream Distance (km)							Upstream Duration (days)							Upstream Rate (km/day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
Year 1	12	289.20	50.00	1.60	24.10	17.56	5.07	13.15	1077.77	441.44	12.52	89.81	117.76	33.99	88.15	2.88	0.02	0.79	0.85	0.25	0.64
Year 2	6	107.00	54.60	1.60	17.83	21.10	8.61	27.25	1069.02	440.15	10.87	178.17	194.95	79.59	251.77	0.85	0.00	0.44	0.38	0.15	0.49
Year 3	6	49.60	8.60	6.60	8.27	0.82	0.33	1.05	852.83	696.61	6.97	142.14	272.63	111.30	352.09	1.23	0.01	0.48	0.52	0.21	0.67
Year 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Year 6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
All Years (Avg)	**24**	148.60	37.73	3.27	18.575	-	-	-	999.87	526.07	10.12	124.9842	-	-	-	1.65	0.01	0.6246	-	-	-

Table 6.11. Movement metrics summarized by emigration year after tagging for bull trout tagged as small adults in the SFWWR that moved downstream of Harris Park Bridge(rkm 97) in 2002 – 2011.

Year Emigrated after tagging	N	Downstream Distance (km)							Downstream Duration (days)							Downstream Rate (km/day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
Year 1	23	-800.80	-258.00	-1.00	-34.82	54.39	11.34	27.28	4374.93	682.25	3.99	190.21	182.39	38.03	91.48	13.88	0.00	1.70	3.26	0.68	1.64
Year 2	4	-46.00	-25.80	-3.00	-11.50	9.89	4.95	20.66	1217.71	567.25	53.07	304.43	218.78	109.39	456.87	0.60	0.01	0.20	0.28	0.14	0.58
Year 3	2	-12.60	-8.60	-4.00	-6.30	3.25	2.30	58.54	810.29	797.58	12.71	405.15	554.99	392.44	9988.14	0.68	0.01	0.34	0.47	0.34	8.55
Year 4	1	-8.60	-8.60	-8.60	-8.60	-	-	-	182.44	182.44	182.44	182.44	-	-	-	0.05	0.05	0.05	-	-	-
All Years (Avg)	**30**	-217.00	-75.25	-4.15	-28.93	-	-	-	1646.34	557.38	63.05	219.5123	-	-	-	3.80	0.02	1.35	-	-	-

Year Emigrated after tagging	N	Upstream Distance (km)							Upstream Duration (days)							Upstream Rate (km/day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
Year 1	14	564.60	213.40	6.00	40.33	55.64	14.87	37.66	3027.27	764.91	5.01	216.23	280.36	74.93	189.77	1.72	0.03	0.75	0.62	0.16	0.42
Year 2	3	35.60	28.40	2.60	11.87	14.35	8.29	51.42	877.49	424.58	47.50	292.50	212.39	122.62	760.92	0.29	0.01	0.12	0.15	0.09	0.54
Year 3	1	2.60	2.60	2.60	2.60	-	-	-	30.50	30.50	30.50	30.50	-	-	-	0.09	0.09	0.09	-	-	-
Year 4	1	5.60	5.60	5.60	5.60	-	-	-	1124.65	1124.65	1124.65	1124.65	-	-	-	-	-	-	-	-	-
All Years (Avg)	**19**	152.10	62.50	4.20	32.021	-	-	-	1264.98	586.16	301.92	266.3111	-	-	-	0.70	0.04	0.58	-	-	-

Table 6.12. Movement metrics summarized by emigration year after tagging for bull trout tagged as large adults in the SFWWR that moved downstream of Harris Park Bridge (rkm 97) in 2002 – 2011.

Year Emigrated after tagging	N	Downstream Distance (km)							Downstream Duration (days)							Downstream Rate (km/day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
Year 1	62	-1379.40	-99.40	-2.00	-22.25	17.51	2.22	5.11	8084.23	598.90	0.73	130.39	132.52	16.83	38.68	17.94	0.01	2.42	3.43	0.44	1.00
Year 2	4	-57.40	-28.20	-8.60	-14.35	9.37	4.69	19.57	966.93	403.19	33.71	241.73	172.13	86.07	359.46	2.59	0.03	0.73	1.24	0.62	2.59
All Years (Avg)	**66**	-718.40	-63.80	-5.30	-21.77	-	-	-	4525.58	501.05	17.22	137.1388	-	-	-	10.26	0.02	2.31	-	-	-

Year Emigrated after tagging	N	Upstream Distance (km)							Upstream Duration (days)							Upstream Rate (km/day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
Year 1	40	682.60	80.40	1.60	17.07	14.92	2.36	5.50	5097.89	724.27	4.14	127.45	177.94	28.13	65.59	1.65	0.03	0.43	0.36	0.06	0.13
Year 2	4	39.00	17.20	5.60	9.75	5.12	2.56	10.69	142.92	64.32	10.37	35.73	25.99	13.00	54.28	0.83	0.09	0.43	0.31	0.15	0.64
All Years (Avg)	**44**	360.80	48.80	3.60	16.40	-	-	-	2620.41	394.30	7.26	119.1094	-	-	-	1.24	0.06	0.43	-	-	-

Table 6.13. Total number of bull trout PIT tagged by USFWS in the mainstem WWR, 2004 – 2011.

Size class at tagging	2004	2005	2006	2007	2008	2009	2010	2011	Total
Juveniles	4	1	1	9	11	9	0	0	35
Sub-adults	4	5	11	46	184	125	196	86	657
Small Adults	1	0	1	32	47	30	48	40	199
Large Adults	0	1	0	8	3	2	9	12	35
	9	7	13	95	245	166	253	138	**926**

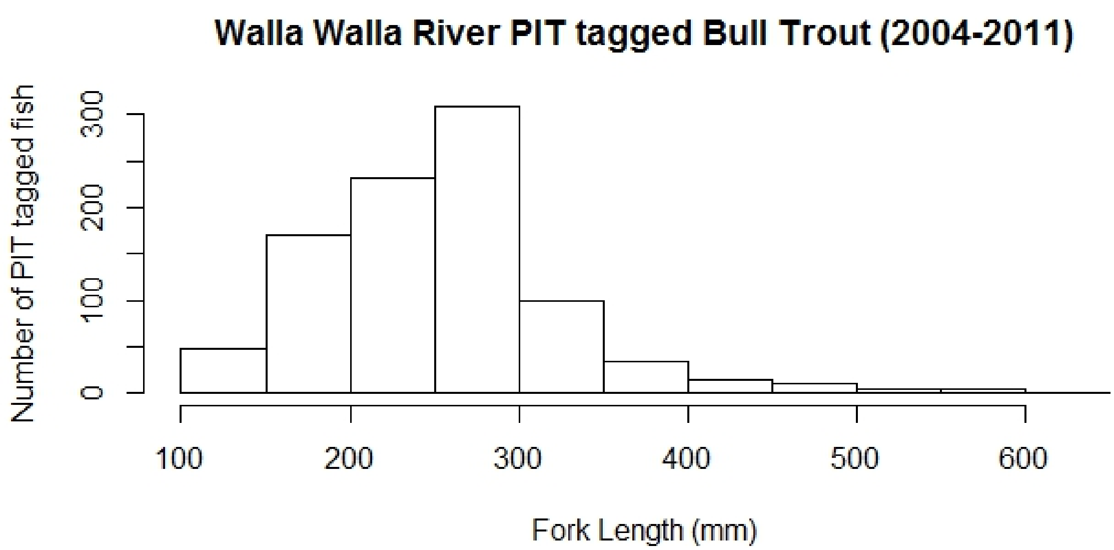

Figure 6.12. Length frequency distribution of bull trout PIT tagged in the mainstem WWR, 2004 – 2011.

Table 6.14. Number of bull trout PIT tagged in the WWR by size class. Number of migratory fish, % that migrated downstream, and % detected migrating upstream.

Size Class at Tagging (mm)	Migratory Tagged	Migratory Moved Downstream	Downstream Movement (%)	Upstream Movement (%)
Juveniles (< 144)	35	10	29%	10%
Sub-adults (144 - 290)	657	266	40%	24%
Small Adults (291 - 406)	199	95	48%	45%
Large Adults (> 406)	35	21	60%	62%

Table 6.15. Movement metrics summarized by emigration year after tagging for all bull trout tagged in the WWR and detected more than one time during 2004 – 2011.

Year Tagged	N	Downstream Distance (km)							Downstream Duration (days)							Downstream Rate (km / day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
2004	1	-60.20	-60.20	-60.20	-60.20	-	-	-	302.66	302.66	302.66	302.66	-	-	-	0.76	0.76	0.76	-	-	-
2005	3	-29.20	-17.20	-6.00	-9.73	6.47	3.73	23.17	211.76	96.95	20.49	70.59	43.40	25.06	155.50	1.62	0.06	0.66	0.84	0.49	3.01
2006	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2007	37	-789.00	-88.20	-2.00	-21.32	22.53	3.70	8.66	2648.74	717.09	2.22	71.59	134.38	22.09	51.67	13.82	0.02	1.78	2.50	0.41	0.96
2008	110	-2451.20	-135.80	-2.00	-22.28	27.74	2.64	6.01	8815.83	493.88	0.53	80.14	97.48	9.29	21.12	21.57	0.01	1.66	2.96	0.28	0.64
2009	75	-1604.00	-95.60	-2.00	-21.39	24.25	2.80	6.41	6692.04	408.79	0.46	89.23	96.79	11.18	25.57	18.70	0.01	1.74	3.09	0.36	0.82
2010	117	-2783.80	-130.00	-2.00	-23.79	24.79	2.29	5.21	7972.75	408.88	0.29	68.14	78.49	7.26	16.48	13.64	0.01	1.46	2.26	0.21	0.47
2011	49	-1360.00	-67.00	-2.00	-27.76	25.54	3.65	8.44	2279.60	187.25	0.77	46.52	52.71	7.53	17.42	19.78	0.04	2.02	3.15	0.45	1.04
Avg	**392**	-1296.77	-84.86	-10.89	-23.16	-	-	-	4131.91	373.64	46.77	73.7841	-	-	-	12.84	0.13	1.6602	-	-	-

Year Tagged	N	Upstream Distance (km)							Upstream Duration (days)							Upstream Rate (km / day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
2004	2	94.20	77.20	17.00	47.10	42.57	30.10	766.10	1763.39	1389.73	373.66	881.70	718.47	508.04	12930.35	0.20	0.05	0.12	0.11	0.08	2.01
2005	1	38.20	38.20	38.20	38.20	-	-	-	213.37	213.37	213.37	213.37	-	-	-	0.22	0.22	0.22	-	-	-
2006	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2007	14	651.20	116.60	13.00	46.51	28.16	7.52	19.06	3052.33	860.93	6.70	218.02	226.85	60.63	153.55	1.94	0.07	0.69	0.59	0.16	0.40
2008	27	1293.60	125.20	2.00	47.91	37.97	7.31	17.38	5620.49	637.71	10.81	208.17	190.07	36.58	87.01	6.99	0.02	0.85	1.28	0.25	0.59
2009	31	1190.20	80.60	6.10	38.39	21.71	3.90	9.20	4790.18	645.03	3.99	154.52	171.05	30.72	72.49	1.80	0.02	0.69	0.43	0.08	0.18
2010	43	1319.00	87.00	2.00	30.67	17.84	2.72	6.32	6387.73	474.51	0.75	148.55	125.79	19.18	44.59	4.30	0.05	0.73	0.83	0.13	0.29
2011	2	101.00	65.00	36.00	50.50	20.51	14.50	369.05	272.16	137.64	134.52	136.08	2.21	1.56	39.70	0.48	0.27	0.37	0.15	0.11	2.68
Avg	**120**	669.63	84.26	16.33	39.0617	-	-	-	3157.09	622.70	106.26	184.16	-	-	-	2.28	0.10	0.7228	-	-	-

Table 6.16. Movement metrics summarized by emigration year after tagging for bull trout tagged as juveniles in the WWR and detected more than one time during 2004 – 2011.

Year Tagged	N	Downstream Distance (km)							Downstream Duration (days)							Downstream Rate (km / day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
2005	1	-6	-6.00	-6.00	-6.00	-	-	-	20.49	20.49	20.49	20.49	-	-	-	0.29	0.29	0.29	-	-	-
2007	3	-27	-19.00	-2.00	-9.00	8.89	5.13	31.84	71.28	59.49	5.36	23.76	30.95	17.87	110.88	0.93	0.37	0.62	0.29	0.16	1.02
2008	5	-22	-6.00	-2.00	-4.40	2.19	0.98	3.42	80.98	70.16	1.35	16.20	30.20	13.51	47.21	4.44	0.09	1.63	1.72	0.77	2.68
2009	1	-19	-19.00	-19.00	-19.00	-	-	-	2.38	2.38	2.38	2.38	-	-	-	7.98	7.98	7.98	-	-	-
Avg	**10**	-18.50	-12.50	-7.25	-7.40	-	-	-	43.78	38.13	7.40	17.51	-	-	-	3.41	2.18	1.83	-	-	-

Year Tagged	N	Upstream Distance (km)							Upstream Duration (days)							Upstream Rate (km / day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
2007	1	13.00	13.00	13.00	13.00	-	-	-	-	11.41	11.41	11.41	-	-	-	1.14	1.14	1.14	-	-	-
Avg	**1**	13.00	13.00	13.00	13.00	-	-	-	-	11.41	11.41	11.41	-	-	-	1.14	1.14	1.14	-	-	-

Table 6.17. Movement metrics summarized by emigration year after tagging for bull trout tagged as sub-adults in the WWR and detected more than one time during 2004 – 2011.

Year Tagged	N	Downstream Distance (km)							Downstream Duration (days)							Downstream Rate (km / day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
2004	1	-60.20	-60.20	-60.20	-60.20	-	-	-	302.66	302.66	302.66	302.66	-	-	-	0.76	0.76	0.76	-	-	-
2005	1	-6.00	-6.00	-6.00	-6.00	-	-	-	94.32	94.32	94.32	94.32	-	-	-	0.06	0.06	0.06	-	-	-
2007	18	-307.00	-64.00	-2.00	-17.06	19.82	4.67	11.48	737.06	132.74	2.22	40.95	44.04	10.38	25.51	4.04	0.02	1.24	1.29	0.30	0.75
2008	77	-1616.00	-135.80	-2.00	-20.99	26.34	3.00	6.87	6633.00	447.86	0.53	86.14	88.98	10.14	23.19	21.57	0.01	1.53	3.23	0.37	0.84
2009	56	-1102.40	-95.60	-2.00	-19.69	21.58	2.88	6.65	4724.86	408.79	2.42	84.37	86.52	11.56	26.64	8.72	0.01	1.02	1.67	0.22	0.52
2010	84	-2048.40	-130.00	-2.00	-24.39	26.36	2.88	6.57	6136.91	408.88	0.49	73.06	81.15	8.85	20.21	13.64	0.01	1.38	2.30	0.25	0.57
2011	29	-886.00	-67.00	-2.00	-30.55	26.91	5.00	11.84	1698.76	187.25	3.75	58.58	61.96	11.51	27.25	6.75	0.04	1.76	2.01	0.37	0.88
Avg	**266**	-860.86	-79.80	-10.89	-23.55	24.20	3.69	8.68	2903.94	283.21	58.06	81.45	72.53	10.49	24.56	7.94	0.13	2.10	2.10	0.30	0.71

Year Tagged	N	Upstream Distance (km)							Upstream Duration (days)							Upstream Rate (km / day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
2004	1	77.20	77.20	77.20	77.20	-	-	-	1389.73	1389.73	1389.73	1389.73	-	-	-	0.20	0.20	0.20	-	-	-
2007	1	36.00	36.00	36.00	36.00	-	-	-	45.04	45.04	45.04	45.04	-	-	-	1.84	1.84	1.84	-	-	-
2008	14	622.80	120.80	2.00	44.49	37.41	10.00	25.32	2928.96	637.71	11.91	209.21	210.94	56.38	142.78	6.99	0.02	0.97	1.77	0.47	1.20
2009	23	810.00	80.60	6.10	35.22	22.02	4.59	11.05	4055.95	645.03	3.99	176.35	190.74	39.77	95.67	1.53	0.02	0.62	0.39	0.08	0.19
2010	24	659.00	66.00	2.00	27.46	15.02	3.06	7.35	2933.45	474.51	5.53	122.23	131.55	26.85	64.39	2.35	0.05	0.71	0.60	0.12	0.29
Avg	**63**	441.00	76.12	24.66	35.00	24.82	5.89	14.57	2270.63	638.40	291.24	180.2084	177.74	41.00	100.95	2.64	0.52	0.74	1.08	0.28	0.69

Table 6.18. Movement metrics summarized by emigration year after tagging for bull trout tagged as small adults in the WWR and detected more than one time during 2004 – 2011.

Year Tagged	N	Downstream Distance (km)							Downstream Duration (days)							Downstream Rate (km / day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
2007	11	-280.80	-80.60	-2.00	-25.53	23.71	7.15	18.83	733.00	307.00	2.88	66.64	89.73	27.05	71.25	5.75	0.06	1.73	1.88	0.57	1.49
2008	25	-631.40	-124.00	-2.00	-25.26	28.42	5.68	13.59	1583.44	493.88	1.67	63.34	107.23	21.45	51.28	7.78	0.02	1.99	2.38	0.48	1.14
2009	17	-480.60	-95.60	-2.00	-28.27	32.15	7.80	19.28	1964.34	396.49	3.60	115.55	125.76	30.50	75.43	18.70	0.03	3.58	5.11	1.24	3.07
2010	26	-590.20	-66.00	-2.00	-22.70	20.46	4.01	9.57	1285.81	248.40	1.45	49.45	64.21	12.59	30.03	8.97	0.01	1.61	2.14	0.42	1.00
2011	16	-404.00	-64.00	-2.00	-25.25	24.06	6.01	14.98	514.31	114.49	1.62	32.14	30.25	7.56	18.83	6.17	0.05	1.53	1.61	0.40	1.00
Avg	**95**	-477.40	-86.04	-2.00	-25.126	25.76	6.13	15.25	1216.18	312.05	2.24	64.0095	83.43	19.83	49.36	9.47	0.03	2.06	2.62	0.62	1.54

Year Tagged	N	Upstream Distance (km)							Upstream Duration (days)							Upstream Rate (km / day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
2004	1	17.00	17.00	17.00	17.00	-	-	-	373.66	373.66	373.66	373.66	-	-	-	0.0455	0.0455	0.0455	-	-	-
2007	7	321.80	116.60	13.00	45.97	33.61	12.70	37.72	1650.33	860.93	6.70	235.76	296.67	112.13	332.88	1.94	0.07	0.70	0.63	0.24	0.71
2008	10	410.40	122.00	13.00	41.04	31.65	10.01	26.87	1728.14	465.15	10.81	172.81	166.77	52.74	141.60	1.20	0.07	0.76	0.36	0.11	0.31
2009	8	380.20	80.60	31.60	47.53	19.17	6.78	19.26	734.23	207.25	17.51	91.78	70.60	24.96	70.92	1.80	0.28	0.91	0.48	0.17	0.48
2010	15	514.80	87.00	2.00	34.32	22.47	5.80	14.56	2698.70	337.82	0.75	179.91	120.35	31.08	77.99	4.30	0.05	0.87	1.18	0.30	0.76
2011	2	101.00	65.00	36.00	50.50	20.51	14.50	369.05	272.16	137.64	134.52	136.08	2.21	1.56	39.70	0.48	0.27	0.37	0.15	0.11	2.68
Avg	**43**	290.87	81.37	18.77	40.586	25.48	9.96	93.49	1242.87	397.08	90.66	173.42	131.32	44.49	132.62	1.63	0.13	0.78	0.56	0.19	0.99

Table 6.19. Movement metrics summarized by emigration year after tagging for bull trout tagged as large adults in the WWR and detected more than one time during 2004 – 2011.

Year Tagged	N	Downstream Distance (km)							Downstream Duration (days)							Downstream Rate (km / day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
2005	1	-17.2	-17.2	-17.2	-17.2	-	-	-	96.95	96.95	96.95	96.95	-	-	-	1.62	1.62	1.62	-	-	-
2007	5	-174.20	-88.20	-8.60	-34.84	31.34	14.02	48.99	1107.40	717.09	5.35	221.48	315.55	141.12	493.27	13.82	1.11	4.51	5.36	2.40	8.38
2008	3	-181.80	-112.20	-8.60	-60.60	51.80	29.91	185.59	518.41	423.56	1.90	172.80	221.88	128.10	794.93	4.53	0.36	2.15	2.14	1.24	7.68
2009	1	-2.00	-2.00	-2.00	-2.00	-	-	-	0.46	0.46	0.46	0.46	-	-	-	4.35	4.35	4.35	-	-	-
2010	7	-145.20	-67.60	-2.00	-20.74	22.57	8.53	25.33	550.03	228.63	0.29	78.58	94.11	35.57	105.60	6.90	0.11	1.85	2.51	0.95	2.82
2011	4	-70.00	-51.00	-2.00	-17.50	23.16	11.58	48.36	66.53	43.61	0.77	16.63	18.64	9.32	38.92	19.78	0.19	5.91	9.30	4.65	19.43
Avg	**21**	-98.40	-56.37	-6.73	-29.75	-	-	-	389.96	251.72	17.62	120.65	-	-	-	8.50	1.29	3.56	-	-	-

Year Tagged	N	Downstream Distance (km)							Downstream Duration (days)							Downstream Rate (km / day)					
		Sum	Max	Min	Avg	SD	SE	95% CI	Sum	Max	Min	Avg	SD	SE	95% CI	Max	Min	Avg	SD	SE	95% CI
2005	1	-17.2	-17.2	-17.2	-17.2	-	-	-	96.95	96.95	96.95	96.95	-	-	-	1.62	1.62	1.62	-	-	-
2007	5	-174.20	-88.20	-8.60	-34.84	31.34	14.02	48.99	1107.40	717.09	5.35	221.48	315.55	141.12	493.27	13.82	1.11	4.51	5.36	2.40	8.38
2008	3	-181.80	-112.20	-8.60	-60.60	51.80	29.91	185.59	518.41	423.56	1.90	172.80	221.88	128.10	794.93	4.53	0.36	2.15	2.14	1.24	7.68
2009	1	-2.00	-2.00	-2.00	-2.00	-	-	-	0.46	0.46	0.46	0.46	-	-	-	4.35	4.35	4.35	-	-	-
2010	7	-145.20	-67.60	-2.00	-20.74	22.57	8.53	25.33	550.03	228.63	0.29	78.58	94.11	35.57	105.60	6.90	0.11	1.85	2.51	0.95	2.82
2011	4	-70.00	-51.00	-2.00	-17.50	23.16	11.58	48.36	66.53	43.61	0.77	16.63	18.64	9.32	38.92	19.78	0.19	5.91	9.30	4.65	19.43
Avg	**21**	-98.40	-56.37	-6.73	-29.75	-	-	-	389.96	251.72	17.62	120.65	-	-	-	8.50	1.29	3.56	-	-	-

Chapter 7 : Quantifying Survival and Population Trends in the Upper South Fork Walla Walla River

authored by

Mary Conner
Phaedra Budy
Tracy Bowerman
Robert Al-Chokhachy

Utah State University

Introduction

Population trend is an important vital rate that describes the cumulative effects of survival at different life stages on the population as a whole. Understanding whether this trend is stable, increasing, or decreasing across relevant temporal scales is a key component for recovery for most species listed under the Endangered Species Act (ESA; McElhany et al. 2000). Integrating estimates of population trends with measures of abundance and inherent variability in abundance over time can allow for robust assessments of population persistence.

Developing effective management strategies, however, also requires information regarding how extrinsic and intrinsic factors can influence population abundance and trends within a hypothesis-driven framework (Holmes and York 2003; Saether et al. 2005). Concomitantly, targeting specific management actions can require information on how such factors (e.g., climate) can influence vital rates across life stages, which in turn, affect population abundance and trends.

For bull trout, maintaining stable or increasing population trends is a key component of recovery planning. Monitoring bull trout populations to evaluate population trends, however, has proven difficult (Ham and Pearsons 2000; Al-Chokhachy et al. 2009), as bull trout often naturally occur at low densities (Rieman and McIntyre 1993; Al-Chokhachy and Budy 2007), are behaviorally cryptic (Thurow et al. 2006; Banish et al. 2008), and exhibit clumped distributions within stream networks (Al-Chokhachy et al. 2009). While there have been a number of efforts to quantify trends in bull trout abundance (e.g., Myers et al. 2014), there have been surprisingly few analyses that evaluate factors influencing bull trout trends explicitly and, more specifically, the vital rates that drive those trends (Bowerman and Budy 2012). Here, we address this need by employing 10 years of mark-recapture data (Appendices I,II) to assess how biotic and abiotic factors influence bull trout vital rates (survival, emigration) and population trends (population growth rates, recruitment). We compliment these mark- recapture data with long-term redd count data for a multifaceted assessment to specifically evaluate: 1) life-stage (juvenile, sub-adult, adult, and large adult) and life-history expression (migratory, resident, and unknown) specific trends in bull trout abundance; 2) bull trout survival and emigration rates across life stages; and 3) hypotheses of how biotic and abiotic factors influence such patterns.

Methods

Capture-recapture methodology

We estimated long-term growth rates and survival rates for the population of bull trout in the South Fork Walla Walla River (SFWWR) based on ten years of capture-mark-recapture data (CMR; Figure 7.1). We marked bull trout with unique passive integrated transponder (PIT) tags, and subsequently recaptured fish via systematic sampling (see Appendix II for more details on capture and tagging methods). Each year the active capture period took place during the summer (mid-June through mid-August), as this time period included the majority of adult seasonal migrations upstream (Homel and Budy 2008). In this dataset, we also included passive resights at stationary passive in-stream antennas (PIAs), which were located at several locations throughout the SFWWR and mainstem Walla Walla River (WWR; detailed description in Appendix I; Al-Chokhachy and Budy 2008), that occurred during the discrete summer sampling season. All data collected during the discrete summer sampling period were considered capture (initial marking) or recapture (both active and passive PIA detections) data, and used in the population trend analysis (described below). In addition, we collected additional resight data at the PIAs during the remainder of the year outside of the discrete summer sampling period. Please see Appendix I-II for more detail.

Pradel population growth rate analyses

We used a temporal symmetry model implemented in Program MARK (White and Burnham 1999) to estimate the annual rate of population change (λ_t) for adult bull trout. For the Pradel model, we restricted our population of interest to bull trout > 300 mm total length (TL) as this corresponded to the true adult population within the SFWWR (Al-Chokhachy and Budy 2008), as well as to bull trout recovery goals, and because this size class holds the greatest proportion of individuals exhibiting larger migratory patterns within the SFWWR and WWR. The temporal symmetry model (also called Pradel model) simultaneously models the capture history of each individual using both forward-time and reverse-time modeling to estimate capture probability (*p*), recruitment to the adult stage (*f*), apparent survival (*f*), and consequently, population growth rate (i.e., lambda, *λ*; Pradel 1996; Nichols and Hines 2002).

The goal of this analysis was to estimate annual population growth rates (Λt) and a central estimate of population growth rate (mean or median) for the study period (Λ). We considered population trends for the entire population of adults (>300 mm) and trends for those adults that were considered migratory (i.e., recaptured any location outside of the SFWWR study area), which we ran as completely separate analyses. As such, we allowed model parameters to vary by time. We followed model development protocols established for estimating population growth rate for endangered northern spotted owls (Franklin et al. 2004; Anthony et al. 2006) and refined for California spotted owls (Blakesley et al. 2010). In particular, we followed goodness-of-fit procedures (described below) and constructed models that allowed *f* and 1 to vary from year to year, but we did not constrain *f* more than 1 because that required that recruitment would completely drive 1 each year. We diverged from the previous analyses by using a Bayesian approach, rather than random effects models, to estimate mean 1 and overall population change during the study period (described below). For each of the parameters we tested for individual year effects (*t*); however, we did not consider any environmental or biotic covariates for this trend analysis, as we explore the influence of these factors in the Barker survival model framework (see below).

To evaluate model goodness-of-fit, we estimated overdispersion from extrabinomial variation (median $\hat{c}$) using a simulation procedure in Program MARK with a Cormack-Jolly-Seber model framework for the model with the greatest complexity. Deviations of $\hat{c}$ above 1.0 indicate overdispersion, and a $\hat{c}$ >2–3 often indicates a lack of fit for the model (Lebreton et al. 1992; Cooch and White 2013). If median $\hat{c}$ was >1, we adjusted AIC by $\hat{c}$ ($QAIC_c$) for model selection and used $\hat{c}$ to inflate variances of parameter estimates.

To compare among competing models, we used Akaike's Information Criterion corrected for small sample size (AICc) and compared models using ΔAICc (Lebreton et al. 1992; Burnham and Anderson 2002) and normalized AICc weights (w_i; Burnham and Anderson 2002). Models with the lowest AICc values were most supported by the data and generally, models <2 ΔAICc units of the best model were considered competing models.

To estimate probabilities of population declines, we used a Bayesian approach via MCMC sampling implemented in Program MARK to estimate posterior distributions of annual trend estimates ($1t$) using the top model structure for each trend analysis. The posterior distribution of 1_t was also used to estimate median population trend estimates (1_{MCMC}) and the overall realized population change (D_t) for the study period. Based on sample size estimation within Program

MARK for the data sets, for all MCMC simulations, we used 40 tuning samples, 100 burn in samples, and 20,000 realizations, of which we kept every other realization to meet first order MCMC independence (thus we kept 10,000 realizations). We used vague priors for all parameters included in the model. For estimating median 1_{MCMC}, we used a hyperprior for mean (m) and variance (s) of 1_t. For m, we used a normally distributed prior with mean = 0 and standard deviation = 100 and for s we used a gamma prior to model its transformation, $1/s^2$, with a = 1.00001 and b = 0.000001. Although estimates of f and p were not used in the hyperprior to estimate m and s of 1_t, they were included in the model and required a prior distribution. Because they were logit transformed parameters, we used a normal prior distribution with mean of 0 and a standard deviation of 1.75, which is a vague prior when back transformed to the real scale (2.5th and 97.5th percentiles of approximately 0.02 and 0.98, with a uniform distribution between those percentiles). We determined if the Markov chains converged using the Gelman-Rubin statistic, R-hat (Gelman et al. 2004). For each parameter, we used 10 chains of 1000 each and used a threshold of R-hat < 1.1 to evaluate whether the posterior distribution was adequately sampled.

Using Bayesian MCMC methods, a posterior distribution of D_t can be used to calculate the probability of any decline of interest (Conner et al. 2013). We used D_t to evaluate the probability of decline of bull trout population size for different thresholds including ICUN (2001) standards used as part of their criteria to determine threatened or vulnerable populations. In particular, we evaluated the ICUN (2001) criterion that there was “an estimated population size reduction of ≥ 50% (part of criteria for endangered species) and ≥ 30% (part of criteria for vulnerable species) over the last 10 years or three generations, whichever is the longer”.

Trends in redd counts

To complement the Pradel analysis, we also evaluated population trend via linear regression of log-transformed annual changes in population growth rate (λ) as a function of time step (Morris and Doak 2002) based on redd count data. We used this approach because redd counts are a widely available metric that can be used to represent the abundance and trend of spawning adults, and this provided a useful comparison to Pradel trend estimates based on individual mark-recapture. Further, data from redd counts provided a much longer time series to assess long-term population status. Thus, we estimated population growth rate based on two different time periods, one that included all available redd count data from 1994 to 2011, and a second that mirrored the time period over which we collected mark-recapture data (2002 to 2011). Redd counts were conducted by the Oregon Department of Fish and Wildlife (ODFW) within index reaches in the SFWWR. The index reaches encompassed approximately 40% of the available spawning habitat in the SFWWR study area, and all index reaches were surveyed between 3 and 5 times during each spawning season.

Barker survival rate analyses

We used Program Mark (White and Burnham 1999) to estimate annual survival probabilities from 2002-2011 based on encounter histories generated for each individual PIT tagged bull trout (Cooch and White 2013). As described above, encounter histories included active mark and recapture events during discrete summer sampling periods as well PIA detections throughout the rest of the year.

Because data from arrays are continuously collected, we used the Barker model (Barker 1997) rather than a Cormack-Jolly-Seber (CJS) model to estimate survival. The Barker model is a re-parameterization of the CJS model that can accommodate continuously collected resight and recovery data between sampling occasions (Barker et al. 2004). There are 7 parameters in the Barker model (from Cooch and White 2013): S_i = the probability an animal alive at i is alive at i +1, p_i = the probability an animal at risk of capture at i is captured at i, r_i = the probability an animal that dies in interval i to i +1 is found dead, R_i = the probability an animal that survives from i to i + 1 is resighted (alive) sometime between i and i +1, R'_i = the probability an animal that dies in i, i +1 without being found dead is resighted alive in i, i + 1 before it died, F_i = the probability an animal at risk of capture (i.e., on study area) at i is at risk of capture at i +1, and F'_i = the probability an animal not at risk of capture at i is at risk of capture at i + 1 (this differs from the definition in Barker 1997).

Our main goals were to estimate annual survival by size class and to assess impacts of several annual covariates which we hypothesized could affect capture probability (parameters p, R, and R'), and survival probabilities (S). We set r as constant for all models because recovery rates of dead fish were extremely low (e.g., <0.001; Bowerman and Budy 2012). We delineated fish into 4 groups based on size, which we refer to as: juveniles (<150 mm), small adults (151 to 300 mm; likely including both subadult migratory fish and resident adults), adults (301 to 420 mm), and large adults (> 420 mm). We modeled survival of individual size classes such that fish transitioned to a larger class each year (until fish reached the largest class; *a* in model notation).

Based on preliminary analysis, we split the data into 2 data sets; one for fish marked as juveniles and small adults (i.e., small fish) and one for fish marked as adults and large adults (i.e., large fish). Many more bull trout were tagged as small fish (n = 4,321, 91%) than as large fish (n = 430, 9%). When the two data sets were combined in a single analysis, small fish dominated model selection and temporal patterns of estimates. There were not enough data for the large fish to support interactive effects (e.g., S(a x t)) and additive models (e.g., S(a + t)) were top models. However, the patterns of parameter estimates for the numerically dominant small fish drove the patterns for the larger fish and masked different survival patterns of the larger fish. Thus, we separated encounter histories for small and large fish into different input files. We followed the same model selection procedures for both data sets, although the set of models varied slightly because the small fish could age into the larger size classes so that there were 4 possible age classes, while there were only 2 possible age classes for the large fish. To minimize the number of models assessed simultaneously and avoid false significance issues (Burnham and Anderson 2002), our model development procedure was a sequential process beginning with an evaluation of temporal and group patterns (Nichols et al. 1997). We began by constructing a global model with interactive size class and year effects (a x t in model notation) for all parameters. Then, leaving survival with a global structure, we constructed models with more parsimonious structures for the remainder of the parameters (e.g., p(a + t), p(a) p(t) etc.). We also tried an additive model for survival to evaluate if the age classes fluctuated similarly though time. For analysis of small fish (which aged to 4 size classes), we constructed additional models with 2 age groups versus 4 to determine if there were common patterns between smaller and larger size classes. We then used the top model (or models if within 2 ΔAICc of top model) and added annual environmental covariates where appropriate (e.g., high and low flow years as an index for S, change in sampling intensity for p).

We did not evaluate model fit (i.e., $\hat{c}$; see above) using the Barker model given the lack of verification of any procedure for evaluating the fit of Barker Models (Cooch and White 2013). There are several potential ad hoc strategies that can be used to evaluate fit, such as using only the mark-recapture data and evaluating fit with the CJS model, which we performed using the Pradel model ($\hat{c}$ = 1.083; see above). Because the recapture data were the same except for the inclusion of the smallest size classes in the Barker analysis, we assumed there was no lack of fit for the Barker model. We evaluated and compared all models using AICc as described for to the Pradel model (see above).

Results and Discussion

Population growth rates

<u>All adult fish</u>

The top Pradel model for analysis including all adult fish (≥ 300 mm) included time-varying estimates of apparent survival, and an interaction between group and time for population growth rate (Table 7.1). In the top-ranked model p varied as a function of PIA efficiency during the summer sampling period. The top model was nearly 7 $\Delta QAIC_c$ units above the next highest model indicating it performed substantially better than any other models evaluated.

Based on the top model, both population growth rates (λt) and realized population change (Δt) for all adult fish combined (migratory, non-migratory, and unknown) were greater than one near the start of the time series, declined significantly until 2006-2007, but then increased for the last three years, albeit with wide confidence intervals that overlap 1 (i.e., stable population trend) in all years except 2006-2007 (Figure 7.2). The estimated median λ_{MCMC} for the time series was 1.001 (95% CI = 0.71-1.42). Based on the posterior distributions of overall realized population change (Figure 7.3; top), the probability that these fish have declined in abundance by the IUCN threshold is small (IUCN 2001). There is a 1% chance they decreased ≥50% (endangered threshold), and a 5% chance they decreased ≥ 30% (threatened threshold).

Noting that true survival as estimated in the Baker model and described below is much more accurate and informative, across the time series Pradel apparent survival (Φ) for this group ranged from ~20-40% and was relatively stable (Figure 7.4). In contrast, recruitment was greater than 50% for the first three years of the time series, but dropped significantly to 20% in 2006-2007; however, recruitment dramatically increased for the remainder of the time series (Figure 7.4). Thus changes in recruitment (*f*), and not survival, explain most of the variation in population growth rates across time.

<u>Migratory bull trout</u>

The top Pradel model for the analysis including only adult fish (≥ 300 mm) that migrated from the study area included an additive effect of time (year) for apparent survival (Φ), hypothesis 8 (H8; Table 7.2) for recapture probability, and an interaction between group and time for population growth rate (λ). Again the top model was > 6.5 $\Delta QAIC_c$ units above the next highest model indicating it performed clearly better than any other models evaluated for migratory fish.

Based on the top model, both population growth rates (λt) and realized population change (Δt) were more stable for the migratory fish than observed for the entire adult population (see above) and hovered near one, with wide confidence intervals that overlap 1 in all years (Figure 7.5). The estimated median λ_{MCMC} for the time series was 0.99 (95% CI = 0.81-1.12). Based on the posterior distributions of overall realized population change (Figure 7.3; bottom), the probability that these fish have declined in abundance by the IUCN threshold is also small. There is a 5% chance they decreased ≥50% (endangered threshold), but a 22% chance they decreased ≥ 30% (threatened threshold) (Figure 7.3).

Trends in redd counts

Trends in bull trout redd counts varied considerably during the last 2 decades in the SFWWR (Figure 7.6), which is consistent with patterns from proximate populations of bull trout in the Blue Mountains (Bowerman 2013). In general, trends of bull trout redd counts were largely dependent on the temporal period considered in the analysis. The estimated trend in bull trout redds for the entire period of record (1994 to 2011) was 1.09 (95% CI = 0.90-1.32). However, the redd count trend during the period of our mark-recapture study (2002 to 2011) was considerably lower (λ = 0.97, 95% CI = 0.84-1.13). Previous results suggested redd counts were most similar to population trends observed for large, adult bull trout (Al-Chokhachy et al. 2005); this pattern is consistent with the Pradel findings described above. More specifically, we found years with the lowest observed redd data (2005 to 2007) mirrored the pattern found for Pradel estimates of population trend for all bull trout > 300 mm.

Survival

The tremendous asymmetry in the number of fish tagged and recaptured in small (< 300 mm; n = 4,321, 91% of data) versus large (> 300 mm; n = 430, 9.1% of data) groups required that these size/age groups of fish be modeled separately. If the small and large fish were not separated into different files, but rather modeled as different groups in a single analysis, the small fish dominated model selection and temporal patterns of estimates. There were not enough data for the large fish to support interactive effects (e.g., S(a x t)) and additive models (e.g., S(a + t)) were top models. However, the patterns of parameter estimates for the dominant small fish drove the patterns for the larger fish. Nonetheless, these greater size groupings are biologically reasonable given that most fish >300 mm in the SFWWR are reproductively mature (Bowerman 2013), and use similar habitat (Al-Chokhachy and Budy 2007). Unfortunately, estimates from models in which known migratory, known non-migratory fish were modeled with migratory covariates were strongly positively biased by migratory fish that migrated and survived; these fish have a much greater chance of getting detected. As such those models were removed from the analysis.

Survival (S) varied over time and among age/size classes but with no clear time trend for small fish (< 300 mm; Figure 7.7). Specifically, in the top Barker model, survival rate (S) differed among three age/size groups of small fish, and was the lowest for the smallest size class of juveniles (< 150 mm) and less than 30% in most years. Low survival rates for small size classes are typical for many fish populations, as susceptibility to predation decreases with size.

Survival rates were similar on average for size/ages of large, adult fish (> 300 mm), but with very different patterns across years relative to small fish (Figure 7.8). For example, survival rates for the largest fish (>300 mm) were lowest in 2005, 2006 and 2009 (when other groups showed high survival) and generally remained above 50% in other years. In contrast survival rates for the small adults (150-300 mm) varied little across time but were greatest in 2006 and 2010. The pattern of survival across time and age/size groups strongly suggests that different factors determine survival in the upper river, where small adults stay and migrate, versus the lower river, where most large fish attempt to migrate.

The observed low survival of large adults in 2005 and 2006 may correspond with the low observed recruitment during the following years (2006-2007) estimated in the Pradel analysis above. Because we modeled recruitment into the largest size classes of adults (>300 mm TL), high recruitment estimates between 2007 and 2010 may reflect a combination of three separate demographic parameters, 1) survival for all adult size classes, 2) growth and survival of unmarked fish in the juvenile size class, and 3) high reproductive success of spawners 4-6 years prior (e.g., 2001-2005).

Resight probability (R) for large fish (> 420 mm) was extremely high and ranged from 50% to more than 95% (Figure 7.8; bottom panel). These high resight probabilities were unsurprising as most of these fish attempt to migrate and thus have a high probability of getting detected at a PIA when migrating out of the system. In contrast, resight probability for medium-sized adults (300-420 mm) was much lower, less than about 30% for the first part of the time series and near 40% for the later part of the time series (Figure 7.8; bottom panel).

Future analyses will include full hypothesis tests of environmental influences and factors likely to affect recapture probability (antennae efficiency). While survival and resight estimates will change little, fidelity and recapture probability estimates could be different depending on which hypotheses rise to the top.

The size frequency distribution is shown in Figure 7.9 and the annual population abundance estimates (± 95% CI) for three size groupings are shown in Figure 7.10; both are for all bull trout in the SFWWR, 2002-2011.

Literature Cited

Al-Chokhachy, R., and P. Budy. 2007. Summer microhabitat use of fluvial bull trout in Eastern Oregon streams. North American Journal of Fisheries Management 27:1068-1081.

Al-Chokhachy, R., and P. Budy. 2008. Demographic characteristics, population structure, and vital rates of a fluvial population of bull trout in Oregon. Transactions of the American Fisheries Society 137:262-277.

Al-Chokhachy, R., P. Budy, and M. Conner. 2009. Detecting declines in the abundance of a bull trout (Salvelinus confluentus) population: understanding the accuracy, precision, and costs of our efforts. Canadian Journal of Fisheries and Aquatic Sciences 66: 649–658.

Al-Chokhachy, R., P. Budy, and H. Schaller. 2005. A comparison of redd counts and mark/resight methods for estimating abundance and monitoring bull trout population trends. North American Journal of Fisheries Management 25:1505-1512.

Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. D. Nichols, J. E. Hines, G. S. Olson, S. H. Ackers, L. S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, K. M. Dugger, K. E. Fehring, T. L. Fleming, R. P. Gerhardt, S. A. Gremel, R. J. Guttierez, P. J. Happe, D. R. H erter, J. M. Higley, R. B. Horn, L. L. Irwin, P. J. Loschl, J. A. Reid, and S. G. Sovern. 2006. Status and trends in demography of northern spotted owls, 1985-2003. Wildlife Monographs 163.

Banish, N. P., J. T. Peterson, and R. F. Thurow. 2008. Physical, biotic, and sampling influences on diel habitat use by stream-dwelling bull trout. North American Journal of Fisheries Management 28:176–187.

Barker, R. J. 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. Biometrics 53:666-677.

Barker, R. J., K. P. Burnham, and G. C. White. 2004. Encounter history modeling of joint mark-recapture, tag-resighting and tag-recovery data under temporary emigration. Statistica Sinica 14:1037-1055.

Blakesley, J. A., M. E. Seamans, M. M. Conner, A. B. Franklin, G. C. White, R. J. Gutiérrez, J. E. Hines, J. D. Nichols, T. E. Munton, D. W. H. Shaw, J. J. Keane, G. N. Steger, and T. L. McDonald. 2010. Population dynamics of spotted owls in the Sierra Nevada, California. Wildlife Monographs 174.

Bowerman, T. and P. Budy. 2012. Incorporating movement patterns to improve survival estimates for juvenile bull trout North American Journal of Fisheries Management 32:1123-1136.

Bowerman, T. 2013. A multi-scale investigation of factors limiting bull trout viability. Doctoral dissertation, Utah State University, Logan, Utah.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: Second edition. Springer-Verlag, New York, New York, USA.

Cooch, E. G., and G. C. White. 2013. Program MARK: "A gentle introduction", 11th Edition. in Available at http://www.phidot.org/software/mark/docs/book.

Franklin, A. B., R. J. Gutiérrez, J. D. Nichols, M. E. Seamans, G. C. White, G. S. Zimmerman, J. E. Hines, T. E. Munton, W. S. LaHaye, J. A. Blakesley, G. N. Steger, B. R. Noon, D. W. H. Shaw, J. J. Keane, T. L. McDonald, and S. Britting. 2004. Population dynamics of the California spotted owl (Strix occidentalis): a meta-analysis. Ornitholgical Monograph 54.

Gelman, A., J. A. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian data analysis. Second Edition. Chapman & Hall/CRC, Boca Raton, Florida, USA.

Ham, K.D. and T.N. Pearsons. 2000. Can reduced salmonid population abundance be detected in time to limit management impacts? Canadian Journal of Fisheries and Aquatic Sciences 57:17-24.

Holmes, E. E., and A. E. York. 2003. Using age structure to detect impacts on threatened populations: a case study with Steller sea lions. Conservation Biology 17(6):1794-1806.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67-118.

International Union for Conservation of Nature and Natural Resources (IUCN). 2001. IUCN red list categories and criteria, version 3.1. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

McElhany, P., M. H. Ruckleshaus, M.J. Ford, T.C. Wainwright, and E.P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionary significant units. US Department of Commerce. NOAA Memorandum NMFS-NWFSC-42, 156 p.

Morris, W.M. and D.F. Doak. 2002. Quantitative conservation biology. Sinauer Associates Inc. Sunderland, Massachusetts.

Myers, K. A., E. O. Garton, and D. J. Schill. 2014. Bull trout trends in abundance and probabilities of persistence in Idaho. North American Journal of Fisheries Management 34:202-214.

Nichols, J. D., J. E. Hines, and P. Blums. 1997. Tests for senescent decline in annual survival probabilities of common pochards, Aythya ferina. Ecology 78:1009–1018.

Nichols, James D., and James E. Hines. 2002. Approaches for the direct estimation of u, and demographic contributions to u, using capture-recapture data. Journal of Applied Statistics 29 539-568.

Pradel, R. 1996. Utilization of capture-mark-capture for the study of recruitment and population growth rate. Biometrics 52: 703-709.

Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Department of Agriculture General Technical Report INT-302.

Sæther, B. E., Lande, R., Engen, S., Weimerskirch, H., Lillegård, M., Altwegg, R. & Visser, M. E. 2005. Generation time and temporal scaling of bird population dynamics. Nature, 436(7047). 99-102.

Thurow, R. F., J. T. Peterson, and J. W. Guzevich. 2006. Utility and validation of day and night snorkel counts for estimating bull trout abundance in first-to third-order streams. North American Journal of Fisheries Management 26:217–232.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 Supplement:120-138.

Table 7.1. Top models for the Pradel analysis for all groups of fish. Hypothesis "H8" describes monthly antenna efficiencies.

Model	*K*	*DQAIC$_c$*	*w_i*	*QDeviance*	QAICc
Phi(2g+t) p(2g+H8) Lambda(2g*t)	31	0.000	0.965	8411.600	8474.685
Phi(2g+t) p(2g) Lambda(2g*t)	30	6.992	0.029	8420.661	8481.676
Phi(t) p(3g) Lambda(3g*t)	39	10.818	0.004	8405.790	8485.503
Phi(2g*t) p(2g) Lambda(2g*t)	38	12.974	0.001	8410.033	8487.659
Phi(3g*t) p(3g) Lambda(3g*t)	57	27.779	0.000	8384.798	8502.464
Phi(t) p(H8) Lambda(2g*t)	29	36.311	0.000	8452.046	8510.995
Phi(3g*t) p(3g*t) Lambda(3g*t)	78	43.901	0.000	8355.673	8518.585
Phi(3g*t) p(.) Lambda(3g*t)	55	48.405	0.000	8409.679	8523.090
Phi(3g*t) p(t) Lambda(3g*t)	62	51.433	0.000	8397.775	8526.118
Phi(t) p(.) Lambda(3g*t)	37	52.767	0.000	8451.910	8527.451
Phi(t) p(t) Lambda(3g*t)	44	54.449	0.000	8438.954	8529.133

Table 7.2. Top models for the Pradel analysis for only migratory fish. A fish was determined to be migratory if it was detected at the Harris Park Bridge PIA or any other downstream passive in-stream antennas.

Model	*K*	*DAIC$_c$*	*w_i*	*Deviance*	AICc
Phi(2g+t) p(2g+H8) Lambda(2g*t)	31	0.000	0.962	123.386	1502.538
Phi(2g+t) p(2g) Lambda(2g*t)	30	6.587	0.036	132.413	1509.124
Phi(t) p(3g) Lambda(3g*t)	39	12.588	0.002	115.843	1515.126
Phi(2g*t) p(2g) Lambda(2g*t)	38	17.132	0.000	122.965	1519.670
Phi(t) p(H8) Lambda(2g*t)	29	18.604	0.000	146.853	1521.141
Phi(t) p(.) Lambda(3g*t)	37	33.900	0.000	142.292	1536.438
Phi(3g*t) p(3g) Lambda(3g*t)	57	36.114	0.000	89.714	1538.651
Phi(t) p(t) Lambda(3g*t)	44	38.791	0.000	128.887	1541.329
Phi(3g*t) p(t) Lambda(3g*t)	62	46.575	0.000	85.184	1549.112
Phi(3g*t) p(.) Lambda(3g*t)	55	53.989	0.000	113.430	1556.526
Phi(3g*t) p(3g*t) Lambda(3g*t)	78	76.709	0.000	63.304	1579.246

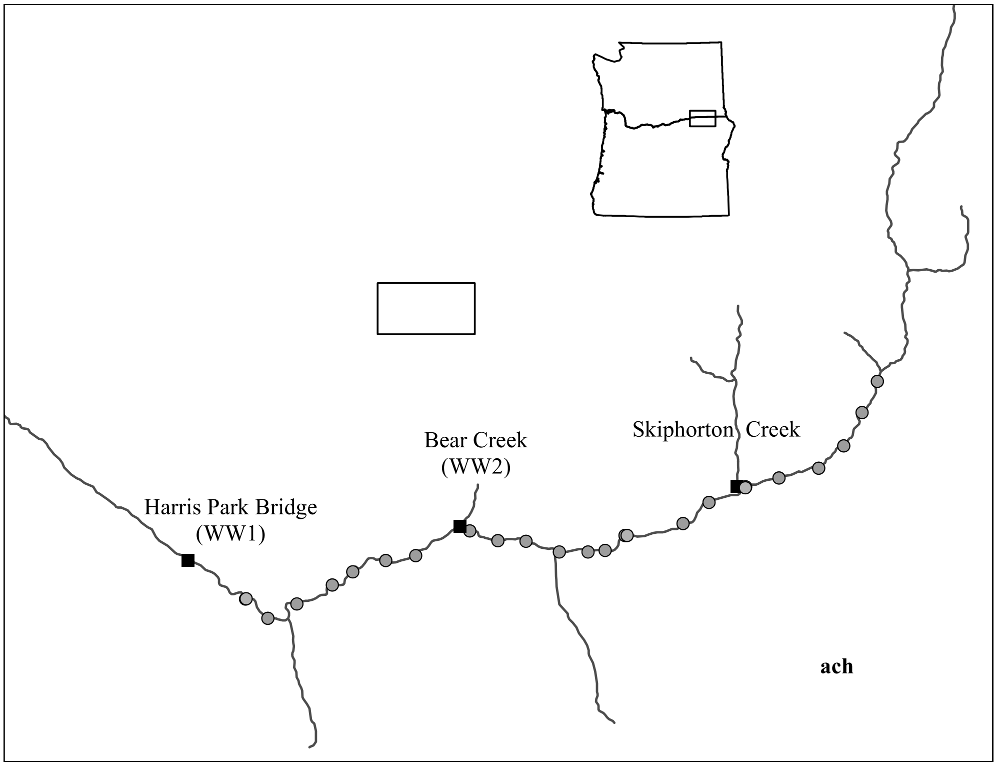

Figure 7.1. Map of the study area in the SFWWR showing the locations of active samples reaches and passive integrated antennae.

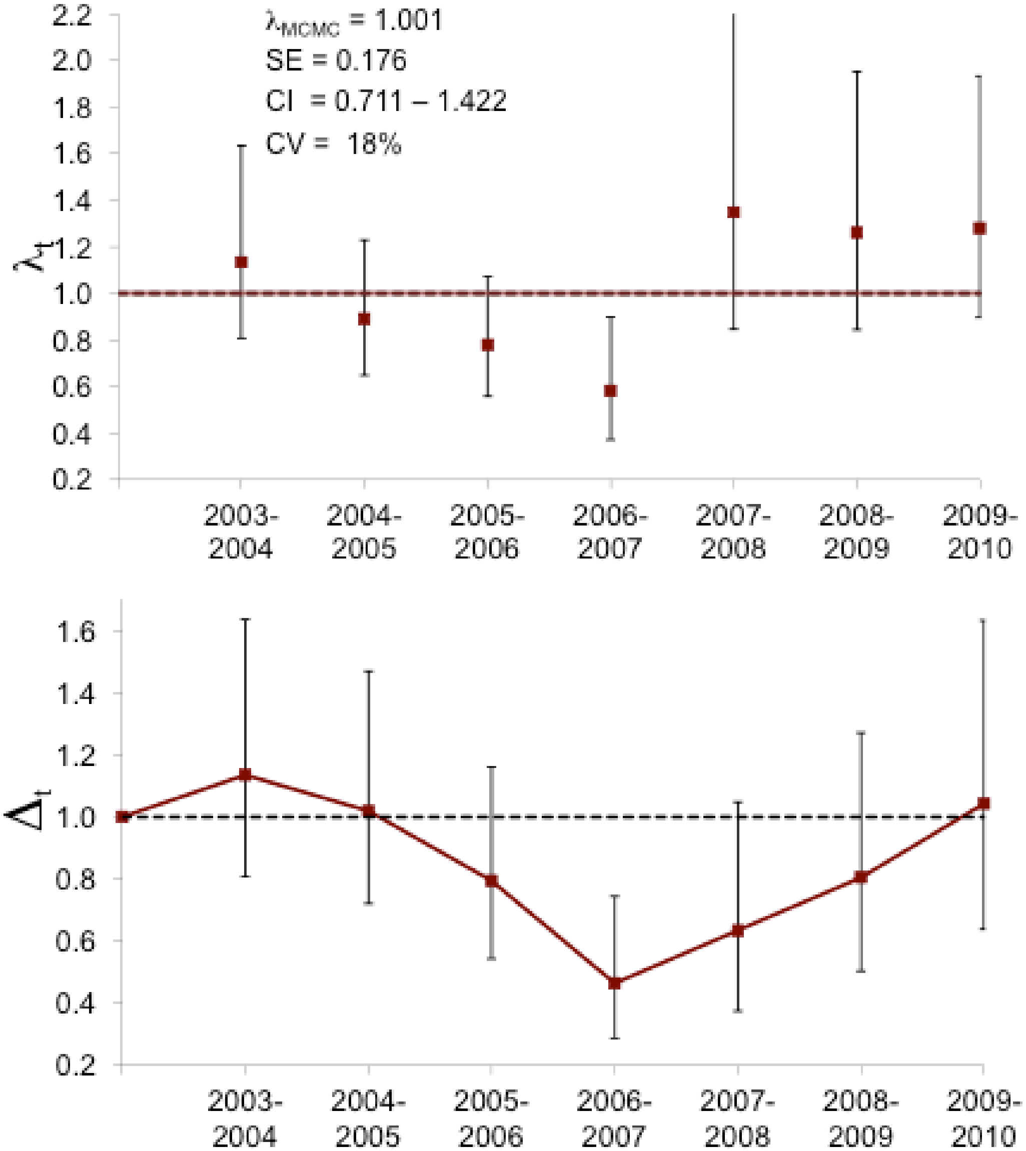

Figure 7.2. Population growth rates (λ_t; top panel) and realized population change (Δ_t; bottom panel) from the top model (Table 7.1) for all adult fish ≥ 300 mm, migratory, non-migratory, and unknown combined (n=1,706).

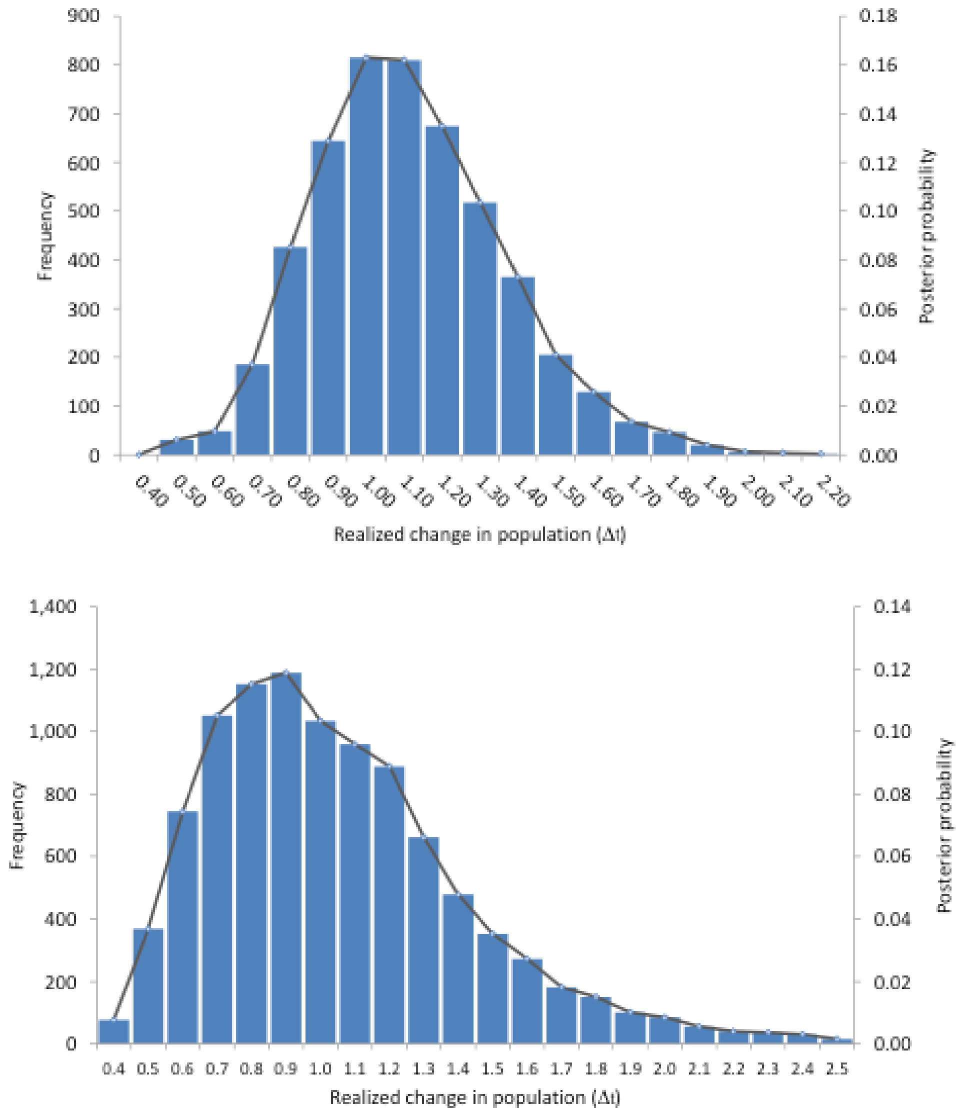

Figure 7.3. Estimated posterior distributions of overall realized population change (Δt) based on posterior distributions of λt from 20,000 Markov chain Monte Carlo (MCMC) simulations, from the Pradel top model for all adult fish (top) and only migratory adult fish (bottom). We excluded the first 2 and last estimates because of confounding or potential bias. Overall realized population change is the proportion of the initial population size remaining at the end of the monitoring time period.

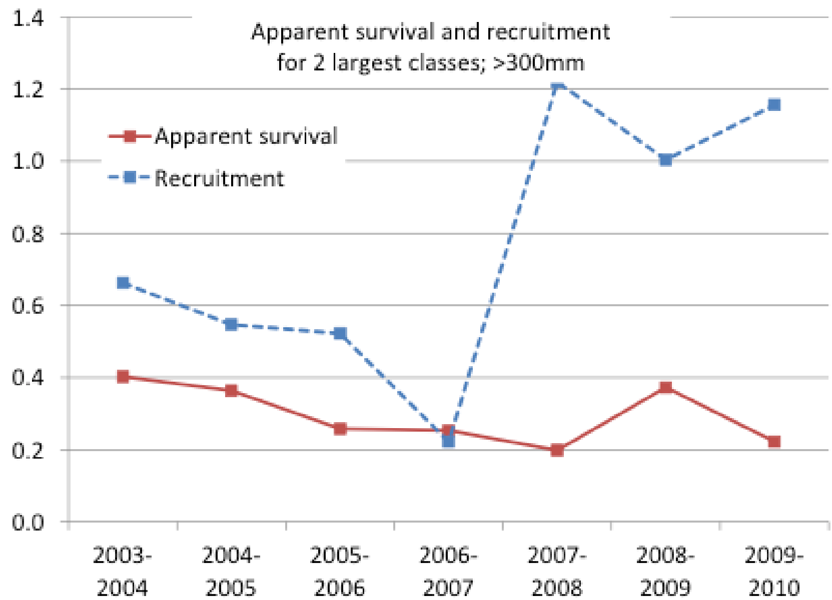

Figure 7.4. Apparent survival (Φ) and recruitment (*f*) from the Pradel top model (Table 7.1) for all adult fish ≥ 300 mm, migratory, non-migratory, and unknown combined (n=1,706).

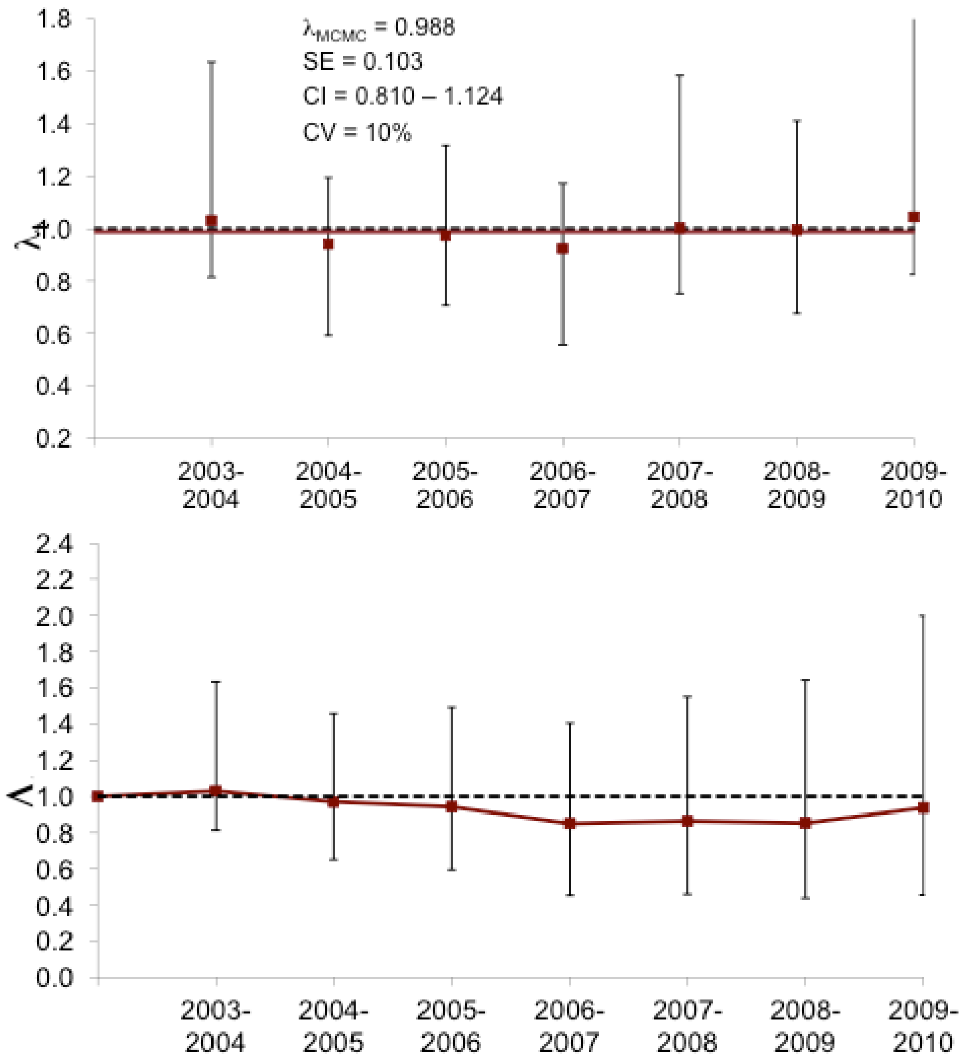

Figure 7.5. Population growth rates (λ_t; top panel) and realized population change (Δ_t; bottom panel) for all adult fish ≥ 300 mm that migrated from the study area (n=329).

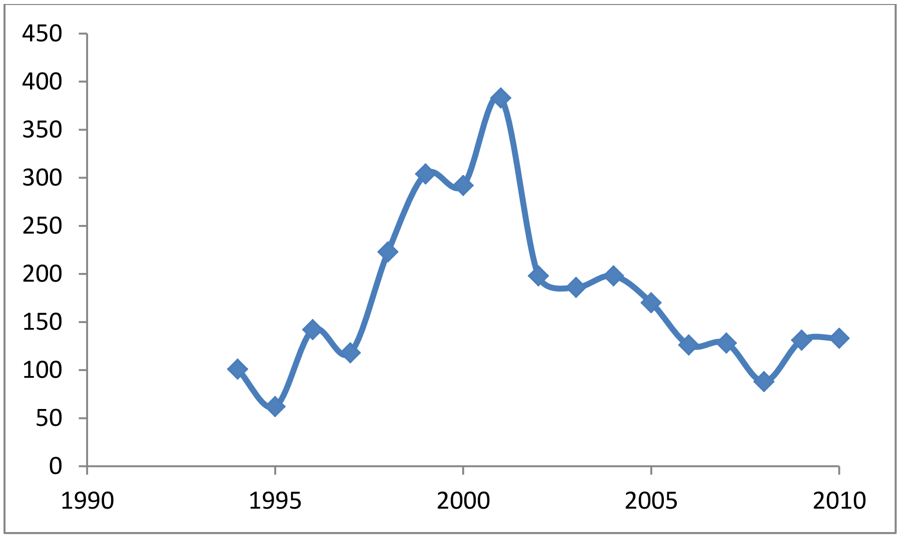

Figure 7.6. Bull trout redd counts for the SFWWR populations from 1994 to 2011.

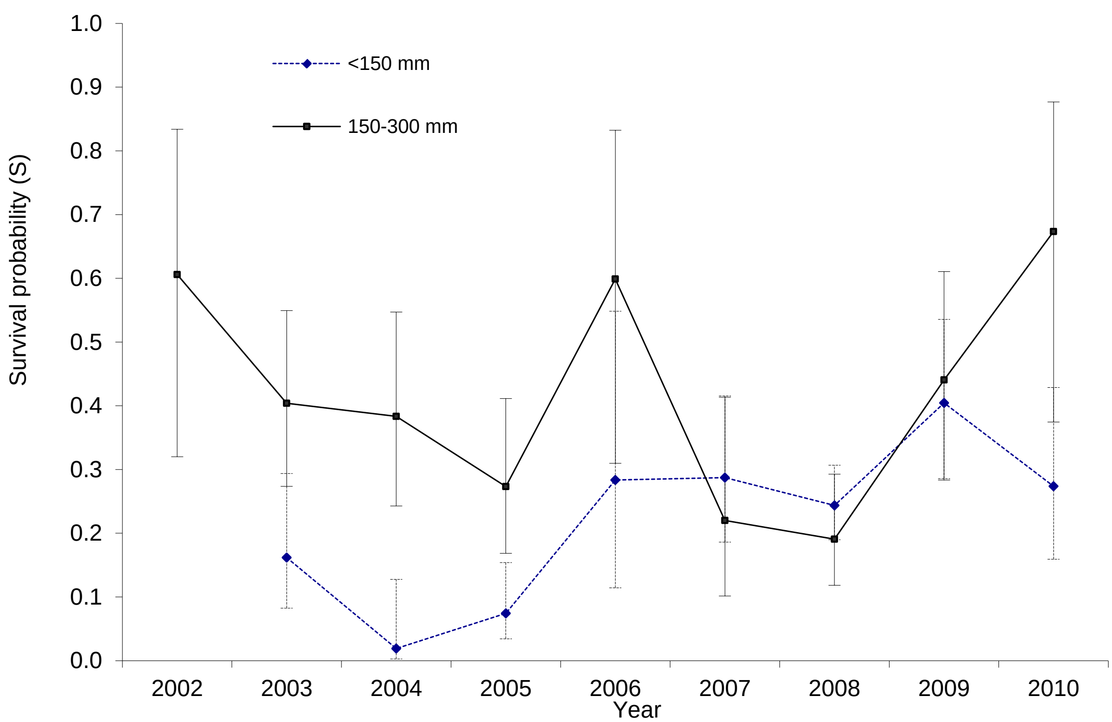

Figure 7.7. Survival probability (*S;* top panel) from the top Barker model for two size/age classes of small fish, < 150 mm and 150-300 mm.

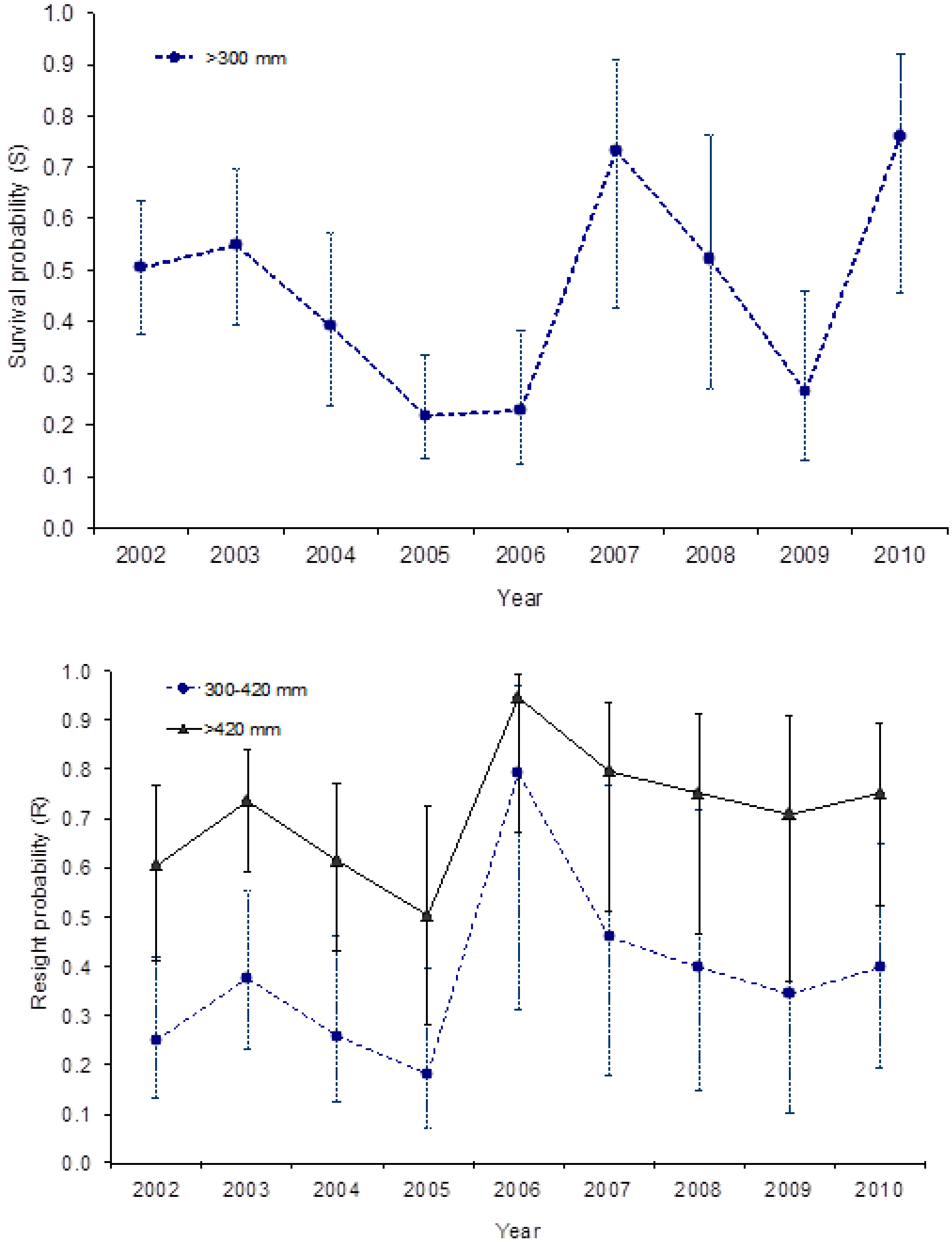

Figure 7.8. Survival probability (*S;* top panel) from the top Barker model for all large (> 300 mm) fish. Resight probability (R; bottom panel) from the top Barker model for two largest size/age groups of fish.

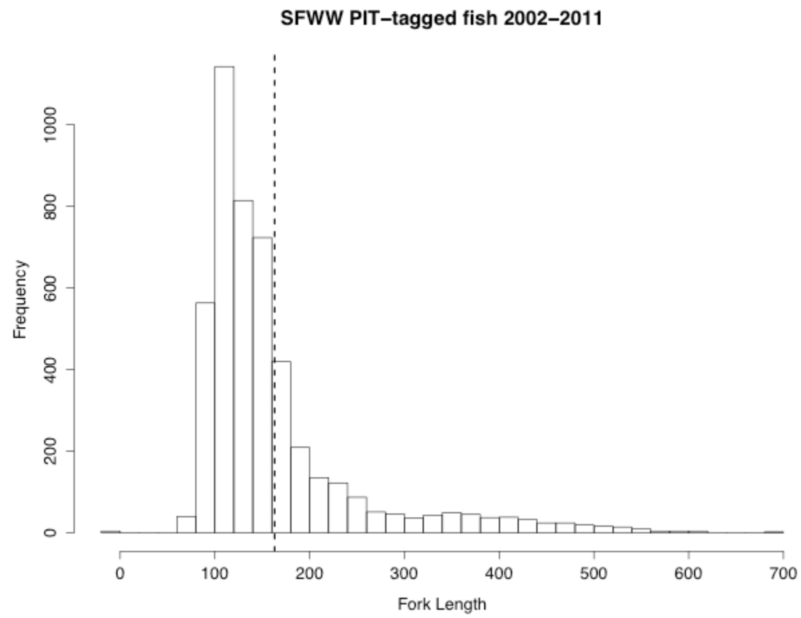

Figure 7.9. Size frequency distribution of all fish tagged in the SFWWR 2002 - 2011.

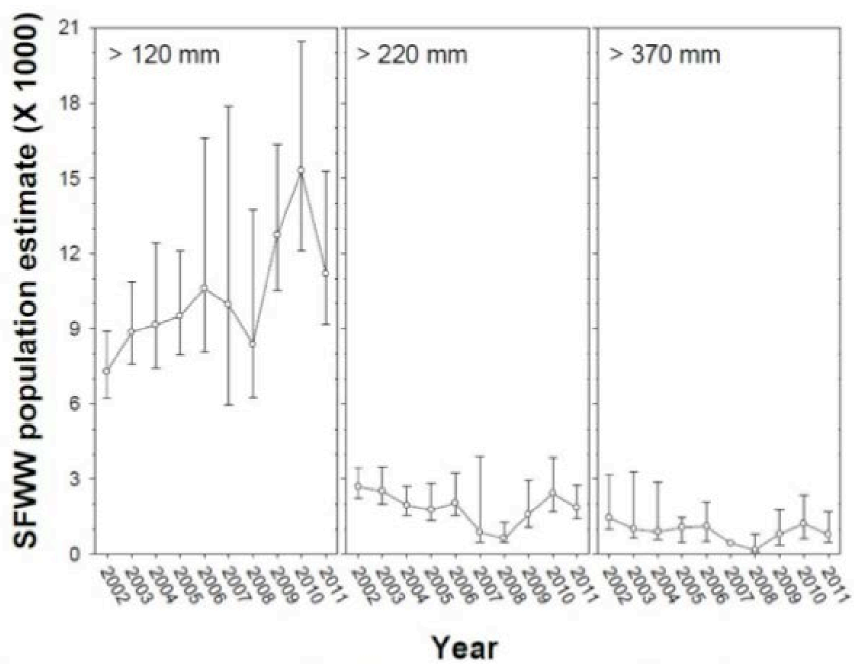

Figure 7.10. Annual population abundance estimates (± 95% CI) for three size groupings of bull trout in the SFWWR, 2002-2011. Due to low sample size, no confidence intervals were obtainable for the bull trout population component > 370 mm in TL in 2007. Estimates were expanded to represent the entire stream area from Harris Park Bridge upstream to Reser Creek.

Chapter 8 : Estimates of Survival Rates for South Fork and lower Walla Walla River Bull Trout

authored by

Steven Haeseker

U.S. Fish and Wildlife Service

Introduction

Estimation of survival rates is a key element towards the development of effective conservation and recovery strategies. Evaluation of survival rates and associated variability within a population can provide critical information on how habitat conditions and phenotypic characteristics influence individual and population viability (Dempson et al. 2011; Norris et al. 2013; Pine et al. 2013). Survival rates often vary within and across life stages for species that migrate through variable habitat conditions (Al-Chokhachy and Budy 2008; Dempson et al. 2011; Halfyard et al. 2013). These issues are particularly relevant for bull trout in the Walla Walla River basin, which display several life-history strategies (e.g., resident, fluvial, adfluvial) and experience different habitats as a result of life-history strategy and over time (AL-Chokhachy and Budy 2008; Homel and Budy 2008; Tyre et al. 2011; Pinto et al. 2013).

In this analysis we focus on migratory bull trout that have left their natal spawning and rearing areas and were captured in the lower Walla Walla River (WWR). Flow in the lower WWR is heavily impacted by irrigation withdrawals during late spring and summer, resulting in elevated water temperatures and migratory barriers. In addition, channel and riparian development have dramatically altered the river habitat conditions in several areas (USFWS 2002). For comparative purposes, we examine the lower WWR survival estimates against those for the South Fork Walla Walla River (SFWWR) derived using similar methodologies.

Methods

Bull trout were captured using angling, measured for fork length and weight, tagged with a passive integrated transponder (PIT) tag, and released. Fish were captured throughout the year, with peak numbers generally occurring in June and November (Figures 8.1, 8.2). We were interested in understanding how survival rates vary across seasons, so we divided the overall release dataset into two periods: fish that were tagged and released in the spring-summer period (March 1 – August 31) and fish that were tagged and released in the fall-winter period (September 1- February 28). Fork length at tagging varied across individuals, but fish that were tagged in the spring-summer period were generally smaller than fish in the fall-winter period, with mean fork lengths of 208 mm and 288 mm, respectively (Figure 8.3). During the spring-summer period, fish were primarily captured at two sites (Nursery Bridge Dam and Cemetery), while during the fall-winter period, fish were primarily captured at three sites (Nursery Bridge Dam, Cemetery Bridge, and Burlingame Diversion, Figure 8.1). Methods for capturing and tagging bull trout in the SFWWR are described in Appendix II.

Most mark-recapture survival estimation models require the duration of the sampling occasions (i.e., to mark or recapture individuals) to be short (almost “instantaneous”) relative to the period of survival estimation (Williams et al. 2002). However, due to bull trout migratory behaviors in combination with the available detection arrays, subsequent detections of tagged bull trout occurred over an extended period of time and thus did not meet this requirement. In addition, these models also require homogeneity of capture and survival probabilities among individuals. Because individuals were tagged and released over an extended period of time, survival probabilities likely varied across individuals, with fish tagged early in the season (e.g., in November) expected to have lower survival probabilities than fish tagged late in the season (e.g., in January).

To address these challenges, we used a logistic regression approach that incorporated the time-since-tagging to estimate the return rate, an index of survival. Return rates are an index of survival because they do not account for detection probability or emigration from the study area. However, Bowerman and Budy (2012) found that juvenile bull trout return rates in the SFWWR (i.e., proportion of fish detected nine or more months after tagging) were similar to true annual survival estimates derived using a Barker model, a model that accounts for detection probability and emigration. In addition, the study area monitored using PIT tag detection arrays is sufficiently large to cover the majority of the range of lower WWR bull trout, thus the effect of emigration from the study area on the return rate is likely small. The advantage of the survival index was that it allowed for comparisons between fish released in the upper and lower sections using a consistent analytical approach. The disadvantage of the survival index is that it does not account for recapture probability and does not estimate emigration rates. As a result, the survival indices are known to be biased low to some degree. Despite this bias, the survival indices do provide a consistent analytical approach for quantifying and comparing patterns of survival for the lower (WWR) and upper (SFWWR) sections.

In our application, a return was defined as any tagged fish with a subsequent detection that occurred after August 31st for spring-summer tagged fish or after February 28th for fall-winter tagged fish. Return rates were the proportion of fish released in each season that were categorized as returns. Logistic regression was used to estimate return rates for each release period, along with evaluating whether time-since-tagging, tagging site, fork length, and release year were important factors for explaining patterns of variation in the return rates.

For each release period, the full logistic regression equation was of the form

$$logit(p_i) = \beta_0 + \beta_1 Year + \beta_2 Site + \beta_3 Length + \beta_4 Time + \beta_5 Length \cdot Year + \beta_6 Site \cdot Year + \varepsilon_i,$$

where $\beta_0, \beta_1, \beta_2, \beta_3, \beta_{4,}\beta_5, \beta_6$ are estimated parameters, *Year* is year of release (2008-2011), *Site* is release site (Burlingame Dam, Cemetery Bridge, Nursery Bridge), *Length* is fork length at tagging, *Time* is number of days between the day of tagging and the end of the period (August 31st for spring-summer releases and February 28th for fall-winter releases), $Length \cdot Year$ is an interaction term allowing for length effects to potentially vary by year, and $Site \cdot Year$ is an interaction term allowing for site effects to vary by year. In this formulation, the *Time* variable represents the number of days that fish were vulnerable to mortality prior to the end of the period, with the expectation that fish released earlier in the time period would have higher mortality than fish released later in the time period (i.e., *Time* was used to account for the continuous release of individuals).

An all-subsets approach was used to fit all combinations of the parameters in the full model defined above. The models were ranked according to AICc, the model with the minimum AICc was identified, and Akaike weights (w_i) were calculated for each model (Burnham and Anderson 2002). Using the AICc-ranked set, we calculated model-averaged predictions for the return rate for each of the release years and sites. Model-averaged predictions were calculated using:

$$\hat{\bar{\theta}} = \sum_{i=1}^{R} w_i \hat{\theta},$$

where $\hat{\bar{\theta}}$ denotes the model-averaged prediction of θ (i.e., return rate) across the R models and w_i denotes the Akaike weight for model i = 1, 2, …, R (Burnham and Anderson 2002). Predictions for return rates at each combination of release *Site* and *Year* were generated with *Length* fixed at the average length observed during the spring-summer and fall-winter releases and the *Time* variable set at 91 d for the spring-summer releases and 180 d for the fall-winter releases. In addition, we generated predictions for return rate across the range in *Length* values and across *Years*, with the *Time* variable set at 91 d for the spring-summer releases and 180 d for the fall-winter releases.

The sets of best fitting models were also used to evaluate the relative importance of each predictor variable used in regressions (Burnham and Anderson 2002). The relative variable importance is a quantitative measure of the degree to which variables are consistently included among the best-fitting models based on AICc, relative to the other variables considered. The relative variable importance for variable j among a set of R models is calculated as

$$\sum_{i=1}^{R} w_i I_j(g_i),$$

where w_i is the Akaike weight for model i and $I_j(g_i)$ is an indicator variable equal to one if variable j is in model i (g_i) and equal to zero otherwise. Variables with relative variable importance values near one are consistently in the top fitting models while variables with relative variable importance values near zero are rarely, if ever, included in the top fitting models.

In addition to the seasonal return rates estimated above, we also generated annual return rates using a similar logistic regression approach to the one described above. Based on the date of release for each individual fish, we defined a return as a subsequent recapture at any location at least one year after release. Releases were organized by calendar year and we evaluated length, year, and length*year interactions using logistic regression techniques and model averaging as described above. Identical procedures were applied to both the lower WWR and SFWWR releases, allowing for comparisons between the two locations. Results were summarized as a continuous function of length at release using logistic regression, as well as by binning the data into the sub-adult (145-290 mm) and the small adult (291-406 mm) size classes and using a binomial estimate of the return rate.

Results

Releases of PIT-tagged bull trout occurred throughout the spring-summer and fall-winter periods, with the majority occurring after June 1 for the spring-summer releases and after September 1 for the fall-winter releases (Figures 8.2, 8.3, Table 8.1). The average length of bull trout tagged in the spring-summer period was 208 mm while the average length in the fall-winter period was 288 mm (Figure 8.4). Larger fish were captured during the fall-winter releases, with 27% greater than 300 mm, while only 1% of the spring-summer releases were greater than 300 mm.

The *Length* and *Time* variables were consistently in the top-fitting models of return rate (Tables 8.2, 8.3), resulting in high relative variable importance values for *Length* and *Time* (Figures 8.5, 8.6). The signs of the estimated coefficients indicated that return rates increase with *Length* and decrease with *Time*. The relative variable importance values indicated that there was some support for *Site* and *Year* effects, but little support for *Length*Year* or *Site*Year* interactions (Figures 8.5, 8.6).

Fish length was an important factor for explaining variability in return rates. Model-averaged predictions for return rate showed an increasing pattern with *Length* for both spring-summer and fall-winter released fish (Figures 8.7, 8.8). There was little indication that this pattern varied across years.

Estimated return rates for the spring-summer releases showed little variation across years or across release sites (Figure 8.9). Similarly, the fall-winter releases showed little variation in estimated return rates across years or across release sites (Figure 8.10).

It is important to note that the duration of the fall-winter period (180 d) was double the duration of the spring-summer period used in this analysis (91 d). To compare the two periods on similar temporal scales, we generated model-averaged predictions for return rate as a function of length using a standardized 91 d period for both the fall-winter and the spring-summer releases (Figure 8.11). When standardized using similar *Time* durations, the two periods showed similar increasing patterns in return rate with increasing length.

The annual estimates of survival based on the relative return rate for both locations (i.e., both WWR and SFWWR) showed that survival varied by release year and by fish length, with higher survival for larger fish compared to smaller fish (Figures 8.12, 8.13). However, the strength of the survival advantage for larger fish also varied by year, with some years showing a high survival advantage and some years showing only a moderate survival advantage for large fish. For example, sub-adult (145-290 mm) and small adult fish (291-406 mm) from the SFWWR survived at similar rates during 2004, 2006, 2008, and 2009 (Figure 8.14). In other years such as 2003, 2007, and 2011, small adults displayed much higher survival than sub-adults. Average survival of sub-adult fish from the SFWWR was low, with a mean of 12% across years (range: 3-23%, Figure 8.14). Survival of small adult fish from the SFWWR was higher, with a mean of 25% across years (range: 9-43%). Over the years when fish were released in both locations (i.e., 2008-2010), annual length-specific survival patterns were similar between WWR and SFWWR releases, suggesting that shared factors influenced survival of fish released at both locations (Figure 8.14).

Discussion

Fish length was the most important examined covariate affecting return rate for migratory bull trout in the WWR. Al-Chokhachy and Budy (2008) found generally lower survival rates for bull trout between 120-170 mm TL, as compared to larger fish. They found little distinction between survival rates for larger fish based on group size; however, sample sizes may have been too small to detect such differences in survival modeling. Often larger fish have higher survival than smaller conspecifics (Sogard 1997); however, specific relationships between size and survival may not always be that simple and may vary by life stage, behavior, or environmental conditions (Halfyard et at. 2013; Pinto et al. 2013; Tattam et al. 2013). These results potentially suggest that differences between sites (i.e., differences in habitat) and among years (i.e. annual environmental variability) could be influential, although not as important as individual differences in fish length. Differences in habitat and environmental variability have been shown to impact survival for various species (Stoner 2009; Halfyard et al. 2013). Identifying environmental mechanisms that impact survival can be challenging since they occur at a variety of spatial and temporal scales. Results from this study suggest that both individual and environmental differences could affect survival rates for bull trout. Since the WWR experiences multiple anthropogenic impacts that could affect bull trout survival in variable ways (USFWS 2002), research to evaluate survival under specific environmental conditions would be informative for conservation and population viability assessment.

Differences between spring-summer releases and fall-winter releases could indicate seasonal patterns in survival. Although the relationship between survival and fish size was fairly similar by release period, there was some evidence that return rates were slightly higher, for the spring-summer releases as compared to the fall-winter releases for fish of similar sizes. These results could be caused by increased survival, increased capture probability, sampling variability, or a combination. Seasonal patterns can be evident in both movement rates and survival (Alexiades et al. 2012). Increased capture probability during the spring-summer could be a result of either increase movement through the area or reduced movement out of the area as a result of summer low-flow passage barriers. The biggest difference between spring-summer releases and fall-winter releases was fish size. Potentially, fall-winter releases were composed of a higher proportion of spawning individuals, which would be less available in the sampling area during the summer spawning period (Al-Chokhachy and Budy 2008). Differences in survival could also potentially be impacted by previous spawning.

Although return rates may underestimate true survival, they could provide a useful index when other methods are financially or practically prohibitive. Estimates from Al-Chokhachy and Budy (2008) for presumed migratory bull trout captured in the SFWWR suggest that annual survival is ~0.2-0.5 for small individuals (120-170 mm TL) and ~0.5-0.8 for larger individuals. Return rates from this study would produce much lower annual estimates, which could be a function of differences in survival by location, or differences in sampling design. Return rates do not incorporate capture probability or emigration and while Bowerman and Budy (2012) observed that the return rates in their study were similar to annual survival rates from the Barker model, this may be related to capture probability, which would vary based on antenna numbers and placement in the sampling area. Since, in some situations, it can be too costly or practically difficult to acceptably complete mark-recapture studies (Miranda and Bettoli 2007), the approach developed in this study could prove useful for identifying factors that affect survival and to identify changes in survival over time and as a result of environmental change or restoration activities.

Seasonal, annual, and individual differences in survival based on return rates should be evaluated with caution, since capture probability is not evaluated. Capture probability can vary based on fish size and behavior, as well as environmental and habitat conditions (Al-Chokhachy and Budy 2008) and when capture probability is not considered, it can be difficult to tease apart relationships with survival from those with capture probability (Kéry and Schaub 2012). Maintaining high and stable detection probability throughout the populations' area of use would be helpful for separating changes in survival versus changes in detection probability.

Literature Cited

Al-Chokhachy, R., and P. Budy. 2008. Demographic characteristics, population structure, and vital rates of a fluvial population of bull trout in Oregon. Transactions of the American Fisheries Society 137:1709-1722.

Alexiades, A. V., M. M. Peacock, and R. Al-Chokhachy. 2012. Movement patterns, habitat use, and survival of Lahontan cutthroat trout in the Truckee River. North American Journal of Fisheries Management 32:974-983.

Bowerman, T., and P. Budy. 2012. Incorporating movement patterns to improve survival estimates of juvenile bull trout. North American Journal of Fisheries Management 32:1123-1136.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretic approach. Second Edition. Springer, New York.

Dempson, J. B., M. J. Robertson, C. J. Pennell, G. Furey, M. Bloom, M. Shears, L. M. N. Ollerhead, K. D. Clarke, R. Hinks, and G. J. Robertson. 2011. Residency time, migration route and survival of Atlantic salmon Salmo salar smolts in a Canadian fjord. Journal of Fish Biology 78:1976-1992.

Halfyard, E. A., A. J. F. Gibson, M. J. W. Stokesbury, and D. E. Ruzzante, and F. G. Whoriskey. 2013. Correlates of estuarine survival of Atlantic salmon postsmolts from the Southern Upland, Nova Scotia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 70:452-460.

Homel, K., and P. Budy. 2008. Temporal and spatial variability in the migration patterns of juvenile and subadult bull trout in northeastern Oregon. Transactions of the American Fisheries Society 137:869-880.

Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Waltham, Massachusetts.

Miranda, L. E., and P. W. Bettoli. 2007. Mortality. Pages 229-277 in C. S. Guy and M. L. Brown, eds. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Norris, D. R., D. T. T. Flockhart, and D. Strickland. 2013. Contrasting patterns of survival and dispersal in multiple habitats reveal an ecological trap in a food-caching bird. Oecologia 173:827-835.

Pine, W. E, III, B. Healy, E. Omana Smith, M. Trammell, D. Speas, R. Valdez, M. Yard, C. Walters, R. Ahrens, R. Vanhaverbeke, D. Stone, and W. Wilson. 2013. An individual-based model for population viability analysis of humpback chub in Grand Canyon. North American Journal of Fisheries Management 33:626-641.

Pinto, M. C., J. R. Post, A. J. Paul, F. D. Johnston, C. J. Mushens, J. D. Stelfox. 2013. Lateral and longitudinal displacement of stream-rearing juvenile bull trout in response to upstream migration of spawning adults. Transactions of the American Fisheries Society 142:1590-1601.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60(3):1129-1157.

Stoner, A. 2009. Habitat-mediated survival of newly settled red king crab in the presence of a predatory fish: Role of habitat complexity and heterogeneity. Journal of Experimental Marine Biology and Ecology 382:54-60.

Tattam, I. A., J. R. Ruzycki, H. W. Li, and G. R. Giannico. 2013. Body size and growth rates influence emigration timing of Oncorhynchus mykiss. Transactions of the American Fisheries Society 142:1406-1414.

Tyre, A. J., J. T. Peterson, S. J. Converse, T. Bogich, D. Miller, M. Post van der Burg, C. Thomas, R. Thompson, J. Wood, D. C. Brewer, M. C. Runge. 2011. Adaptive management of bull trout populations in the Lemhi Basin. Journal of Fish and Wildlife Management 2(2):262-28.

U.S. Fish and Wildlife Service (USFWS). 2002. Chapter 11, Umatilla-Walla Walla Recovery Unit, Oregon and Washington. 153p. In: U.S. Fish and Wildlife Service. Bull trout (Salvelinus confluentus) Draft Recovery Plan. Portland Oregon.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: Modeling, estimation, and decision making. Academic Press, San Diego, CA.

Table 8.1. Number of Walla Walla River PIT-tagged bull trout released and the number of returns by release year and sampling season. Time since marking refers to the minimum, mean, and maximum number of days between release and the end of the sampling season (August 31st for spring summer releases and February 28th for fall-winter releases) for fish released in each year.

				Time since marking		
Year	Season	Releases	Returns	min	mean	max
2008	Spring-Summer	76	33	5	56	131
2009	Spring-Summer	24	9	19	47	77
2010	Spring-Summer	93	30	1	51	78
2011	Spring-Summer	47	18	2	53	85
2008	Fall-Winter	118	20	88	114	145
2009	Fall-Winter	91	23	61	137	172
2010	Fall-Winter	150	38	33	132	159
2011	Fall-Winter	82	28	3	117	156

Table 8.2. Table of estimated model coefficients, the number of estimated parameters (k), AICc values, AICc differences (delta), and AICc weights for spring-summer releases of bull trout in the Walla Walla River. For variables defined as factors, a plus sign (+) indicates that the factor was included in the model.

Time	Length	Site	Year	Length:Year	Site:Year	k	AICc	delta	weight
-0.020	0.011					3	297.7	0.0	0.35
-0.020	0.013		+			6	298.5	0.8	0.23
-0.020	0.011	+				4	299.6	1.9	0.14
-0.020	0.012	+	+			7	300.4	2.7	0.09
-0.018	0.012	+	+		+	10	300.8	3.1	0.08

Table 8.3. Table of estimated model coefficients, the number of estimated parameters (k), AICc values, AICc differences, and AICc weights for fall-winter releases of bull trout. For variables defined as factors, a plus sign (+) indicates that the factor was included in the model.

Time	Length	Site	Year	Length:Year	Site:Year	k	AICc	delta	weight
	0.009					2	470.8	0.0	0.19
-0.010	0.008		+			6	471.0	0.2	0.17
-0.006	0.009					3	471.0	0.2	0.17
-0.011	0.016		+	+		9	472.2	1.4	0.09
	0.008	+				4	472.6	1.8	0.08
	0.008		+			5	472.8	1.9	0.07
	0.008	+	+			7	472.9	2.1	0.07
-0.007	0.008	+	+			8	473.6	2.8	0.05
-0.004	0.008	+				5	474.1	3.3	0.04

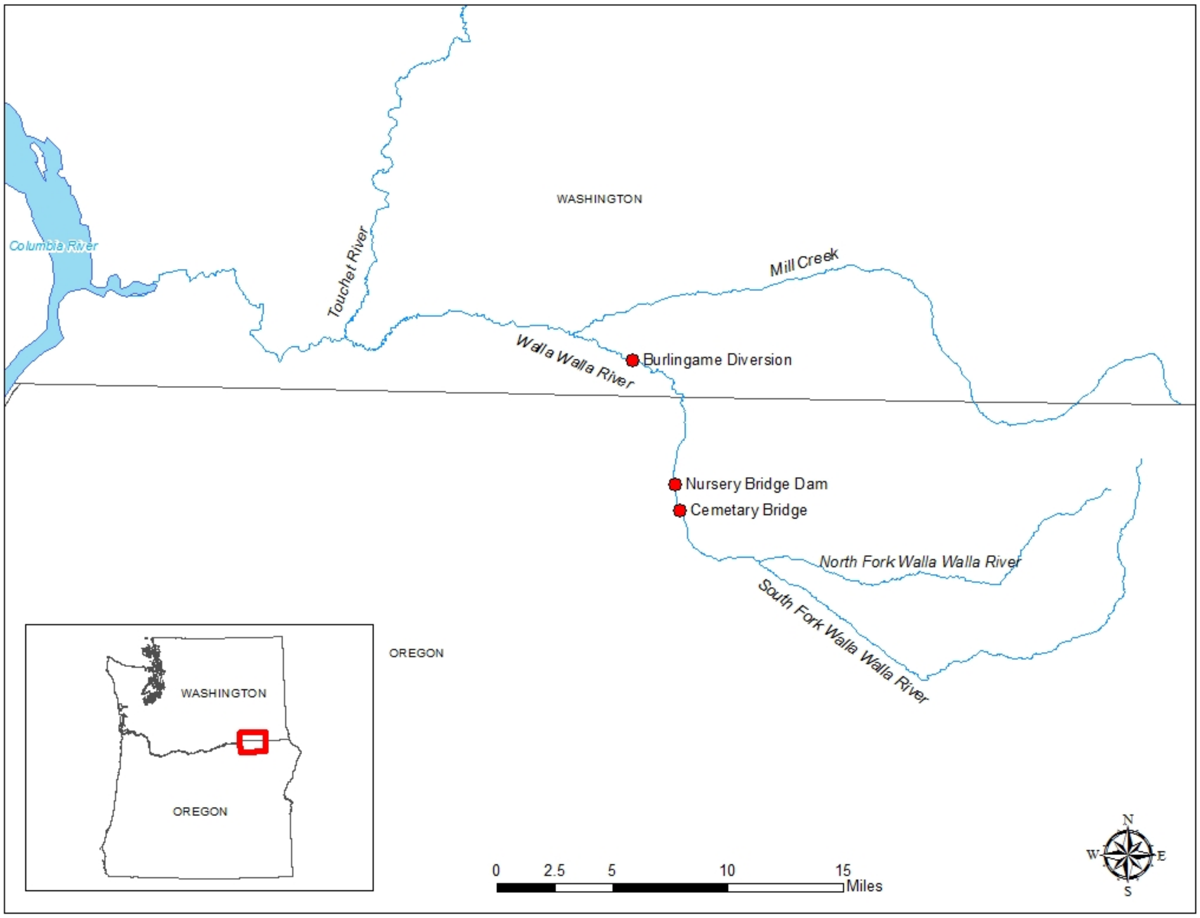

Figure 8.1. Lower Walla Walla River study area, with locations of Burlingame Diversion, Nursery Bridge Dam, and Cemetary Bridge release sites.

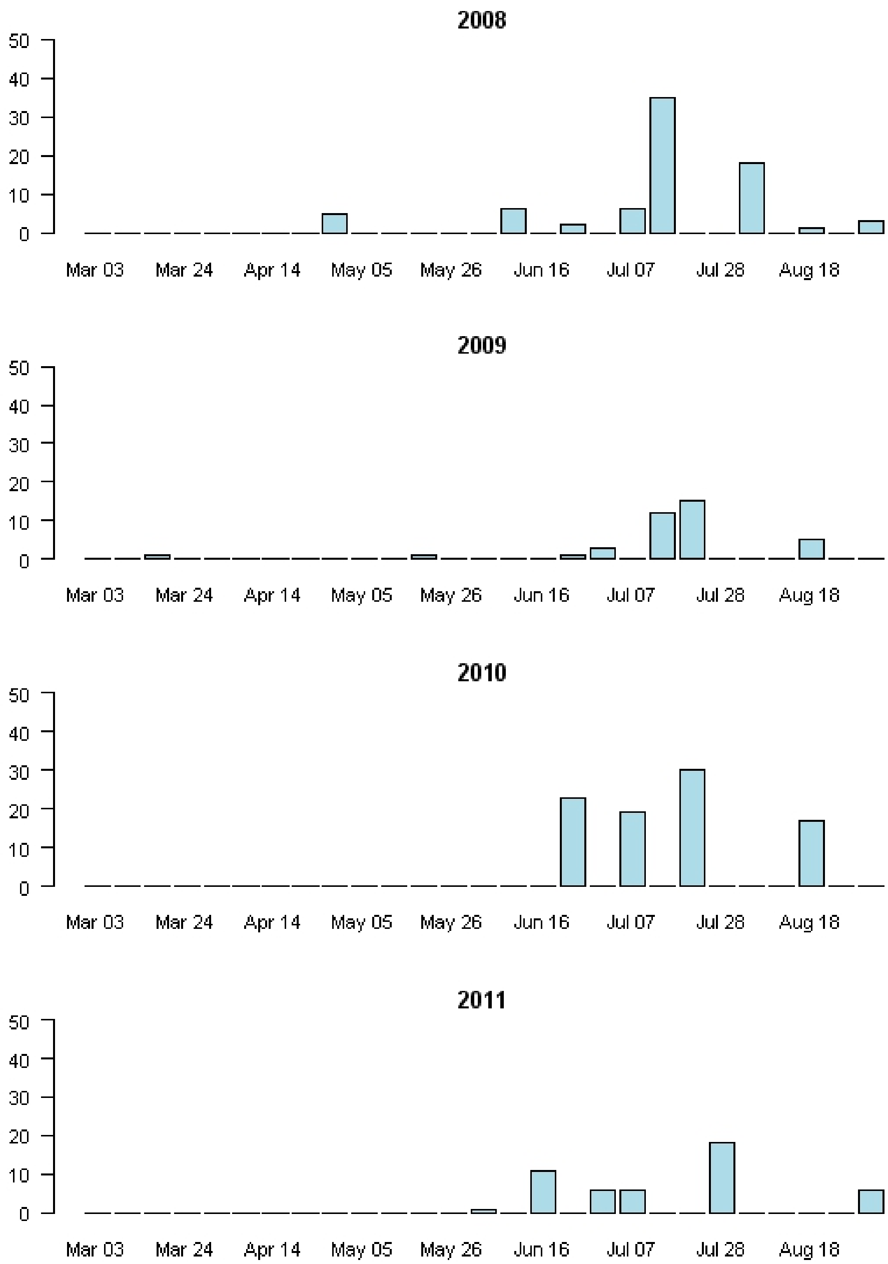

Figure 8.2. Weekly number of bull trout that were captured, PIT-tagged, and released during the spring-summer periods of 2008-2011 in the Walla Walla River.

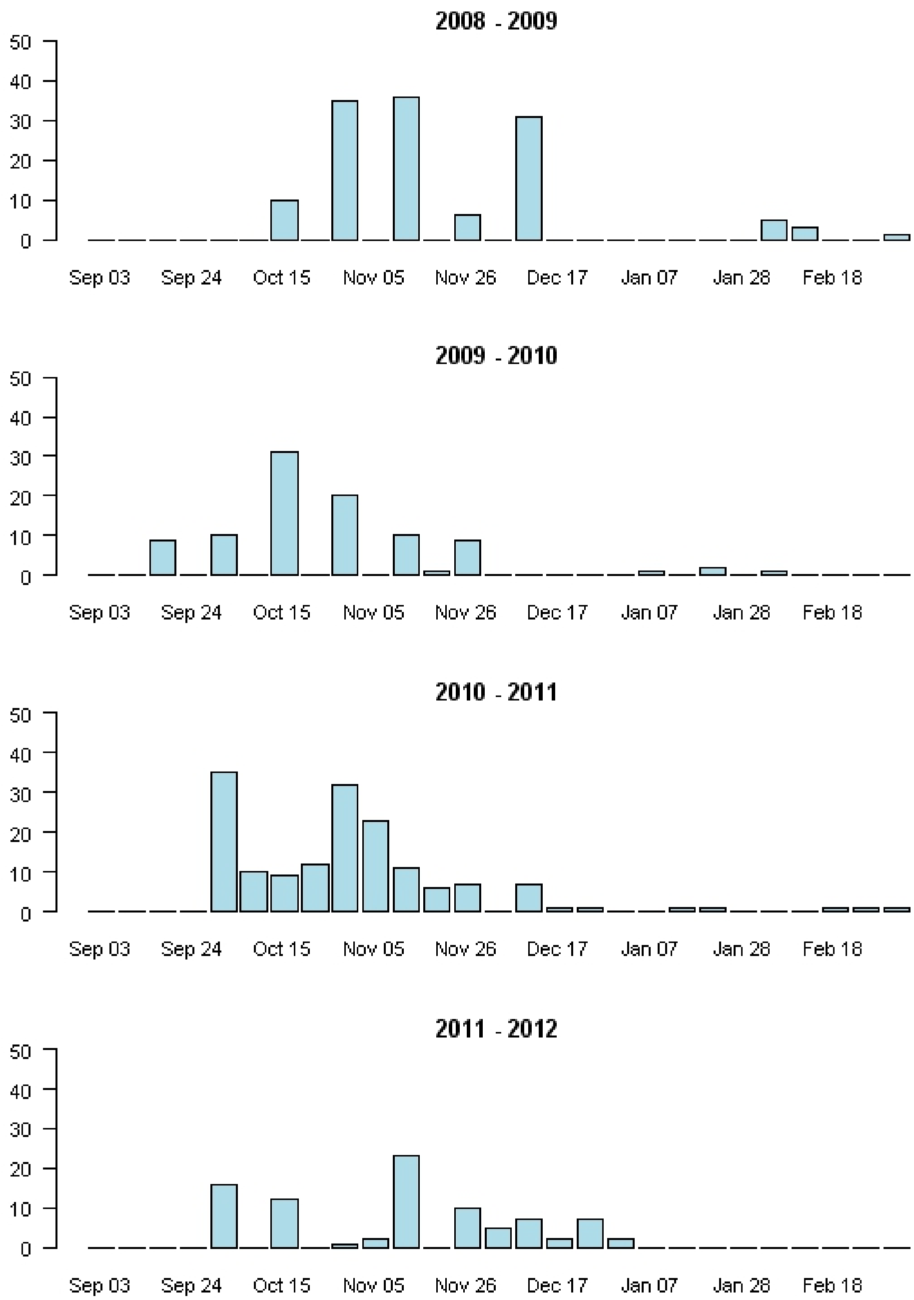

Figure 8.3. Weekly number of bull trout that were captured, PIT-tagged, and released during the fall-winter periods of 2008-2012 in the Walla Walla River.

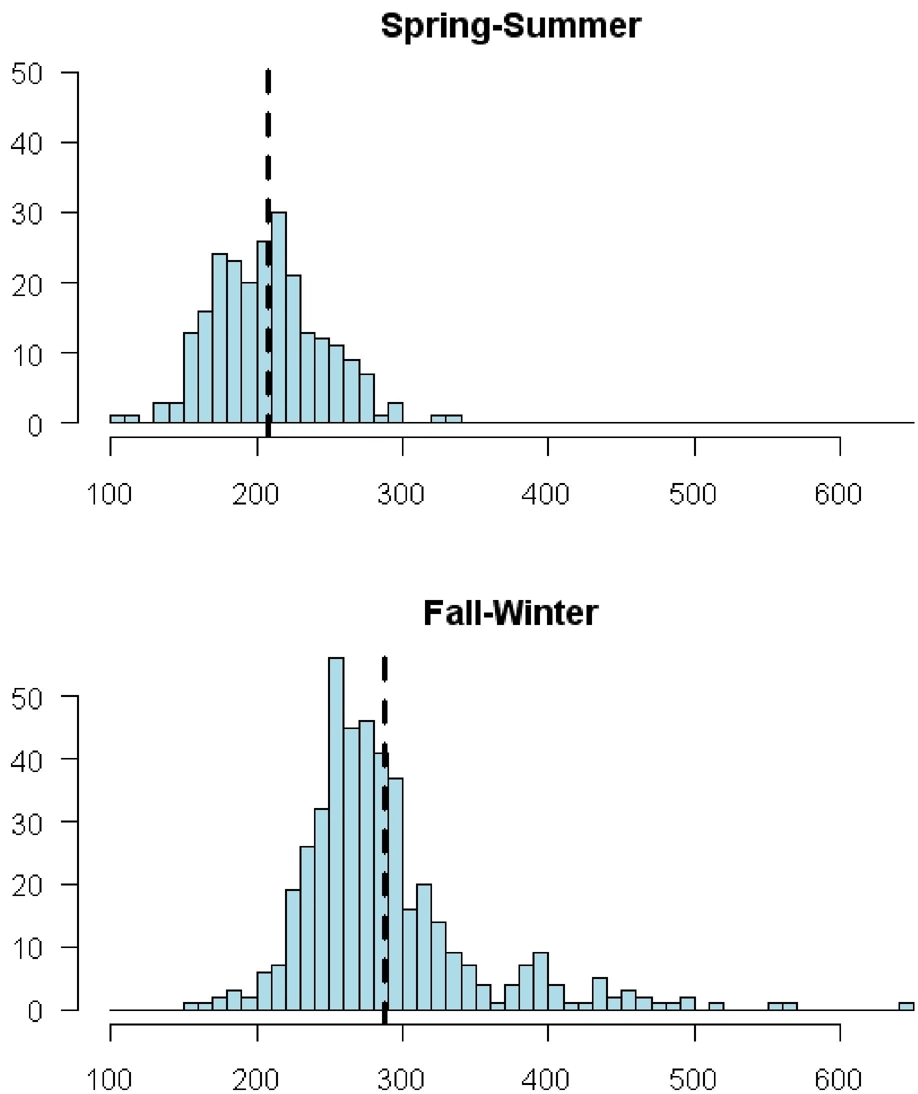

Figure 8.4. Fork length of bull trout that were captured, PIT-tagged, and released during the spring-summer period and the fall-winter period, 2008-2012, in the Walla Walla River. The vertical, dashed lines represent the mean lengths of 208 mm for the spring-summer group and 288 mm for the fall-winter group.

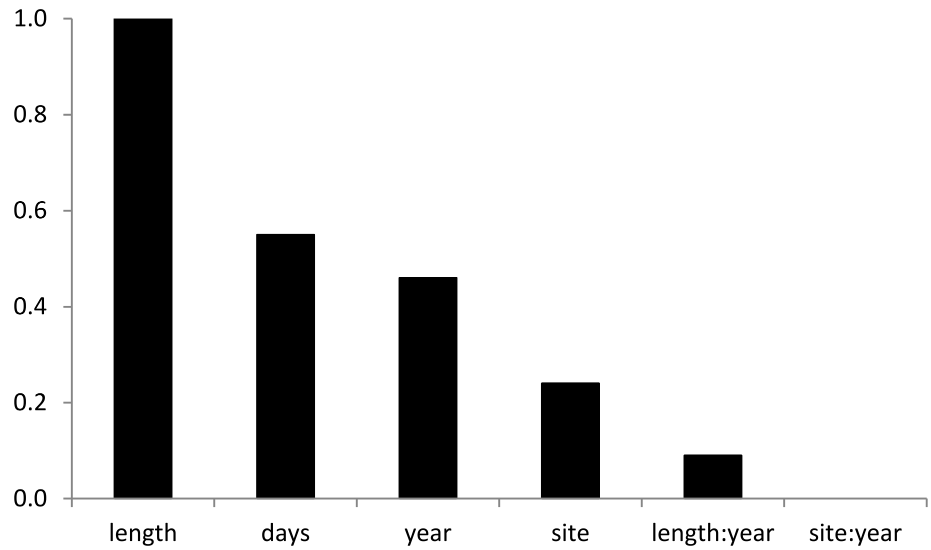

Figure 8.5. Relative variable importance values for fall-winter releases of bull trout in the Walla Walla River.

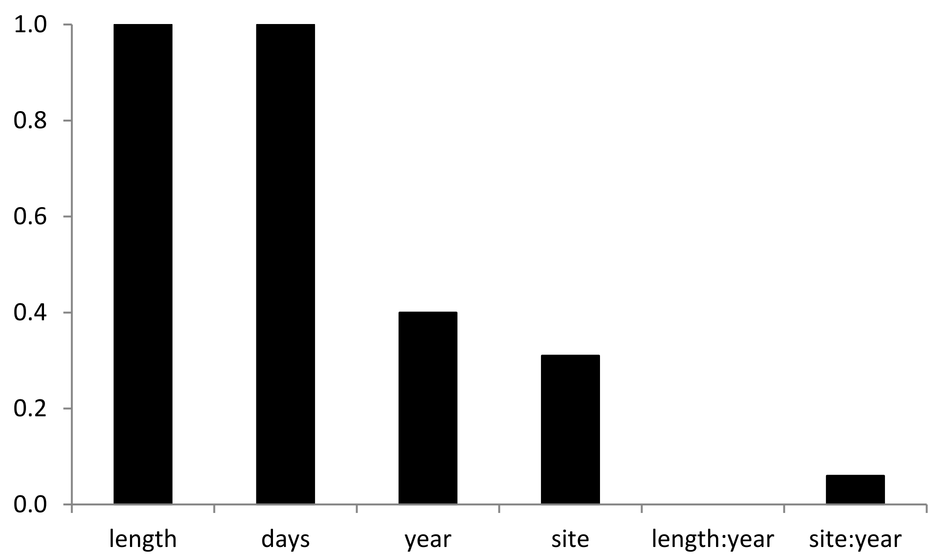

Figure 8.6. Relative variable importance values for spring-summer releases of bull trout in the Walla Walla River.

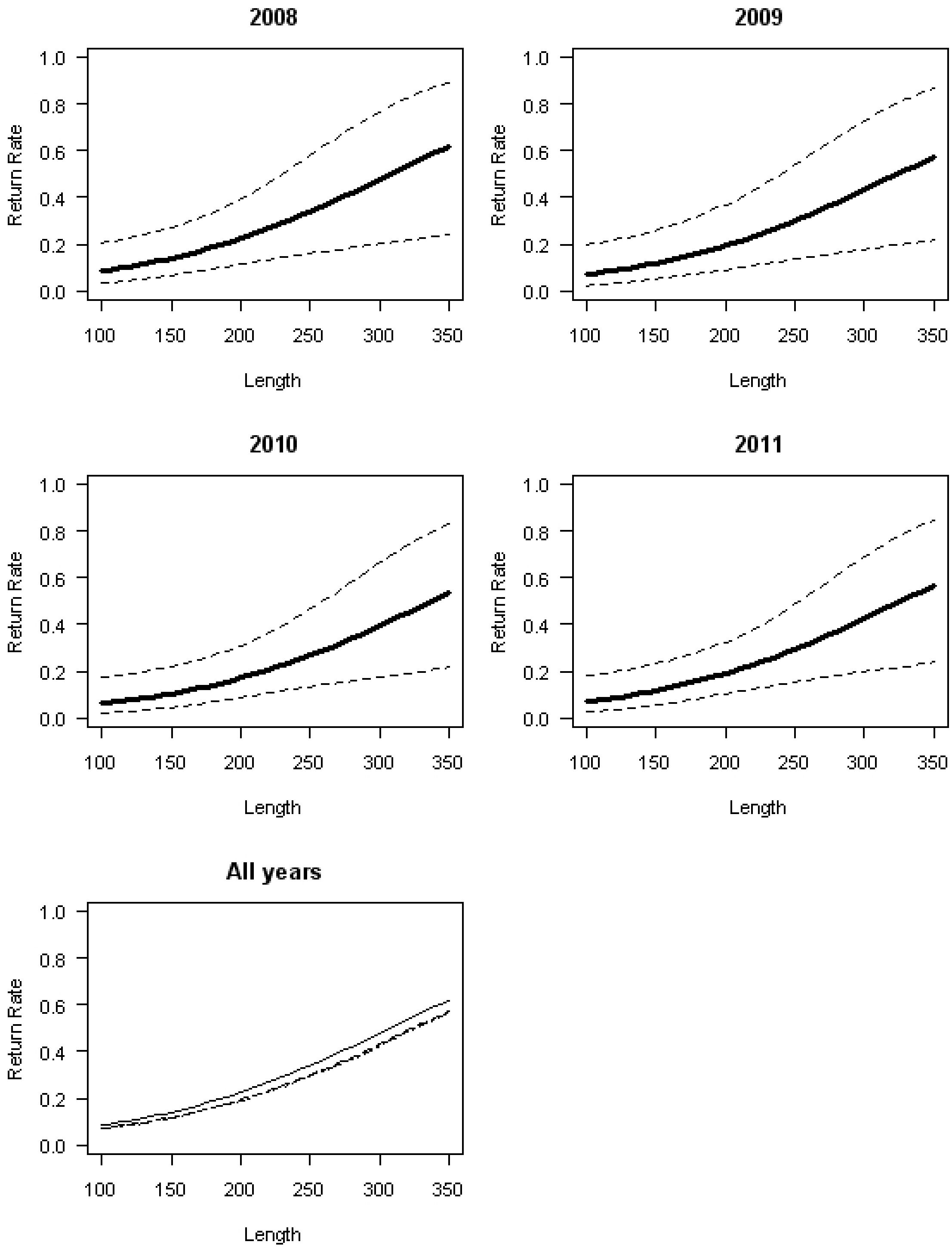

Figure 8.7. Model-averaged predictions of survival versus length with 95% confidence intervals for spring-summer releases of PIT-tagged bull trout, 2008-2011, in the Walla Walla River. Predictions were based on *Time* fixed at 91 d and *Site* set to Cemetary Bridge. The mean responses by year are plotted on the “All years” panel.

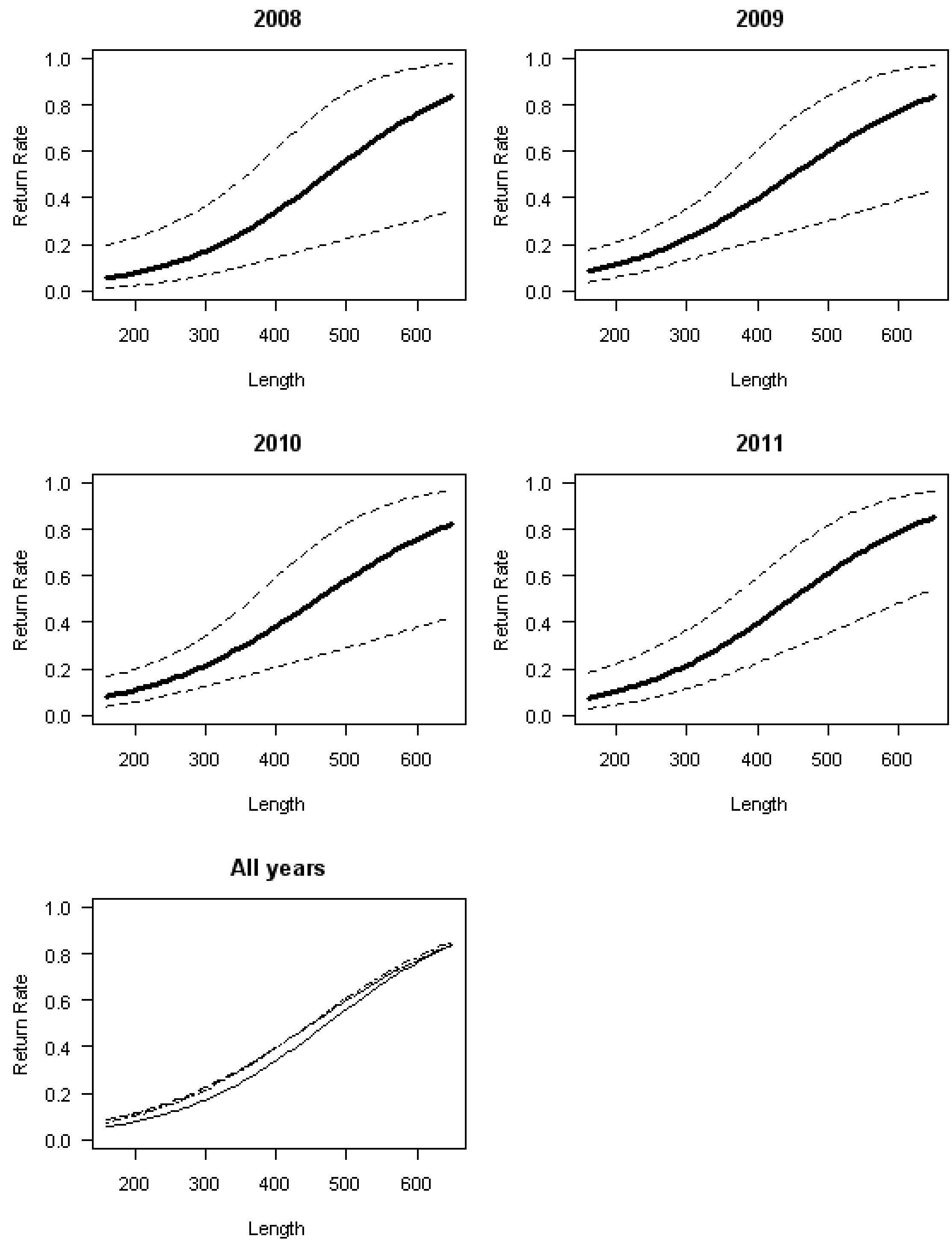

Figure 8.8. Model-averaged predictions of survival versus length with 95% confidence intervals for fall-winter releases of PIT-tagged bull trout, 2008-2011, in the Walla Walla River. Predictions were based on *Time* fixed at 180 d and *Site* set to Cemetary Bridge. The mean responses by year are plotted on the “All years” panel.

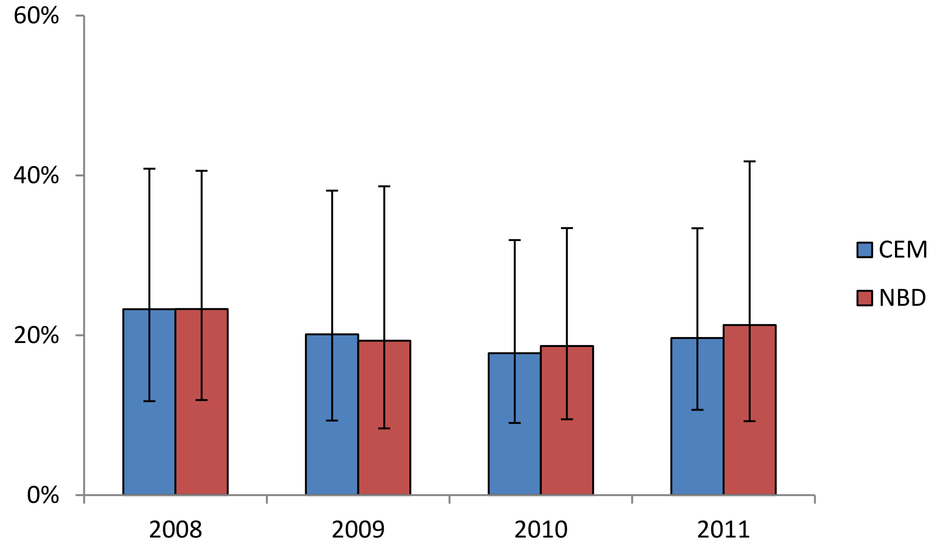

Figure 8.9. Model-averaged predictions of survival by *Year* and *Site* (CEM = Cemetary, NBD = Nursery Bridge Dam) for spring-summer releases of PIT-tagged bull trout, 2008-2011. Predictions were based on *Time* fixed at 91 d and *Length* set to 208 mm.

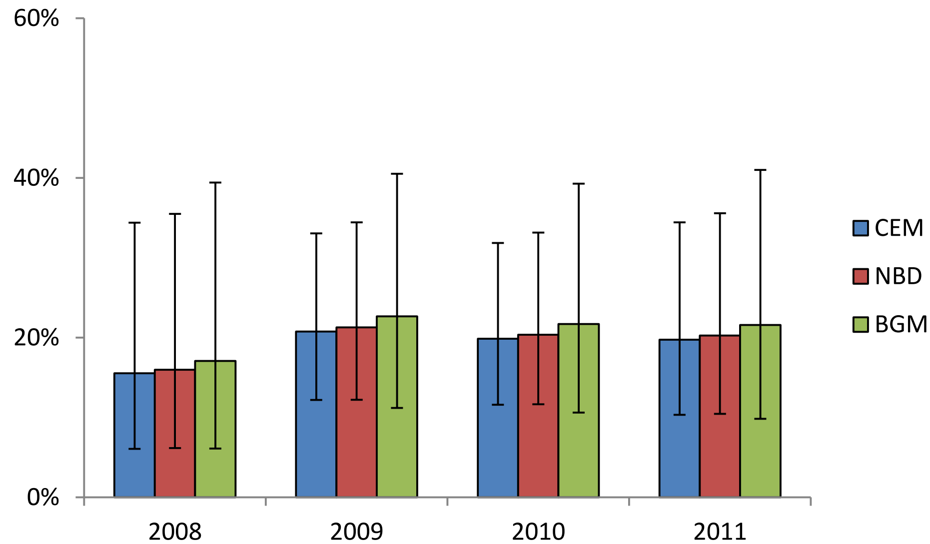

Figure 8.10. Model-averaged predictions of survival by Year and Site (CEM = Cemetary, NBD = Nursery Bridge Dam, BGM = Burlingame) for fall-winter releases of PIT-tagged bull trout, 2008-2011. Predictions were based on Time fixed at 180 d and Length set to 288 mm.

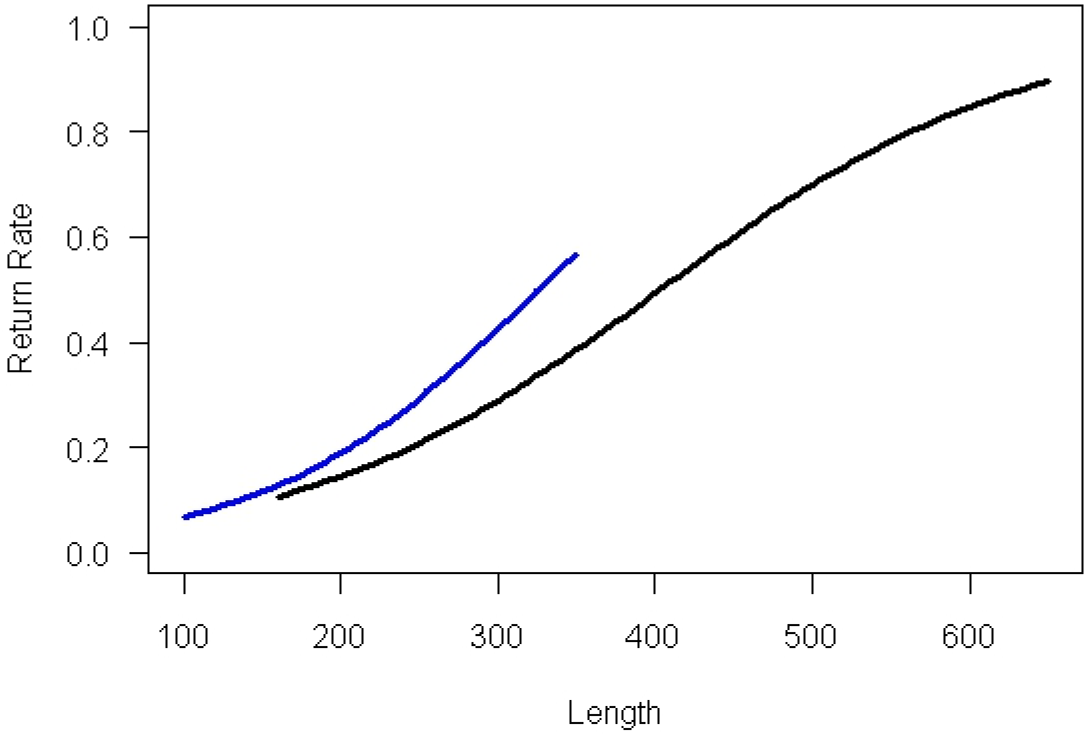

Figure 8.11. Model-averaged predictions of seasonal survival indices (i.e., return rates) versus length for fall-winter releases (black line) and spring-summer releases (blue line) of PIT-tagged bull trout, 2008-2011. Predictions were based on *Time* fixed at 91 d and *Site* set to Cemetary Bridge.

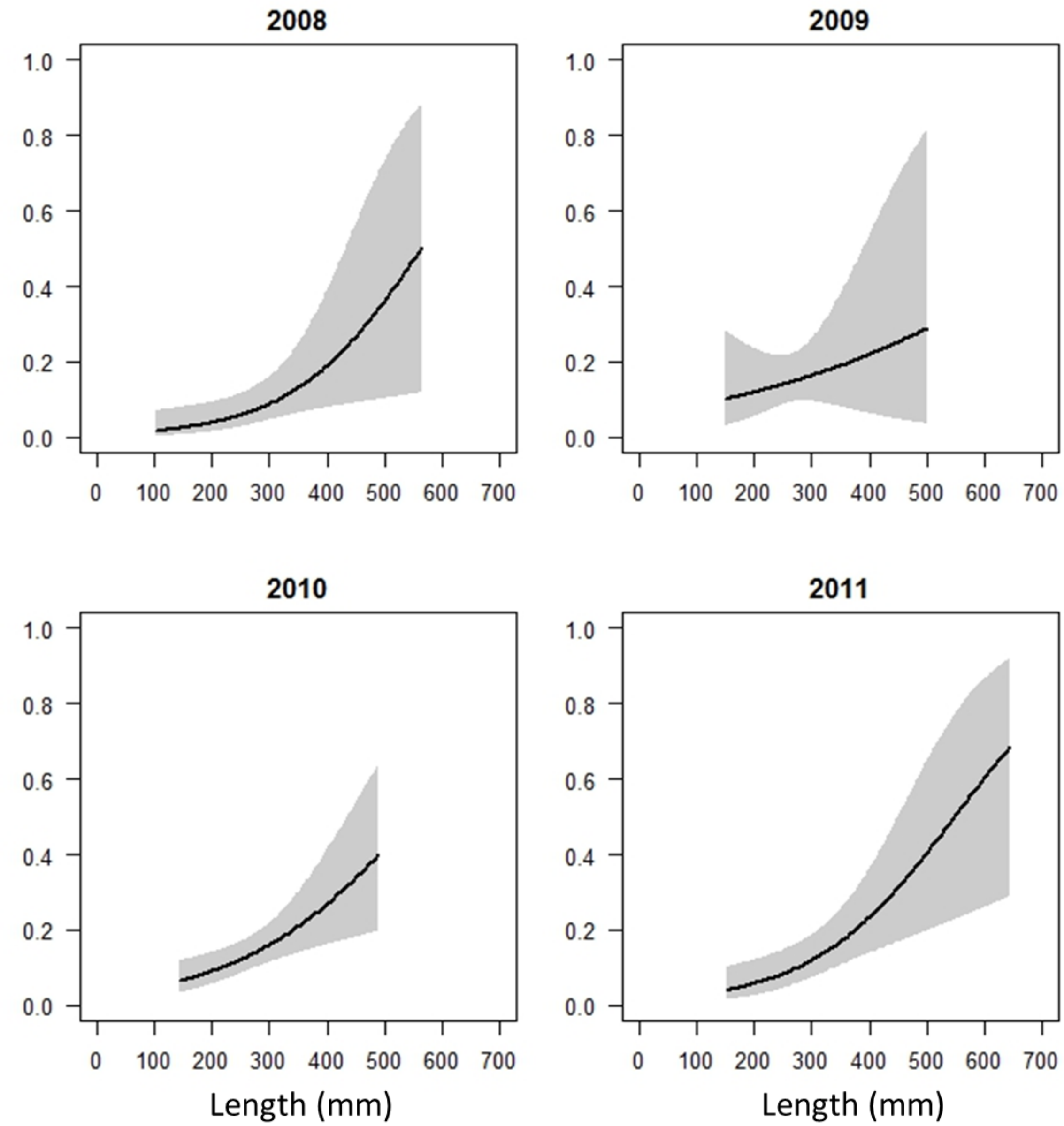

Figure 8.12. Model-averaged predictions of annual survival indices (i.e., return rates) versus length at tagging for lower Walla Walla River PIT-tagged bull trout, 2008-2011. Shaded areas represent 95% confidence intervals on the annual survival rates.

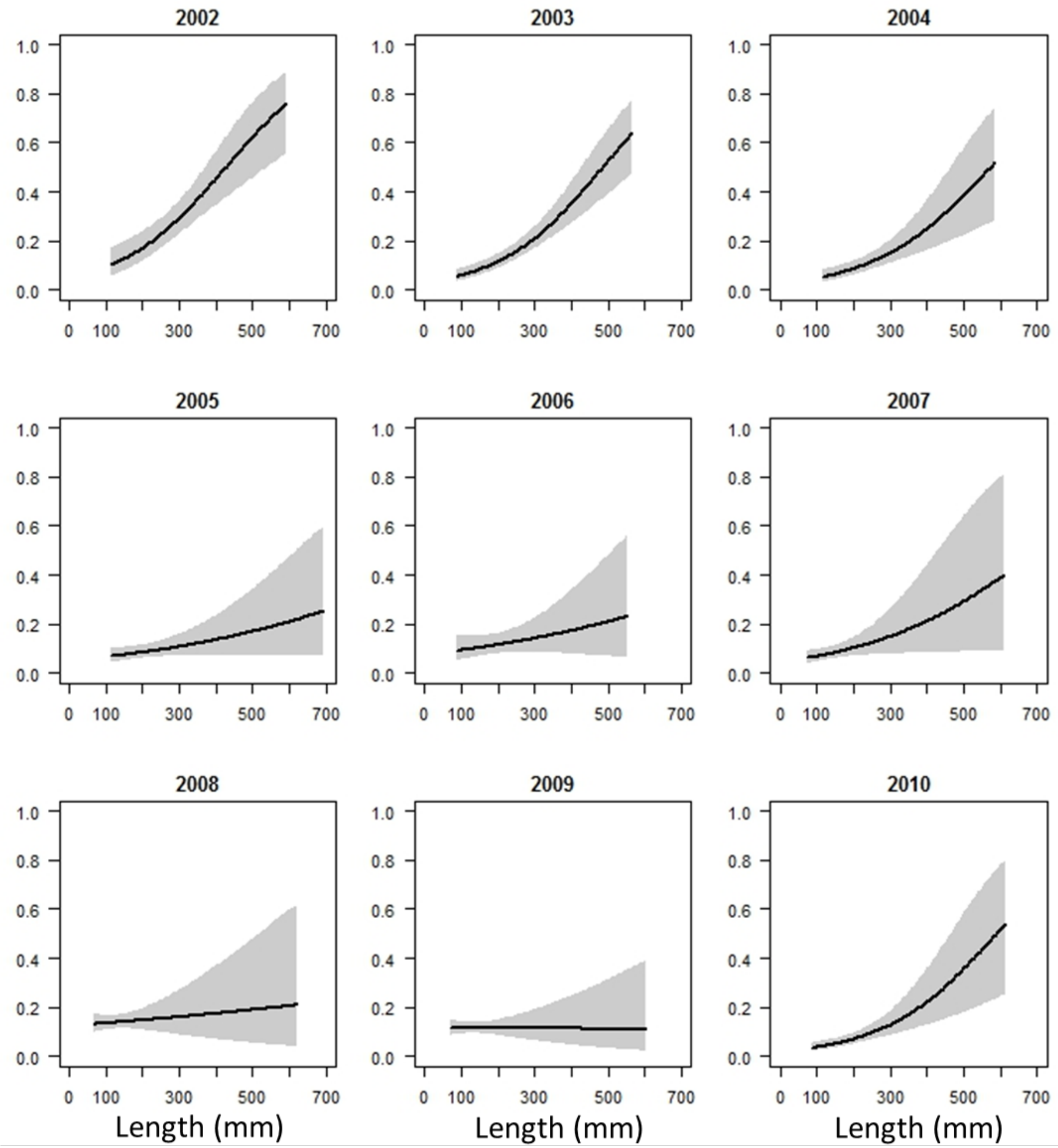

Figure 8.13. Model-averaged predictions of annual survival indices (i.e., return rates) versus length at tagging for South Fork Walla Walla River PIT-tagged bull trout, 2008-2011. Shaded areas represent 95% confidence intervals on the annual survival rate indices.

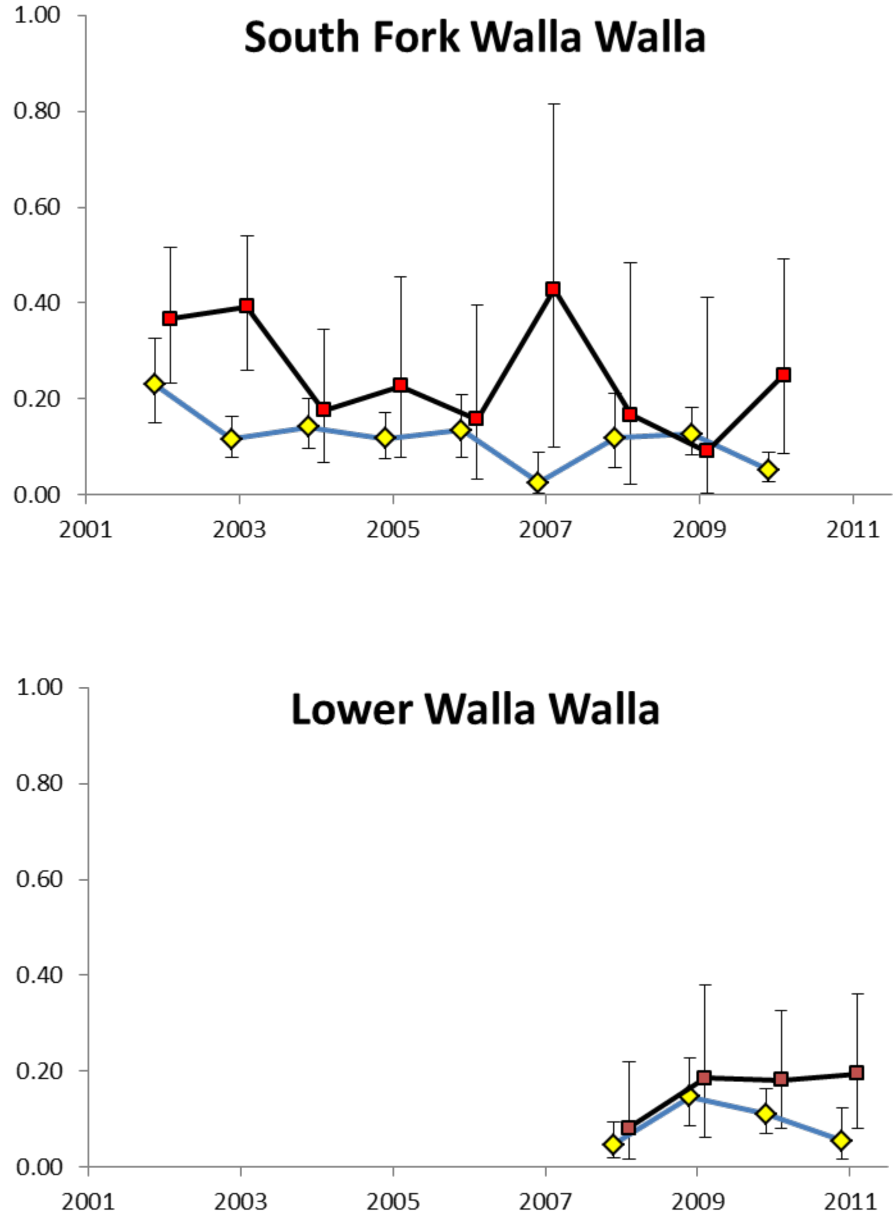

Figure 8.14. Binomial estimates of annual survival indices (i.e., return rates) for sub-adult (145-290 mm, yellow diamonds) and small adult (291-406 mm, red squares) size categories for South Fork Walla Walla River (2002-2010) and lower Walla Walla River (2008-2011) PIT-tagged bull trout. Whiskers represent 95% exact confidence intervals on the annual survival rates.

Chapter 9 : Conservation Implications of Multiple Life-history Strategies and Metapopulation Structure in a Stream Dwelling Char, Bull Trout

authored by

Tracy Bowerman
Phaedra Budy
Howard Schaller

Utah State University
U.S. Fish and Wildlife Service

Introduction

Conservation practitioners are often called upon to predict how populations will respond to management actions or environmental disturbances. Informed predictions require knowledge about local processes that affect birth and death rates, as well as landscape-scale factors that influence interactions with other populations via immigration and emigration. However, empirical estimates of specific demographic rates such as survival, fertility, and dispersal among populations are uncommon for many imperiled species, particularly those with multiple life stages and complex life histories (Heppell et al. 2000). When this information does exist, it can be used to populate detailed demographic models, which are valuable tools for endangered species recovery (Brook et al. 2000). Such models are often used to evaluate the relative contribution of specific demographic processes to overall population growth and to assess extinction risks for imperiled populations (Doak et al. 1994; Hiraldo et al. 1996). For example, stage-structured demographic models have been used to analyze the cause of decline in whale populations (Fujiwara and Caswell 2001), and to identify management actions to aid recovery of endangered woodpeckers (Heppell et al. 1994). Evaluation of vital rates within the context of life-history variation can also help ecologists better understand how population structure and life-history expression might affect population growth. For example, populations composed mostly of resident versus migratory individuals may vary considerably in their response to habitat loss (Bender et al. 1998).

Although management of endangered species often occurs at the population level, the long-term fate of many populations may ultimately depend on interactions with other populations (Brown and Kodric-Brown 1977). For species that occupy patchy or fragmented habitats, a complete understanding of factors limiting populations may entail evaluation of the connectivity among populations in addition to survival and reproductive rates within a population. The risk of extinction is often higher when populations are isolated, compared with when breeding individuals can move among populations (White 2000; Mills 2007). Conspecific populations that occupy discrete habitat patches and interact via dispersal can generally be defined as a metapopulation (Hanski and Gilpin 1991; Hanski and Simberloff 1997).

Salmonid fishes are among the many organisms thought to occur as metapopulations, and the spatial distribution of salmonid populations is an important consideration in conservation (Dunham and Rieman 1999; Gotelli 1999; Schtickzelle and Quinn 2007). Salmonids typically spawn in discrete patches of suitable habitat within a river system and are known to show site fidelity to their natal spawning patch (Dunham et al. 2001a; Isaak and Thurow 2006), but may occasionally stray and reproduce in another patch (i.e., dispersal). Like many other mobile organisms, the occurrence of stream-dwelling fishes may be related to habitat patch size and degree of isolation (Rieman and Dunham 2000; Dunham et al. 2001a; Koizumi and Maekawa 2004), suggesting that connectivity plays an important role in population persistence (Fagan 2002). Despite the relevance of metapopulation theory to research on salmonid populations, the concept has not been widely applied (Schtickzelle and Quinn 2007). A lack of empirical studies on metapopulation dynamics may be due in part to the difficulty of obtaining accurate estimates of dispersal among populations (Nathan et al. 2003; Schtickzelle and Quinn 2007).

We compiled life stage-specific demographic rates for a threatened stream-dwelling salmonid, bull trout *Salvelinus confluentus*, to evaluate population-level responses to environmental perturbations and to assess the role of connectivity in maintaining bull trout metapopulations. Bull trout, a species of char native to the northwestern United States and Canada, have complex life cycles and exhibit multiple life-history strategies (Rieman and McIntyre 1993;

McPhail and Baxter 1996). Bull trout are often categorized into two distinct life-history types, resident and migratory (Nelson et al. 2002; Howell and Sankovich 2012). Both resident and migratory life-history types spawn in cold headwater streams (Rieman and McIntyre 1993). Resident bull trout may spend their entire lives in natal rearing areas, where they grow slowly, and mature adults typically range from 140 to 300 mm in fork length (FL; Goetz 1989; Hemmingsen et al. 2001; Howell and Sankovich 2012). In contrast, migratory bull trout may remain in headwater streams with residents for several years before moving as far as 200 km downstream into larger rivers (fluvial life-history strategy), lakes (adfluvial strategy), or the ocean (anadromous strategy; Brenkman and Corbett 2005; Fraley and Shepard 1989). Migratory individuals generally overwinter in larger water bodies, and move upstream into headwater streams between June and October to spawn. Migratory bull trout typically mature at sizes greater than 300 mm FL and can exceed 800 mm FL (Goetz 1989; Johnston and Post 2009).

Despite general differences in behavior, growth, and size at reproduction among life-history types, the degree of life-history separation is more ambiguous in many systems where migration timing and distances can be highly variable (Downs et al. 2006; DuPont et al. 2007; Homel and Budy 2008). Growth rates and maturation timing can also differ greatly among individuals within a single system, as well as among populations (Al-Chokhachy and Budy 2008). This variability has led some researchers to suggest that life-history traits in bull trout can occur along a continuum, and that populations are likely to be composed of individuals that express different life-history strategies (Homel and Budy 2008; Homel et al. 2008). Due to diversity in bull trout behavior and biology, as well as the wide range of habitat used throughout the life cycle, well-informed management decisions rely on a complete understanding of the influence of specific demographic rates on the overall population growth rate, particularly within the context of life-history variation (Johnston et al. 2007).

On a larger spatial scale, conservation of bull trout populations will benefit from an understanding of how populations interact from both genetic and demographic perspectives. Bull trout are extremely philopatric, and genetic research indicates low rates of interbreeding between populations (Leary et al. 1993; Ardren et al. 2011). However, patterns of occurrence suggest that bull trout exist as metapopulations (i.e., core area populations), with migratory corridors in large, mainstem rivers connecting isolated spawning habitat patches located in headwater streams (Dunham and Rieman 1999). Current knowledge of dispersal rates between spawning habitat patches and the effect of dispersal on metapopulation dynamics is extremely limited. A greater understanding of how populations interact via dispersal, and the effect of physical barriers on those dispersal patterns, will help guide management of migratory corridors and define the spatial scale at which bull trout conservation should be considered.

To characterize the diversity in bull trout demography, we developed stage-based models to represent a range of life-history characteristics exhibited by different bull trout populations. We used these models to explore possible effects of natural or anthropogenic factors that influence particular portions of habitat or specific life stages, and evaluated the population-level and metapopulation response to such changes (Figure 9.1). The intent of this study was to use available data on bull trout demographic rates to characterize populations and to explore potential effects of environmental changes on bull trout population viability. Within this framework, we had four primary objectives. Our first objective was to develop life-stage-specific demographic models based on empirical vital rate estimates to describe different bull trout life-history types. Second, we assessed the relative sensitivity of bull trout populations to changes in specific demographic parameters. To evaluate the importance of stream connectivity for bull trout, our third objective was to estimate dispersal rates among populations and use this to model metapopulation processes. Finally, we evaluated some potential responses of a metapopulation to changes in dispersal, survival, and growth rates that might result from management actions or climate change.

Methods

Primary data sources and study area

We developed demographic models to describe individual populations and a combined metapopulation based on data from three bull trout populations within the Walla Walla River basin, located on the border of Oregon and Washington: the South Fork of the Walla Walla River (SFWWR), Mill Creek (MC), and the Touchet River (TR; Figure 9.2). Spawning and rearing for each population occurs in headwater tributaries to the Walla Walla River (WWR), and these headwater areas are considered distinct spawning habitat patches (Dunham et al. 2001a; Rieman and McIntyre 1995).

Prior to this study, bull trout from all three populations had been observed migrating throughout the Walla Walla basin, but rates of dispersal among individual populations had not been quantified (Anglin et al. 2008). Genetic comparisons among populations in the basin suggest low levels of genetic exchange (Kassler and Mendel 2007). As such, we hypothesized that bull trout populations within the Walla Walla basin effectively operate as a metapopulation with limited dispersal among all three populations. Current rates of movement and survival throughout the basin may be lower than historic rates due to habitat degradation in migratory corridors in the form of dams, low streamflow during summer months, channel homogenization, and other anthropogenic changes concentrated in lower portions of the watershed.

We estimated vital rates for the population models based on ten years of capture-mark-recapture (CMR) data from the MC and SFWWR populations. In both systems, we marked bull trout with unique passive integrated transponder (PIT) tags, and subsequently recaptured fish via systematic sampling and at several trapping locations (Figure 9.2). We collected additional resight data at stationary passive in-stream antennas (PIAs) located throughout MC, SFWWR, and the mainstem WWR (more detailed descriptions of the system can be found in Howell and Sankovich 2012 and Al-Chokhachy and Budy 2008). We used both active recaptures and passive resights of marked fish to inform vital rate estimates, and henceforth refer to a combination of the two as “detections.”

To represent the complex life cycle of bull trout given the amount of available data, we defined seven life stages based on a length-at-age relationship for bull trout (Table 9.1; see Appendix B for details describing the length-at-age relationship). Based on data from the SFWWR bull trout population, stages corresponded approximately with age. We determined the composition of life-history types for each of the three populations in the Walla Walla basin according to the percentage of marked individuals exhibiting migratory traits and behavior. The population of bull trout in MC is considered mostly migratory, as females typically mature at lengths greater than 300 mm FL and large mature females (e.g., >300 mm FL) have not been observed in spawning areas outside of the spawning season (Howell and Sankovich 2012). In contrast, the SFWWR population is comprised of both migratory and resident bull trout. Large adults exceed lengths of 700 mm total length (TL) and many make long spawning migrations, while others mature at small sizes (200 mm TL) and are not observed downstream of spawning areas (Al-Chokhachy and Budy 2008; Homel and Budy 2008). Monitoring data suggests that the SFWWR bull trout population is composed of approximately 70% fish that exhibit migratory behavior at some stage in their life cycle, and 30% that do not (Budy et al. 2010). To maintain consistent terminology, we called this combination of both migratory and resident life-history strategies a "mixed" life-history type (LHT). Observations of fish size and movement suggest that the TR population is also a mixed LHT (Mendel et al. 2003), but because the proportion of fish exhibiting migratory versus resident behavior is unknown, we used the same mixed LHT model developed for the SFWWR population to also describe the TR population.

Vital rate estimates

We used data from MC and SFWWR bull trout populations to estimate the number of eggs per female, spawning probability, and growth and survival rates for each life stage. We established a standardized relationship between female length and number of eggs from 22 sacrificed mature females between 205 and 674 mm TL. We then determined the number of eggs per female for each life stage based on the median length of each stage (Morris and Doak 2002). We estimated stage-specific spawning probabilities from the ratio of marked fish in each stage that made a spawning migration relative to the total number of marked fish that were detected anywhere in the watershed in a given year. That is, if individuals moved upstream into spawning areas during the summer and downstream in the fall, we considered that a spawning migration (although we could not determine if individuals spawned successfully). We compared the number of fish that exhibited this spawning pattern with the number of fish that were detected during that same year but showed no clear seasonal movement pattern. Estimates of spawning probability for resident fish were unavailable in the literature, so we assumed spawning probabilities similar to those observed for migratory fish, adjusted to describe a population that can reach sexual maturity at 140 mm FL and where individuals typically do not exceed 300 mm FL (Rieman and McIntyre 1993; Howell and Sankovich 2012). Observations of the number of redds compared to the number of mature females in a nearby resident population supported this assumption (Moore et al. 2006).

To estimate stage transition rates, we calculated the proportion of marked survivors from a given stage during one year that grew into another stage in the following year (Morris and Doak 2002). Due to low sample size, we combined annual recapture data from all ten years of the study. We estimated transition rates for all stages of the SFWWR population, but data were unavailable for several stages in both the TR and MC populations. As such, we used estimates of stage-5 and -6 transition probabilities from the MC population to describe transition rates for the migratory LHT, and estimates from the SFWWR as a baseline for all other life stages in both mixed and migratory demographic models. To represent slow growth rates exhibited by the resident LHT, we assumed much lower transition probabilities for all stages except stage 1, when all three LHTs occupy the same habitat.

We estimated survival rates for each of the six largest size classes (stage 2 through stage 7+) from 10 years of CMR data in the SFWWR. We used the Barker model implemented in Program MARK (White and Burnham 1999) to estimate mean survival over time for each of the stages, which we modeled as separate groups. We applied Markov Chain Monte Carlo simulations within a Bayesian framework to analyze a random effects model, with survival estimated on the logit scale and time treated as a random effect (White et al. 2009). We used minimally informative prior distributions for all parameters and retained 10,000 samples from the posterior distribution to estimate the mean survival rate and temporal process variance for each of the six stages (see Appendix B for details). A variance components approach is the preferred method for estimating vital rates in a population viability analysis, as it should provide the least biased estimates of mean survival, as well as isolate process variance from sampling variance (White 2000). We used mean estimates of survival from this analysis in all population models.

We used estimates of process variance (σ^2) in stochastic models to represent biological variation due to temporal differences in survival.

We did not have enough years of data to estimate survival of stage-1 bull trout in the same manner, so we used estimates from the literature (Bowerman and Budy 2012). These estimates were based on only 3 years of data, so temporal variance was not estimable. We therefore used the same estimate of variance from the next larger stage (σ = 0.205), as survival rates were similar between these two size classes (Bowerman and Budy 2012).

Life-history-specific demographic models

We used vital rates described above to develop a stage-based, pre-breeding Lefkovitch matrix model to describe the bull trout life cycle that represented only the female portion of the population (Figure 9.3; Caswell 2001). Initially, we developed a life-cycle model to describe the mixed LHT of the SFWWR population, for which we had empirical estimates to describe nearly every life-history parameter. We then altered parameters within the model to represent what we know about resident and migratory life-histories (Rieman and McIntyre 1993; Howell and Sankovich 2012), and included vital rate estimates from the migratory MC population when possible. In the model for the migratory LHT, individuals matured in stage 5 (> 300 mm TL), had high transition probabilities corresponding with rapid growth rates (e.g., 50-120 mm·year^{-1}), and could reach ages 10 or older (Figure 9.3). The mixed LHT model described a population in which individuals matured between stages 2 and 6, transition probabilities were intermediate, and individuals could reach ages of 8 to 10 years. In contrast, the resident LHT matured as early as stage 2 (> 155 mm TL), had low transition probabilities (e.g., growth rates of 15 to 50 mm·year^{-1}), rarely exceeded 300 mm TL, and reached ages of 8 to 10.

In this study, we developed a model representative of a population with decreasing abundance, as has been observed for bull trout populations of concern (Rieman et al. 1997). We developed base models with a declining population growth rate (λ), with λ = 0.931, a recent estimate based on seven years of CMR data from the SFWWR population (Budy et al. 2010). To represent declining populations, we developed models with conservative levels of survivorship and growth, relative to other estimates in the literature (Pratt 1992; Al-Chokhachy and Budy 2008). Survival and growth probabilities were represented in the matrices by P_i, the probability of surviving and staying in the same stage the following year, and G_i the probability of surviving and moving to the next stage such that $P_i = \hat{s}_i(1-\hat{\gamma}_i)$ and $G_i = \hat{s}_i\hat{\gamma}_i$,where $\hat{s}_i$ is the survival probability and $\hat{\gamma}_i$ is the probability of an individual transitioning from stage *i* to *i*+1 (Caswell 2001). Because temporal variance was associated with $\hat{s}_i$, we apportioned variance between the two survival parameters by multiplying P_i and G_i by the coefficient of variation (CV) associated with each $\hat{s}_i$ (Morris and Doak 2002). All three LHT models included the same estimates of stage-specific survival, but for all stages beyond stage 1, transition rates were greater for the migratory LHT, and considerably lower for the resident LHT, resulting in different estimates of P_i and G_i. Estimates for the mixed LHT were representative of a population with approximately 70% migratory and 30% resident individuals.

We estimated the fertility rate as the number of female offspring produced by a mature female bull trout in each stage *i* that survived to stage 1, as

$$F_i = m_i B_i R S_{egg} S_0,$$

where m_i (fecundity) indicates the average number of eggs produced by a female of the median length for each stage *i*, B_i is the probability of spawning for a female in stage *i*, *R* is the ratio between sexes (assumed 0.5), S_{egg} is the probability of survival between egg deposition and fry emergence, and S_0 is the probability of survival from fry emergence to stage 1 (60 mm TL). We used data from an experiment which evaluated bull trout egg survival in a natural stream to estimate S_{egg} based on the mean egg-to-fry survival rate for eggs reared in incubation capsules in which the sediment composition approximated that of the surrounding redd, as we expected these estimates to be the most representative of natural conditions (Bowerman et al. 2014). Estimates of age-0 survival are lacking for bull trout, so we back-calculated this vital rate after all other life stages had been assembled in the population matrix (Morris and Doak 2002). We set the dominant eigenvalue (the asymptotic population growth rate) equal to λ=0.931 and solved for the unknown parameter, S_0. To assess the validity of S_{egg} and S_0 estimates, we compared them with estimates for other salmonid species in the literature. We assumed consistent rates of S_0 and S_{egg} among the three LHTs, and only m_i and B_i varied among types according to size and length at maturity.

Asymptotic sensitivity analyses

To evaluate the relative effect of changes to individual vital rates on overall population growth rates among the three LHTs, we calculated elasticity and sensitivity values for each, based on an asymptotic λ, assuming a stable stage distribution. Elasticities describe the proportional change in λ resulting from a proportional change in each vital rate independently (Caswell 2001). Elasticity values account for the differences in scale between survival probabilities and fertility rates, and provide a means to assess the relative effect of changes to a single vital rate on the overall population growth rate (Heppell et al. 2000). The sensitivity of λ with respect to a change in an individual vital rate describes the absolute change in the finite rate of population growth resulting from a change in a given vital rate. To examine sensitivity values, we estimated λ across the range of each vital rate (from 0 to 1 for probabilities and from 0 to 200 for fertility values), while holding all other vital rates constant (Morris and Doak 2002). This sensitivity analysis allowed us to evaluate λ within a range of biologically feasible values of each vital rate and assess nonlinear responses in λ to changes in vital rates. We also compared the change in λ relative to specific matrix elements among the three LHTs.

Dispersal rate estimation

Dispersal events for bull trout are infrequent and thus difficult to observe, resulting in a paucity of true long-distance movement and dispersal data (Dunham and Rieman 1999; Nathan et al. 2003). We therefore compared estimates of dispersal based on empirical data to a more general dispersal kernel and to a metric of genetic exchange between populations. This comparison helped us validate our observations, and genetic information allowed us to assess the assumption that movement from one patch to another represented successful dispersal.

First, we estimated dispersal rates based on mark-recapture observations of individuals marked in one spawning patch that were later detected in a different patch during the spawning season. We then calculated a rate by comparing this number to the total number of marked individuals detected again anywhere in the Walla Walla basin. We compared these dispersal rate estimates to estimates generated from a dispersal kernel that models a decrease in the probability of successful dispersal as the distance between populations increases (Fullerton et al. 2011; Schick and Lindley 2007). The dispersal kernel can be described by

$$M_{ij} = \frac{1}{2\alpha}\exp(\frac{-D_{ij}}{\alpha}),$$

where M_{ij} represents the probability of an individual dispersing from spawning patch *i* to patch *j*, α is the maximum dispersal distance (150 km), and D_{ij} is the linear stream distance in km between the two spawning patches.

We also used a genetic approach to assess the relative degree of connectivity among populations in the Walla Walla basin based on an indirect metric of gene flow described as the average number of migrants per generation. We used pairwise F_{st} values estimated from 15 microsatellite loci from individuals in each of the three Walla Walla basin populations (Kassler and Mendel 2007) to assess the average number of migrants per generation (*Nm*; i.e., successful dispersers). Assuming the island model of migration (Allendorf and Luikart 2007),

$$N_m \approx \frac{1-F_{st}}{4F_{st}} \ .$$

As F_{st} is a measure of allele frequency divergence among subpopulations, pairwise F_{st} values are likely to reflect both current and historic gene flow (Mills 2007). For this reason, and because estimation of N_m hinges upon a number of assumptions, these estimates should not be viewed as direct measures of dispersal, but rather can be used as a relative assessment of long-term genetic interaction between populations (Allendorf and Luikart 2007; Mills 2007).

Population capacity based on spawning habitat

Many populations are regulated by density dependent factors, which limit population growth as abundance increases, and it is important to include such biological limitations in population models (Ginzburg et al. 1990). However, for most bull trout populations, there are insufficient data with which to estimate a carrying capacity (but see Johnston and Post 2009). To represent territoriality exhibited by bull trout and limitations on available spawning sites, we established a carrying capacity function to approximate the maximum potential number of redds in each spawning patch based on physical habitat attributes and used this as a ceiling function in population models (Figure 9.1). First, we used 16 years of redd count data from the three Walla Walla bull trout populations (Mahoney et al. 2011) to designate stream reaches in one of four spawning habitat categories based on average redd densities: no spawning, low density mainstem, high density mainstem, and spawning tributaries. Next, for all stream kilometers within the Walla Walla basin, we compiled physical habitat characteristics estimated from 1:24,000 hydrography provided by StreamNet and summarized in Mobrand Biometrics' Ecosystem Diagnosis and Treatment (EDT) analysis (see http://www.nwcouncil.org/edt/ for data and additional information). All environmental variables were taken directly from the Stream Reach Editor and applied in GIS at the scale of stream reaches, which ranged from 0.1 to 8 km in length.

We used classification and regression tree (CART) analysis in the tree package in R 2.13.0 (Ripley 2012) to evaluate the relationship between spawning habitat category and predictive environmental variables. We evaluated habitat variables that had previously been associated with bull trout distributions, such as elevation, channel slope, and maximum summer temperature (McCleary and Hassan 2008; Wenger et al. 2011). We also included variables that we hypothesized might affect spawning habitat availability at a smaller spatial scale (e.g., percent pools, scour). We used results from the CART analysis to establish discrete break-points for continuous predictor variables (e.g., elevation) and to define a rule set for each of the spawning habitat categories based on physical habitat measurements. We applied the rule set to the entire Walla Walla basin to predict the total amount of spawning habitat in each category in each of the three spawning patches. We also calculated the length of stream within each category in spawning survey index reaches (the portions of each spawning habitat patch where spawning surveys are conducted annually to evaluate population trend). We used the 90th percentile of redd densities observed in each spawning habitat category as the redd capacity for that category. We then estimated the maximum number of redds (total spawner capacity; *K*) expected for the spawning index reaches within each patch based on

$$K = \sum_{h}^{n}(L_h * D_L),$$

where *L* indicates the length of a stream reach, *D* is the maximum spawning density, and *h* represents the specific habitat type (Bartz et al. 2006).

Stream temperature change

Based on recent evidence of widespread stream temperature increases over the past two decades in the Western U.S., and the potential for accompanying shifts in species distributions (Isaak et al. 2011), we assessed potential changes to available bull trout habitat within the Walla Walla basin as a result of stream temperature warming (Figure 9.1). We used water temperature measurements taken at four different sites along the profile of the SFWWR to estimate a stream temperature lapse rate, or the average rate of temperature change along the elevational gradient of a stream (°C·100 m^{-1} elevation increase; Isaak and Rieman 2013). We then used the stream lapse rate of 0.5 °C·100 m^{-1} calculated for the SFWWR in conjunction with channel slope and projected long-term rates of stream warming to estimate the rate at which stream temperatures could gradually increase along the longitudinal profile of the stream. The expectation is that as water temperatures increase, the physical location representing a particular temperature threshold will track upward in elevation (Isaak and Rieman 2013). We predicted the rate at which this temperature boundary, or stream temperature isotherm, would shift in the upstream direction based on an equation from Isaak and Rieman (2013):

ISR = (stream warming rate/lapse rate)/sin(channel slope),

where ISR is the isotherm shift rate (km/decade). We evaluated potential ISRs based on a range of long-term stream warming rates ranging from 0.1 to 0.3 °C per decade and for a range of channel slopes. Changes in stream temperature of this magnitude are consistent with those observed in western streams over the past three decades (Isaak et al. 2011).

To apply stream warming rates to capacity function predictions, we assumed that current downstream spawning and rearing distributions for bull trout are currently limited by a critical temperature threshold represented by a temperature isotherm. As stream temperatures warm, we assumed that the downstream boundary of bull trout distributions will move upstream at the rate predicted by the ISR equation, depending upon channel slope. We applied ISRs estimated from the SFWWR to the known distribution of spawning habitat in all three patches within the Walla Walla basin, based on an average stream slope of 2% and 3% for low and high density mainstem habitat, respectively, and 5% for spawning tributary habitat (stream slope data from EDT analysis, Mobrand Biometrics). We used ISRs to predict how far upstream a temperature isotherm could move over the next 25 years. Under the assumption that bull trout distributions will track the temperature isotherm, we estimated the changes in stream length available for spawning within the three patches and within spawning index reaches only. As bull trout distributions appear to be limited by stream size in the upper portions of stream systems, isotherm shifts resulted in habitat loss. Based on these new estimates of available habitat, we then predicted the change in total spawner capacity based on index reaches in the MC, SFWWR, and TR populations over the next 25 years. We modeled population change over a 25 year time span because this is the time frame over which many temperature models are more accurate, and because it is a time frame relevant to many management decisions.

Metapopulation viability assessment

We developed a spatially explicit metapopulation model composed of three distinct bull trout populations within the Walla Walla basin (Figure 9.1). We used the mixed LHT model used to describe the SFWWR and TR populations and the migratory LHT model to describe the MC population. We estimated the initial abundance for each population based on the average number of redds counted during annual surveys of index reaches in each of the three spawning patches between 1996 and 2008 (Figure 9.2). To produce initial population vectors, total spawner abundance was distributed among stages according to the stable stage distribution multiplied by the probability of spawning for each stage. As such, initial population sizes in simulations represented the number of breeding females in spawning survey index reaches only. We used this metric in metapopulation simulations because redd counts are a common measure of bull trout population abundance and trend (Dunham et al. 2001b; Al-Chokhachy et al. 2005), and because changes in spawner abundances would not be observed unless they occurred within index reaches.

We projected future population size with an annual time step based on

$$N_{i(t+1)} = \mathbf{A}N_{i(t)} - \sum M_{ji}N_{i(t)} + \sum M_{ij}\, N_{j(t)}$$

where **A** is the population projection matrix, and $N_{i(t)}$ is a vector of abundances of individuals in each life stage in population *i* in one year, $N_{i(t+1)}$ is the abundance in each stage of the population in the following year, $\sum M_{ji}N_{i(t)}$ is the total number of dispersers emigrating from patch *i* to all other populations *j*, and $\sum M_{ij}\, N_{j(t)}$ is the total number of dispersers immigrating into patch *i* from all other patches *j*. Dispersing individuals were drawn only from reproductive adult stages (stages 5 through 7), as only reproductive migratory adults were assumed to disperse.

For population simulations, we assumed a declining growth rate of $\lambda = 0.931$ in the base model for all populations, and as such, we considered future projections conservative, or worst-case, outcomes. Based on population trend data, this asymptotic growth rate may represent the gradual decline reported in many bull trout populations (Rieman and McIntyre 1993; Rieman et al. 1997). For all scenarios, we included demographic stochasticity by sampling the number of survivors and dispersers from binomial distributions, and the number of age-1 individuals produced at each time step from a Poisson distribution (Akçakaya 2000). We also included environmental stochasticity by sampling survival probabilities from a normal distribution based on estimated mean and variance (σ) for each life stage from our survival analysis, and sampled fertility probabilities from a normal distribution with a mean estimate for each stage, and a naïve estimate of variance (σ = 0.1). We used estimates of maximum spawning capacity as a ceiling for adult abundance in each population, but because we were modeling populations with a long-term declining trend, we did not include other density-dependent effects (Ginzburg et al. 1990). We projected each scenario over 25 years to estimate the probability of the metapopulation declining by a percentage of its current size. We ran 1,000 simulations of each scenario and included variance for each matrix parameter to model environmental stochasticity.

We ran a series of stochastic population simulations in the program RAMAS Metapop to evaluate the potential effects of dispersal rates, management actions, and climate change on long-term persistence of the three individual populations within the Walla Walla basin and the metapopulation as a whole (Figure 9.1). We investigated the hypothesized effect of two management actions: (1) increased survival of stages 3 and 4 by 10% of current values to represent improved sub-adult feeding and rearing habitat, and (2) increased survival of the two largest stages by 10% as a result of improved passage conditions (e.g., removal of barriers to facilitate migration between habitats). We also hypothesized three potential effects of climate change on vital rates.

First, we modeled a decrease in survival of bull trout eggs and alevins by 20% of current estimates to simulate increased scour or sedimentation of redds during embryo development as a result of an earlier peak in the hydrograph (Mantua et al. 2010; Shellberg et al. 2010; Bowerman et al. 2014). Second, we increased juvenile bull trout growth rates by 10% of current rates based on the hypothesis that increased temperatures in headwater areas would be more optimal for growth, assuming that stream productivity also increased concurrently (Zuo et al. 2012). Third, we decreased sub-adult growth rates by 10% under the hypothesis that warmer water temperatures in lower-elevation rearing areas would increase past optimal temperatures for growth. These assumptions were based on bioenergetic measurements of optimal growth and consumption relative to water temperature (Selong et al. 2001; Mesa et al. 2013). To incorporate changes in growth into our models, we altered individual growth rate measurements from recapture data by the specified percentage and then re-calculated transition probabilities. We also ran scenarios in which we combined all climate and management scenarios simultaneously. Percent changes to vital rates represented modest modifications within the 95% confidence intervals of all estimated rates.

To evaluate the effect of dispersal rates on population persistence, we calculated the probability of decline for each of the three populations within the Walla Walla basin, and the metapopulation as a whole, under two different possible scenarios. First, we increased the rate of dispersal between 0 and 0.1 for the base model (all three sub-populations declining; λ = 0.931). Next, we evaluated the effect of the same range of dispersal rates given a scenario in which all populations were subject to the combined effects of climate change (decreased egg survival and sub-adult growth, and increased stage-1 growth). In the latter scenario, management actions were applied to the SFWWR and TR populations (λ = 0.983), but not to the MC population (λ = 0.927). Dispersal rates were selected to represent a range of migration gradients ranging from populations that are completely isolated, to populations with a very high degree of connectivity (10% of adults in each population disperse).

Results

Bull trout vital rates

Sexually mature fish examined in the SFWWR ranged from 205 to 674 mm TL, and the oldest fish aged was 10 years old (supplementary material Figure 8B.1). The relationship between female length and the number of eggs was described by

$$N_{eggs} = 0.0084TL^{2.032},$$

where N_{eggs} is the number of eggs per female, and *TL* is total length in mm (supplementary material Figure B8.2). Based on this relationship, the predicted number of eggs per female of the median size in each class ranged from 227 for stage 2, to 3184 for a 550 mm TL fish (Table 9.2). As there was no terminal length for the largest stage, we estimated the number of eggs for stage 7 based on the average length of captured fish larger than 420 mm in the SFWWR (500 mm TL) for the mixed LHT, and we assumed a slightly larger median size for the migratory LHT (550 mm TL).

In the SFWWR, we observed 124 fish that made distinct spawning migrations, most of them on consecutive years. The proportion of bull trout that made a spawning migration relative to the number detected ranged from 0.05 for stage 3 to 0.7 for stage 7 (Table 9.1; Supplementary material Table B8.2). We considered these estimates conservative owing to incomplete detection probability of migrants and a bias against observing spawning migrations for resident fish. As research suggests that the majority of bull trout in many systems spawn annually (Downs et al. 2006; Johnston and Post 2009; Budy et al. 2010), we used our observations as a conservative baseline for model simulations and increased the spawning probability to 0.9 for the largest stages (Table 9.2).

Annual growth rates for fish recaptured throughout the Walla Walla basin varied greatly among stages, locations, and individual fish. Growth rates ranged from no change in length to an increase of 106 mm in a year (66% of initial length). Growth rates were typically greatest for stages 3 through 5, but there was substantial variability within and among stages, and among populations (supplementary material Figure B8.3). Data from the SFWWR showed that the majority of fish in stages 1 through 4 transitioned into the next stage each year, whereas fish were more likely to remain in stages 5 and 6 for more than one year (Table 9.1; Appendix Table B8.3a). Compared with observations from the SFWWR, recaptured adult bull trout in MC exhibited higher average growth rates and were more likely to transition from stages 5 and 6 into larger stages each year (Table 9.1; Appendix Table B8.3b). The probability of a fish in stage 5 transitioning into stage 6 the following year was 0.3 in the SFWWR compared with 0.83 in MC, and the transition probability from stage 6 to 7 was 0.2 in SFWWR compared with 0.76 in MC.

Mean estimates of annual survival rates across ten years indicated that survival generally increased as bull trout got larger, ranging from estimates of 0.26 for stage-2 fish to 0.47 for stage-7 fish (Table 9.1). Annual survival estimates varied among years, but were the most consistent for stages 5 and 6, and the most variable for stages 2 and 7 (Table 9.1; Appendix Table B8.4). Estimates of temporal process variance (σ) ranged from 0.048 to 0.205, with the highest estimates of variance for stages 2, 4, and 7 (Table 9.1; Table B8.4).

Sensitivity of population growth rate to changes in vital rates

The relative contribution of individual vital rates to overall population growth varied among migratory, mixed, and resident life-history types. For all three LHTs, matrix elements representing sub-adult survival and transition (G_1 and G_2 for all types, in addition to G_3 and G_4 for the migratory LHT) had the highest elasticity values, indicating that survival of pre-reproductive life stages had the greatest proportional contribution to overall population growth (Figure 9.4). Fertility and survival elasticity values for the largest stage were the highest for the migratory type compared with the other LHTs, demonstrating a greater relative contribution of large individuals to overall population growth. In comparison, elasticity values for fertility and the probability of surviving in remaining in the same stage were the highest in stages 2 and 3 for the resident LHT because of slow growth rates and early size at reproduction (Figure 9.4). Elasticity values were relatively more uniform among fertility and adult survival matrix elements for the mixed LHT, reflecting a population structure in which survival and fertility were more evenly distributed across numerous life stages (i.e., more life stages contributed to offspring compared with other LHTs).

Elasticity values represent a proportional change in λ resulting from a proportional change in a vital rate and as such, can be summed together to evaluate the total contribution of a portion of the life cycle. When we summed elasticity values across stages, juvenile survival had the largest proportional contribution to population growth for all LHTs compared with adult survival and fertility (Figure 9.5). However, among LHTs, fertility had the greatest influence on λ for the resident LHT, whereas adult survival had the greatest influence on λ for the migratory LHT. Once again, elasticity values for fertility and adult survival for the mixed LHT was intermediate between the other two.

For each of the LHTs, we illustrate the relative effect of changing representative individual matrix elements on population growth rates across a range of values while holding all other matrix elements constant (Figure 9.6). A line with a steeper slope indicates a greater response of λ to changes in a matrix element. For example, although values of juvenile survival (G_1) were equivalent for all population types, a stable population growth rate (λ = 1) could be reached by increasing G_1 to 0.27 (27% increase) for the resident LHT, to 0.30 for the mixed LHT (43% increase), and to 0.34 for the migratory LHT (62% increase; Figure 9.6 upper panel). In comparison, increased survival of the largest adult stage (largest P) would have a relatively greater influence on λ for the migratory population (Figure 9.6 lower panel). In both examples, the response of the mixed life-history type fell between that of the migratory and resident. Exploring sensitivity values in this manner also demonstrates that increased survival within the 95% credible intervals for the largest stages would not be sufficient for any of the three LHTs to reach a stable population growth rate ($\lambda \approx 1$).

Dispersal rates between populations

Over a ten year period, we observed 33 marked bull trout migrate distances greater than 70 km, and 9 fish traveled farther than 100 km. During this time, two marked individuals from the MC population made spawning migrations into the SFWWR population, and one individual from the TR population migrated into the MC population during spawning. We considered each of these fish successful dispersers. Based on the total number of marked fish that were resighted during the study, the proportionate estimate of dispersal was 0.0052 from MC to SFWWR, and 0.0098 from TR to MC over a 7-year period (Table 9.3a).

Dispersal rates calculated using the dispersal kernel function were 0.0021 between MC and SFWWR populations, 0.0014 between SFWWR and TR, and 0.0015 between MC and TR (Table 9.5b). These dispersal rates were based on distance between spawning patches, and thus, the same rate applied in both directions, even though the potential for dispersal may be greater in one direction than the other.

Based on the general metric from pairwise F_{st} values, we estimated approximately 4 migrants per generation between SFWWR and MC, 3 between SFWWR and TR, and 2 between MC and TR (Table 9.3c). As with the distance function, direction of travel could not be inferred. All three metrics of connectivity suggested similarly low levels of dispersal (e.g., approximately 2 to 6 individuals per generation) among the three populations of bull trout in the Walla Walla basin.

Carrying capacity of spawning habitat

The best predictors of bull trout spawning habitat type were elevation, stream gradient, stream width, and maximum summer temperature. The CART model that included the first three variables had an 86% overall classification success rate, and we included maximum summer temperature post-analysis to distinguish between the remaining sites where spawning had been observed (Table 9.4). In the Walla Walla basin, bull trout spawned at elevations above 700 m, and no spawning was observed where stream gradients exceeded 7.45%. These criteria defined the lower and upper boundaries of most spawning areas in the watershed, respectively. Stream gradient was an important criterion for categorizing all habitat types, and width was used to distinguish between small tributaries and high density mainstem habitat. Based on the defined rule set, we estimated a total of 45 km of spawning habitat in the SFWWR, 22 km in MC, and 43.7 km in the TR under current conditions (Figure 9.7 left panel; Table 9.5b). When only the spawning survey index reaches were considered, total available stream length was 11.9, 17.6, and 22.0 km for the three respective populations (Table 9.5c). The current estimated maximum redd capacity estimated in index reaches was 478 for the SFWWR population, 395 for the MC population, and 690 for the TR population (Table 9.5d).

Stream isotherm shifts and predicted loss of spawning habitat

According to one recent study, streams in the interior Columbia Basin have been warming at a rate of approximately 0.17 °C·decade^{-1} over the past 20 years (Isaak et al. 2011). Based on this rate of warming, we estimated isotherm shift rates of between 1 and 1.6 km·decade^{-1} for spawning habitat in the Walla Walla basin, for reaches with channel slopes of 3 and 2%, respectively, and 0.63 km·decade^{-1} for streams with a 5% slope (0.15 °C·decade^{-1}; Table 9.5a). Under projected accelerated stream warming rates of 0.2 to 0.3 °C·decade^{-1}, isotherms could shift upstream as rapidly as 2 to 3 km·decade^{-1} in spawning areas with 2% slopes, and 1.4 to 2 km·decade^{-1} for stream sections with 3% slopes. Isotherms in bull trout spawning tributaries with steeper slopes (e.g., 5%) would likely shift more slowly (0.8 to 1.25 km·decade^{-1}).

When we applied isotherm shift rates to current spawning habitat distributions in the Walla Walla basin, we estimated a loss of 6.6 km of spawning habitat over the next 25 years in SFWWR, 5.8 km in MC, and 14 km in the TR under current rates of stream warming (Table 9.5b). If stream temperature warming accelerates to 0.2°C·decade^{-1}, in 25 years, spawning habitat could be reduced by as much as 8.7 km in SFWWR, 8.2 km in MC and more than 12.1 km in the TR (Figure 9.7 right panel). When we assessed changes to spawning habitat index areas with a forecasted 0.2 °C·decade^{-1} rate of warming, the amount of available spawning habitat did not change in the SFWWR, as spawning index sites were located 13 km upstream of the current downstream spawning distribution (the location of the baseline isotherm). Predicted available habitat was reduced by 6 and 12 km for the MC and TR populations, respectively (Table 9.5c). Based on our estimates of maximum density in spawning index reaches, the loss of spawning habitat associated with a 0.2 °C·decade^{-1} increase in stream temperatures in 25 years could result in reductions in spawner capacity of 25% for MC and 33% for TR (Table 9.5d).

<u>Metapopulation simulations: effects of management, climate change, and dispersal</u>

The relative effects of changes in vital rates associated with management and climate change scenarios were consistent with elasticity values, but none of the scenarios modeled were sufficient to reverse the declining population trend of the base model. Decreased egg survival resulted in a substantial decrease in λ for both LHTs, although the magnitude of the change was larger for the mixed LHT (Table 9.6). Likewise, a decrease in mean sub-adult survival rates had a greater positive effect on the mixed LHT compared with the migratory. An increase of 10% of the current mean survival rate for the two largest stages resulted in only small increases in the population growth rate for both LHTs, with a larger change for the migratory LHT. For both LHTs, changes to transition probabilities, or mean individual growth, had large effects on λ. In particular, an increase in the transition probability for stage 1 resulted in a larger change to λ than did an increase in sub-adult or adult survival rates. Increased growth in stage 1 resulted in some individuals skipping stage 2 and transitioning directly into stage 3. This accelerated growth reduced the number of time steps it took for an individual to reach reproductive size, as well as move into stages where mortality rates were lower. The positive effect of increased individual growth at this stage was large enough to counteract the negative effect on population trend of decreasing growth rates in two sub-adult stages (Table 9.6).

Based on our extremely conservative estimates, all scenarios we modeled suggested a high probability of the metapopulation declining below 50% of its current size in 25 years. Increased survival rates, as a result of management actions, yielded only a slight decrease in the probability of decline compared with the base model (Figure 9.8a). For the climate change scenarios, a 20% decrease in egg survival resulted in a high probability that the population would decline by more than 90% after 25 years, whereas climate-related changes to growth rates decreased the probability of decline (Figure 9.8b). When we modeled multiple positive changes to vital rates simultaneously, including increased growth and survival, those changes together were sufficient to counteract the negative effect of higher egg mortality and decreased sub-adult growth rates on the metapopulation trajectory, lowering the probability of decline (Figure 9.8c). A reduction in spawner capacity had very little effect on current population projections, because all scenarios were modeled with declining populations, which rarely met or exceeded the capacity threshold.

Changes to dispersal rates had very little effect on either the metapopulation or the individual populations under base model scenarios, in which all three populations were declining (not shown). For a scenario in which both mixed populations had growth rates close to stable (λ = 0.983) and the migratory MC population was declining precipitously (λ = 0.928), dispersal was important for maintaining individual populations. The probability that a population would fall below 75% of its current size in 25 years decreased for both MC, the population with the lowest growth rate, as well as the TR population, which started out with the lowest abundance (Figure 9.9). In contrast, the probability of decline changed very little for the largest population (SFWWR) and the metapopulation as a whole.

Discussion

Bull trout have declined in distribution and abundance across much of their native range, prompting a need to better understand how populations will react to anthropogenic stressors and climatic changes. We present a stage-structured population viability model based on empirical vital-rate estimates, which can be used to explore the response of single and interconnected populations to changes in management, habitat availability, and habitat connectivity. The model serves as a tool with which to assess potential management actions and to better understand the role of life-history variability on population resilience.

Empirical estimates of bull trout vital rates

In this study, we compiled a complete set of vital rate estimates based on multiple long-term capture-mark-recapture studies, an uncommon undertaking for highly mobile species. Although most of our information was from a single population, we also compared population parameters among three neighboring populations, which provided important insight into variability in demographic rates and life-history strategies. We also compared our estimates to those available in the literature, where available. The relationship we established between female length and number of eggs was similar to that from other bull trout populations, including adfluvial migratory populations where fish overwinter in reservoirs or lakes (Johnston et al. 2007). Relative to other studies, our model underestimated fecundity of the largest sizes observed, so care should be taken applying this relationship to bull trout larger than 600 mm. The steep slope of the length-fecundity relationship demonstrates that larger fish produce significantly more eggs than smaller fish and helps illustrate the significant reproductive contribution that large, fluvial fish can make to populations with migratory life-history strategies.

Timing and size at maturation reflect trade-offs between survival, growth, and reproduction (Magnan et al. 2005). For bull trout, such trade-offs have likely led to the substantial amount of variation observed in demographic processes among and within populations. In our study system, bull trout spawned at smaller sizes than has been observed in adfluvial systems (Fraley and Shepard 1989; Johnston and Post 2009). This discrepancy might simply be a characteristic of the slightly smaller body size of the fluvial life-history type compared with adfluvial fish. In the SFWWR population, the variability in size of reproductive individuals and probability of spawning at a given size describes a population that spans a life-history continuum, with mature fish found from sizes representative of resident spawners, to large sizes typical of migratory fish. A range of sizes at maturation may help stabilize population fluctuations and hedge reproductive bets, as fish that spawn earlier in their life cycle will have a higher chance of surviving to spawn, whereas fish that grow larger before spawning have a larger clutch size and therefore a higher probability of offspring survival (Crespi and Teo 2002).

Bull trout within the Walla Walla basin also displayed a wide range of growth rates that could have resulted from numerous factors, including differences in stream temperature and productivity among locations in the watershed, food availability among sites, and variability among individual fish, such as aggressive behavior. It is unclear if the observed difference in transition probabilities between the MC and SFWWR populations was due to environmental characteristics of the two stream systems, a reflection of the percentage of individuals in each population that exhibit migratory behavior, or simply an artifact of low sample sizes (Morris and Doak 2002). In addition, fish capture methods varied between the two systems; bull trout were recaptured annually throughout the SFWWR spawning patch, whereas recaptures in MC only took place at the downstream end of the patch, and thus might have preferentially sampled larger, more mobile individuals.

Faster growth rates for fishes often confer a selective advantage, as larger fish are able to escape gape-limited predators, but the potential for growth is limited by metabolic demands and available resources (Parker 1971). Because of the relationship between growth and survival, these two vital rates should ideally be estimated simultaneously (White 2000), but our low physical recapture rate did not provide sufficient data for such an analysis. Factors affecting bull trout growth in the wild remain an area of uncertainty that warrants additional research, particularly because our population models indicated that changes to individual growth rates (as indicated by higher transition probabilities) had large effects on population trend. As such, factors affecting individual growth may play an important role in the vulnerability of populations to environmental changes.

Reliable stage-specific estimates of survival are critical for stage-based population viability models to produce realistic results. We removed sampling variance from survival rate estimates, which should produce more realistic results (White 2000), but even after doing so, our estimates spanned a range of potential values. Changes to survival rates even within the range of our 95% credible intervals could have substantial effects on the outcome of population viability assessments. We considered our models to be extremely precautionary, as we estimated both λ and survival rates over a period of time during which the SFWWR population appeared to be declining.

Additionally, inclusion of stochastic processes usually provides a more realistic population projection, but may also lead to overly pessimistic extinction risk (White 2000). Our estimates of temporal variance were relatively high for the smallest stage assessed, but also for the largest stage, comprised of migratory individuals. While high variability in smaller animals is expected, the annual variability in large, migratory adults warrants further investigation, as factors that affect survival of this life stage could relate to an interaction between their size and anthropogenic stressors that vary temporally, such as flow regulation and the ability of fish to pass barriers (Naughton et al. 2005). An understanding of the relationship between migratory adult survival and environmental covariates is particularly germane in light of the relative importance of this life stage to overall population growth for the migratory life-history type.

Elasticity patterns across life-history types

Comparison of elasticity values among bull trout life-history types provides some insights into the trade-offs between growth, survival, and reproduction that may help maintain life-history diversity within populations. The optimization approach to life-history theory suggests that organisms maximize the allocation of available resources between growth, survival, and reproduction throughout their lifetimes (Stearns 1989). The two primary bull trout life-history strategies represent different approaches to allocating lifetime resources. Migratory fish allocate more energy toward movement and growth, whereas resident fish allocate a greater portion of overall lifetime energy toward reproduction. The relative magnitude of elasticity values between the two LHTs reflects these different cost-benefit approaches. Adult survival elasticity values were higher for migratory individuals compared with other LHTs, because more of their lifetime reproductive output (and therefore contribution to future population growth) depends upon survival of mature adults. In contrast, resident LHTs have higher fertility elasticity values because more population-level resources are allocated to reproduction than survival. Our results indicate that maintenance of both life-history strategies is likely important for the persistence of bull trout populations. For example, years or environments in which egg survival is low might confer a selective advantage for the migratory LHT, and when adult survival decreases, the resident LHT may fare better.

The elasticity patterns we observed have important implications for management and conservation of bull trout populations. First, juvenile survival appears to play an important role in population persistence regardless of life-history type. However, juvenile bull trout might reside in different parts of a watershed depending upon life-history strategy (Fraley and Shepard 1989), so knowledge of juvenile movement patterns and habitat use are important for conservation of that life stage. Second, the relative sensitivity of population growth to fertility and adult survival may vary among different populations, depending upon the proportion of individuals exhibiting a particular life-history strategy and the composition of different life stages within the population. For example, populations with a stronger migratory component could be more resilient to increased egg or juvenile mortality, but may be more affected by predation of the largest adult sizes (Hebblewhite and Merrill 2009).

Model evaluation will also be most affected by those vital rates with the highest sensitivities (Morris et al. 2002). As such, accurate estimates of juvenile survival are most important for resident populations, whereas in addition to juvenile survival, accurate estimates of adult survival are relatively more important for predictions of migratory populations. For these reasons, future management of bull trout populations can benefit from improved knowledge of representative life-history strategies, age structures, and spatial distributions.

Sensitivity analyses (including elasticity calculations) of population growth rate to changes in vital rates are common tools that provide important insights for management aimed at changing population growth rates for conservation or control (Crouse et al. 1987; Doak et al. 1994; Aubry et al. 2010). However, elasticity analyses should be examined critically prior to prescribing conservation efforts (Wisdom et al. 2000; Koons et al. 2006). By plotting the response of population growth to changes in vital rates, were able to explore the potential for management actions that target a specific part of the life cycle to affect population trend. Prior to using elasticity values to guide management actions, this type of additional evaluation should be conducted to examine the potential for management actions to be effective (Mills et al. 1999).

A second caveat for interpreting elasticity values is that because elasticity analyses assume a stable stage distribution, sudden changes in vital rates will lead to instability in the stage structure (Crowder et al. 1994). Populations with unstable stage structures may respond differently to perturbations than elasticity predictions would suggest (Koons et al. 2006). Future analyses should evaluate the effect of sudden changes to survival rates on age structure stability, and the ensuing transient dynamics (Crowder et al. 1994; Koons et al. 2006).

Evidence of metapopulation structure and the role of connectivity

Our data provide one of the first empirical estimates of long-distance dispersal in contemporary stream conditions. Although we observed only three instances of bull trout dispersing from one population to another, these observations provide evidence that current populations in the Walla Walla basin do operate as a metapopulation. These data also support previous hypotheses that dispersal among populations occurs infrequently (Rieman and McIntyre 1995). Low rates of connectivity (historic and current dispersal combined) have been inferred from strong genetic divergence among bull trout populations, which generally increases in relation to the distance between populations (Meeuwig et al. 2010; Ardren et al. 2011). However, dispersal rates inferred from genetic data are likely a combined metric of historic and current genetic exchange (Mills 2007). Historic levels of dispersal may have been higher than our current estimates suggest, as fish now have to contend with in-stream barriers and degraded habitat in migratory corridors. This theory is supported by evidence of an increase in genetic divergence among populations separated by anthropogenic barriers (Meeuwig et al. 2010).

Based on genetics and the small number of observations in our study, we could not detect differences in the direction of dispersal, and assumed equal dispersal in both directions in our models. Although the SFWWR bull trout population contains the largest number of marked fish within the Walla Walla basin, we did not observe a fish stray from the SFWWR into either of the other two populations, despite numerous opportunities for detection throughout the system. Although our overall sample size of marked bull trout traveling long distances is quite small, we did observe two fish migrate out of MC and into SFWWR, raising the question of whether dispersal rates are directionally asymmetric. Lower stream sections of MC are heavily modified with numerous diversions, which may result in higher stray rates for the MC population. If dispersal is more likely to occur from MC and TR into SFWWR, these populations may act as sources, even though they have fewer individuals than the SFWWR population. Therefore, the direction of dispersal is also important for understanding metapopulation dynamics.

Habitat capacity and predicted changes

In many geographic areas, an important first step in bull trout conservation planning is simply to identify the quality and distribution of available habitat. The rule set we used to estimate bull trout spawning habitat produced reliable results in the Walla Walla basin, and was based on data readily available for the entire Columbia River basin and implemented with GIS software. Further development of this approach could help researchers identify habitat variables that consistently predict bull trout spawning habitat in other similar stream systems (e.g., Bartz et al. 2006). Elevation, stream temperature, and gradient were important predictors of spawning habitat in the Walla Walla basin, and have also been associated with bull trout occurrence in other systems (McCleary and Hassan 2008; Wenger et al. 2011). This consistency among studies suggests that bull trout spawning habitat can be predicted based on physical habitat variables at the stream reach scale from GIS data, which is useful in many places where distribution data are unavailable.

Our estimates of spawning habitat loss due to stream temperature warming varied considerably among spawning patches. The greatest predicted loss of habitat occurred in the TR because the majority of current spawning habitat was located at slightly lower elevations than the other populations, and habitat was distributed in numerous tributaries near the initial isotherm boundary. By comparison, we predicted considerably less habitat loss in the SFWWR because all spawning tributaries were more than 10 km above the isotherm boundary, and there was no tributary habitat lost. Our predictions of potential habitat loss were substantial, but they were based on the assumption that the distribution of bull trout spawning habitat is currently limited by temperature. Numerous other factors also affect spawning distributions, including spawning gravel distribution and groundwater influence, the latter of which could help mitigate stream warming rates (Boulton et al. 1998). Further, like many stream fishes, bull trout may exhibit more behavioral plasticity than habitat models alone would predict (Howell et al. 2010). Estimates of habitat loss associated with stream temperature demonstrate one potential effect of climatic change, and illustrate that the consequences of stream temperature warming could vary considerably among populations depending upon the spatial arrangement of available habitat and the quality of habitat near a temperature boundary.

Metapopulation responses to management and climate change

The current study demonstrates the utility of evaluating a range of potential changes in demographic rates across multiple population types to help evaluate conservation and management actions. Given the inherent uncertainty in parameter estimates and baseline population information, such as initial abundance, population simulations preclude absolute predictions of extinction probabilities or future population sizes. Nonetheless, comparison of responses to changes in survival, reproductive, and growth rates provide valuable insights into potential population responses. Overall, our scenarios demonstrate that small changes to vital rates were insufficient to reverse a population in relatively steep decline, such as we modeled. As such, management actions aimed at reversing a dramatically declining trend would need to have larger effects, or would need to target a positive response from multiple vital rates and multiple life stages, rather than focus on a single portion of the life cycle. Additionally, because the response of a population to such changes will vary depending upon the life-history characteristics of its individuals, metapopulations with different numbers of subpopulations and a different combination of life-history types could respond differently to the same perturbation scenarios we described here. Thus, knowledge of population stage structure and life-history traits are important for management decisions, even at the metapopulation scale.

Our metapopulation projections demonstrated three examples of potential effects of climate change on demographic rates of a migratory freshwater fish, each of which had a very different influence on metapopulation dynamics. Decreases in survival at any life stage resulting from stream temperature warming would clearly be detrimental to population persistence. However, the potential positive effects of changes to the metabolic rates of organisms have garnered much less attention (Doak and Morris 2010). In our simulations, the relative magnitude of the positive population response to increased individual growth rates was sufficient to counteract the combined negative effects of changes to other vital rates. Similar types of compensatory changes in demographic rates have been observed in other species, effectively buffering populations against the negative effects of climate change (Doak and Morris 2010). However, such compensatory mechanisms are unlikely to persist as streams continue to warm. Continued warming can be expected to result in the deterioration of one or more vital rates past the point of compensation, resulting in a rapid population decline once this "tipping point" has been passed (Doak and Morris 2010).

For a stenothermic fish like bull trout, increases in stream temperature above an optimal threshold can lead to a number of other potentially negative biological responses, including reduced fitness via susceptibility to disease, increased metabolic costs, or changes in spawn timing (Crozier et al. 2008; Warren et al. 2012). Our results suggest that the response of bull trout populations to climate change might be difficult to identify or predict, as the effect on individual vital rates could be synergistic or confounding (Crozier et al. 2008). As such, long-term monitoring of representative populations, such as those used in this study, will be important to detect demographic compensation and identify tipping points beyond which compensation can no longer occur (Doak and Morris 2010).

The limited response of metapopulation persistence to decreased carrying capacity was unsurprising, given the declining population growth rates used in our simulations (Ginzburg et al. 1990). Under the scenarios we examined, populations only rarely reached carrying capacity in stochastic simulations. We expect that changes to carrying capacity could have very different effects on populations experiencing positive growth rates, or if a different type of density-dependence function were included in the population model (Ginzburg et al. 1990). Additionally, we based our estimates of reduced capacity on the portion of habitat lost from spawning survey index reaches, which represented only a portion of total habitat lost. Thus, to detect effects of gradually increasing stream temperatures on the distribution of organisms, monitoring should take place throughout the entire habitat of concern.

Results of our metapopulation model indicate that under the scenarios we examined, the importance of dispersal differed for individual populations depending upon the combined dynamics of those populations, whereas the metapopulation response was relatively insensitive. For a metapopulation in which some populations are stable within a stochastic setting, dispersal can help decrease the extinction risk for small and declining populations (Hanski and Simberloff 1997). Although dispersal rates at the upper end of what we evaluated are may not be realistic for bull trout, this effect was apparent even at dispersal rates of less than 2% of the reproductive adult population.

According to metapopulation theory, the low rates of dispersal we observed indicate that the populations of bull trout in the Walla Walla basin could be described as somewhere between a Levins and a non-equilibrium type of metapopulation. In a classical Levins model, a metapopulation is comprised of multiple small subpopulations, and dispersal is sufficient to recolonize extinct or empty patches. In a non-equilibrium metapopulation, subpopulations are separated by large distances and each is extinction-prone because of its isolation and relatively small size (Harrison and Taylor 1997). As ours are some of the first empirical estimates of bull trout dispersal, we have no way of assessing historic or potential levels of movement between populations to evaluate how this metapopulation type may have changed over time. Given our current dispersal estimates, recolonization of extinct or unoccupied patches is unlikely to occur. However, even low rates of dispersal can help stabilize smaller populations, and the exchange of even one or two individuals per generation could be sufficient to help maintain genetic diversity and prevent genetic bottlenecks (Mills and Allendorf 1996).

Implications for bull trout conservation

This research provides a nearly comprehensive set of vital rate estimates for seven size classes of bull trout based on robust empirical estimates from multiple, long-term datasets. These estimates help establish important baseline parameters that can be used to evaluate population-level responses to management actions or environmental changes (e.g., Crowder et al. 1994). The general patterns described by our sensitivity analyses and population projections can help managers develop broad-scale conservation priorities based on life-history strategies (Heppell et al. 2000). We expect bull trout populations to have the greatest response to changes in juvenile survival rates, as well as to individual growth rates. Accordingly, bull trout populations may be particularly susceptible to environmental changes that affect bioenergetics, including stream productivity, food availability, and temperature. Our findings also indicate that resident populations are more responsive to changes in fertility rates and vital rates of early life stages, whereas migratory populations are more sensitive to loss of large, fecund adults, in addition to juvenile survival and growth rates. Further, results of our modeling indicate that to reverse steep population declines, management actions should target improvement of multiple life stages simultaneously.

In a metapopulation context, recolonization of extinct patches may be unlikely under low rates of bull trout dispersal, particularly when patches are separated by large distances (Harrison and Taylor 1997). As such, individual populations warrant unique consideration with regard to conservation actions. However, maintenance of connectivity to facilitate dispersal is still important to promote genetic exchange among populations and to allow the potential for populations to help equalize one another during asynchronous catastrophic events.

Diversity in life-history strategies, migratory patterns, and behavioral plasticity within populations likely helps spread the risk of environmental stochasticity, both spatially as bull trout occupy a range of habitats, and temporally, via numerous co-existing generations that reproduce at different sizes (Rieman and McIntyre 1993). Our findings indicate that this diversity enhances demographic stability and is therefore important for long-term population persistence (Gross 1991). Because vital-rate perturbations affect population growth rates differently among life-history types, the severity of anthropogenic stressors or environmental changes might vary widely among bull trout populations, depending upon the composition of life-history strategies within the population. Variation in demographic responses can help stabilize population growth rates for populations in which vital rates differ considerably among individuals in the same population, such as in the SFWWR. The same could be true for metapopulations composed of populations with different proportions of life-history types (Stacey et al. 1997). To provide as much demographic stability as possible, diversity within and among populations should be maintained along a continuum that emphasizes conservation of the full range of life-history traits expressed by bull trout.

Literature Cited

Akçakaya, H.R. 2000. Population viability analyses with demographically and spatially structured models. Ecol. Bull. 48:23-38.

Al-Chokhachy, R., and Budy, P. 2008. Demographic characteristics, population structure, and vital rates of a fluvial population of bull trout in Oregon. Trans. Am. Fish. Soc. 137:1709-1722.

Al-Chokhachy, R., Budy, P., and Schaller, H. 2005. Understanding the significance of redd counts:a comparison between two methods for estimating the abundance of and monitoring bull trout populations. N. Am. J. Fish. Manage. 25:1505-1512.

Allendorf, F.W., and Luikart, G. 2007. Conservation and the genetics of populations. Blackwell Publishing, Malden, Mass.

Anglin, D.R., Gallion, D., Barrows, M., Newlon, C., and Koch, R. 2008. Current status of bull trout abundance, connectivity, and habitat conditions in the Walla Walla Basin. U.S. Fish and Wildlife Service Columbia River Fisheries Program Office, Vancouver, Wash.

Ardren, W.R., DeHaan, P.W., Smith, C.T., Taylor, E.B., Leary, R., Kozfkay, C.C., Godfrey, L., Diggs, M., Fredenberg, W., Chan, J., Kilpatrick, C.W., Small, M.P., and Hawkins, D.K. 2011. Genetic structure, evolutionary history, and conservation units of bull trout in the coterminous United States. Trans. Am. Fish. Soc. 140(2):506-525.

Aubry, L.M., Rockwell, R.F., and Koons, D.N. 2010. Metapopulation dynamics of mid-continent lesser snow geese: implications for management. Human-Wild. Interact. 4(2):170-191.

Bartz, K.K., Lagueux, K.M., Scheuerell, M.D., Beechie, T., Haas, A.D., and Ruckelshaus, M.H. 2006. Translating restoration scenarios into habitat conditions: an initial step in evaluating recovery strategies for Chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. 63(7):1578-1595.

Bender, D.J., Contreras, T.A., and Fahrig, L. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79(2):517-533.

Boulton, A.J., Findlay, S., Marmonier, P., Stanley, E.H., and Valett, H.M. 1998. The functional significance of the hyporheic zone in streams and rivers. Ann. Rev. Ecol. System. 29:59-81.

Bowerman, T., and Budy, P. 2012. Incorporating movement patterns to improve survival estimates for juvenile bull trout. N. Am. J. of Fish. Manage. 32(6):1123-1136.

Bowerman, T., Neilson, B.T., Budy, P. 2014. Effects of fine sediment, hyporheic flow, and spawning site characteristics on survival and development of bull trout embryos. Can. J. Fish. Aquat. Sci. 71(7):1059-1071.

Brenkman, S.J., and Corbett, S.C. 2005. Extent of anadromy in bull trout and implications for conservation of a threatened species. N. Am. J. Fish. Manage. 25(3):1073-1081.

Brook, B.W., O'Grady, J.J., Chapman, A.P., Burgman, M.A., Akçakaya, H.R., and Frankham, R. 2000. Predictive accuracy of population viability analysis in conservation biology. Nature 404(6776):385-387.

Brown, J.H., and Kodric-Brown, A. 1977. Turnover rates in insular biogeography:effect of immigration on extinction. Ecology 58(2):445-449.

Budy, P., Bowerman, T., and Thiede, G.P. 2010. Bull trout population assessment in northeastern Oregon: a template for recovery planning. 2009 Annual Progress Report to US Fish and Wildlife Service. UTCFWRU 2010.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. 2nd ed. Sinauer Associates, Sunderland, Mass.

Crespi, B.J., and Teo, R. 2002. Comparitive phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. Evolution 56(5):1008-1020.

Crouse, D.T., Crowder, L.B., and Caswell, H. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68(5):1412-1423.

Crowder, L.B., Crouse, D.T., Heppell, S.S., and Martin, T.H. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecol. Appl. 4(3):437-445.

Crozier, L.G., Hendry, A.P., Lawson, P.W., Quinn, T.P., Mantua, N.J., Battin, J., Shaw, R.G., and Huey, R.B. 2008. Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. Evol. Appl. 1(2):252-270.

Doak, D.F., and Morris, W.F. 2010. Demographic compensation and tipping points in climate-induced range shifts. Nature 467(7318):959-962.

Doak, D.F., Kareiva, P., and Klepetka, B. 1994. Modeling population viability for the desert tortoise in the Western Mojave Desert. Ecol. Appl. 4(3):446-460.

Downs, C.C., Horan, D., Morgan-Harris, E., and Jakubowski, R. 2006. Spawning demographics and juvenile dispersal of an adfluvial bull trout population in Trestle Creek, Idaho. N. Am. J. Fish. Manage. 26(1):190-200.

Dunham, J.B., and Rieman, B.E. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecol. Appl. 9(2):642-655.

Dunham, J., Rieman, B., and Davis, K. 2001a. Sources and magnitude of sampling error in redd counts for bull trout. N. Am. J. Fish. Manage. 21(2):343-352.

Dunham, J.B., Rieman, B.E., and Peterson, J.T. 2001b. Patch-based models of species occurrence: lessons from salmonid fishes in streams. *In* Predicting species occurrences: issues of accuracy and scale. *Edited by* J. Scott and P. Heglund. Island Press, Covelo, Calif. pp. 327-334.

DuPont, J.M., Brown, R.S., and Geist, D.R. 2007. Unique allacustrine migration patterns of a bull trout population in the Pend Oreille River drainage, Idaho. N. Am. J. Fish. Manage. 27(4):1268-1275.

Fagan, W.F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology 83(12):3243-3249.

Fraley, J.J., and Shepard, B.B. 1989. Life-history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Sci. 63(4):133-143.

Fujiwara, M., and Caswell, H. 2001. Demography of the endangered North Atlantic right whale. Nature 414(6863):537-541.

Fullerton, A.H., Lindley, S.T., Pess, G.R., Feist, B.E., Steel, E.A., and McElhany, P. 2011. Human influence on the spatial structure of threatened Pacific salmon metapopulations. Conserv. Biol. 25(5):932-944.

Ginzburg, L.R., Ferson, S., and Akçakaya, H.R. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. Conserv. Biol. 4(1):63-70.

Goetz, F. 1989. Biology of the bull trout, *Salvelinus confluentus*: a literature review. Willamette National Forest, Eugene, Ore.

Gotelli, N.J. 1999. Testing metapopulation models with stream-fish assemblages. Evol. Ecol. Res. 1(835-845).

Gross, M.R. 1991. Salmon breeding behavior and life history evolution in changing environments. Ecology 72(4):1180-1186.

Hanski, I.A., and Gilpin, M.E. 1991. Single-species metapopulation dynamics. *In* Metapopulation dynamics: empirical and theoretical investigations. *Edited by* M.E. Gilpin and I.A. Hanski. Academic Press, London. pp. 17-38.

Hanski, I.A., and Simberloff, D. 1997. The metapopulation approach, its history, conceptual domain, and application in conservation. *In* Metapopulation biology: ecology, genetics, and evolution. *Edited by* I.A. Hanski and M.E. Gilpin. Academic Press, San Diego, Calif. pp. 5-26.

Harrison, S., and Taylor, A.D. 1997. Empirical evidence for metapopulation dynamics. *In* Metapopulation biology: ecology, genetics, and evolution. *Edited by* I.A. Hanski and M.E. Gilpin. Academic Press, San Diego, Calif. pp. 27-42.

Hebblewhite, M., and Merrill, E.H. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90(12):3445-3454.

Hemmingsen, A.R., Gunckel, S.L., and Howell, P.J. 2001. Bull trout life history, genetics, habitat needs, and limiting factors in central and northeastern Oregon. Oregon Department of Fish and Wildlife, Portland, Ore.

Heppell, S.S., Walters, J.R., and Crowder, L.B. 1994. Evaluating management alternatives for red-cockaded woodpeckers: a modeling approach. J. Wildl. Manage. 58(3):479-487.

Heppell, S., Caswell, H., and Crowder, L.B. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81(3):654-665.

Hiraldo, F., Negro, J.J., Donazar, J.A., and Gaona, P. 1996. A demographic model for a population of the endangered lesser kestrel in southern Spain. J. Appl. Ecol. 33(5):1085-1093.

Homel, K., and Budy, P. 2008. Temporal and spatial variability in the migration patterns of juvenile and subadult bull trout in Northeastern Oregon. Trans. Am. Fish. Soc. 137(3):869-880.

Homel, K., Budy, P., Pfrender, M.E., Whitesel, T.A., and Mock, K. 2008. Evaluating genetic structure among resident and migratory forms of bull trout (*Salvelinus confluentus*) in Northeast Oregon. Ecol. Fresh. Fish 17(3):465-474.

Howell, P.J., and Sankovich, P.M. 2012. An evaluation of redd counts as a measure of bull trout population size and trend. N. Am. J. Fish. Manage. 32(1):1-13.

Howell, P.J., Dunham, J.B., and Sankovich, P.M. 2010. Relationships between water temperatures and upstream migration, cold water refuge use, and spawning of adult bull trout from the Lostine River, Oregon, USA. Ecol. Fresh. Fish 19(1):96-106.

Isaak, D.J., and Rieman, B.E. 2013. Stream isotherm shifts from climate change and implications for distributions of ectothermic organisms. Glob. Change Biol. 19(3):742-751.

Isaak, D.J., and Thurow, R.F. 2006. Network-scale spatial and temporal variation in Chinook salmon (*Oncorhynchus tsawytscha*) redd distributions: patterns inferred from spatially continuous replicate surveys. Can. J. Fish. Aquat. Sci. 63:285-296.

Isaak, D.J., Wollrab, S., Horan, D., and Chandler, G. 2011. Climate change effects on stream and river temperatures across the northwest U.S. from 1980-2009 and implications for salmonid fishes. Clim. Change:1-26.

Johnston, F.D., and Post, J.R. 2009. Density-dependent life-history compensation of an iteroparous salmonid. Ecol. Appl. 19(2):449-467.

Johnston, F.D., Post, J.R., Mushens, C.R., Stelfox, J.D., Paul, A.J., and Lajeunesse, B. 2007. The demography of recovery of an overexploited bull trout, *Salvelinus confluentus,* population. Can. J. Fish. Aquat. Sci. 64:113-126.

Kassler, T.W., and Mendel, G. 2007. Genetic characterization of bull trout from the Walla Walla River Basin. Washington Department of Fish and Wildlife.

Koizumi, I., and Maekawa, K. 2004. Metapopulation structure of stream-dwelling Dolly Varden charr inferred from patterns of occurrence in the Sorachi River basin, Hokkaido, Japan. Freshwat. Biol. 49(8):973-981.

Koons, D.N., Rockwell, R.F., and Grand, J.B. 2006. Population momentum: implications for wildlife management. J. Wildl. Manage. 70(1):19-26.

Leary, R.F., Allendorf, F.W., and Forbes, S.H. 1993. Conservation genetics of bull trout in the Columbia and Klamath River drainages. Conserv. Biol. 7(4):856-865.

Magnan, P., Proulx, R.I., and Plante, M. 2005. Integrating the effects of fish exploitation and interspecific competition into current life history theories: an example with lacustrine brook trout (*Salvelinus fontinalis*) populations. Can. J. Fish. Aquat. Sci. 62(4):747-757.

Mahoney, B.D., Mendel, G., Weldert, R., Trump, J., Olsen, J., Gembala, M., Gallinat, M., and Ross, L. 2011. The Walla Walla Subbasin salmonid monitoring and evaluation project: 2009 and 2010 annual report. U.S. Deparment of Energy, Bonneville Power Administration, BPA proj. num. 2000-039-00.

Mantua, N., Tohver, I., and Hamlet, A. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Clim. Change 102(1):187-223.

McCleary, R.J., and Hassan, M.A. 2008. Predictive modeling and spatial mapping of fish distributions in small streams of the Canadian Rocky Mountain foothills. Can. J. Fish. Aquat. Sci. 65(2):319-333.

McPhail, J.D., and Baxter, J.S. 1996. A review of bull trout (*Salvelinus confluentus*) life-history and habitat use in relation to compensation and improvement opportunities. Fisheries Management Report No. 104. Fisheries branch, Brit. Col. Minst. Environ.

Meeuwig, M.H., Guy, C.S., Kalinowski, S.T., and Fredenberg, W.A. 2010. Landscape influences on genetic differentiation among bull trout populations in a stream-lake network. Molec. Ecol. 19(17):3620-3633.

Mendel, G.W., Fulton, C., Weldert, R., Uehera, J., and Martin, S. 2003. An investigation into the migratory behavior of bull trout (*Salvelinus confluentus*) in the Touchet River Basin. Washington Department of Fish and Wildlife, Fish Program, Fish Manage. Div.

Mesa, M.G., Weiland, L.K., Christiansen, H.E., Sauter, S.T., and Beauchamp, D.A. 2013. Development and evaluation of a bioenergetics model for bull trout. Trans. Am. Fish. Soc. 142(1):41-49.

Mills, L.S. 2007. Conservation of wildlife populations: demography, genetics, and management. Blackwell Publishing Malden, Mass.

Mills, L.S., and Allendorf, F.W. 1996. The one-migrant-per-generation rule in conservation and management. Conserv. Biol. 10(6):1509-1518.

Mills, L.S., Doak, D.F., and Wisdom, M.J. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. Conserv. Biol. 13(4):815-829.

Moore, T.L., Starcevich, S.J., Jacobs, S., Howell, P.J., and La Grande, O.R. 2006. Migratory patterns, structure, abundance, and status of bull trout populations from subbasins in the Columbia Plateau and Blue Mountain provinces 2005 Annual Report. U.S. Department of Energy, Bonneville Power Administration.

Morris, W.F., and Doak, D.F. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Mass.

Morris, W.F., Bloch, P.L., Hudgens, B.R., Moyle, L.C., and Stinchcombe, J.R. 2002. Population viability analysis in endangered species recovery plans: past use and future improvements. Ecol. Appl. 12(3):708-712.

Nathan, R., Perry, G., Cronin, J.T., Strand, A.E., and Cain, M.L. 2003. Methods for estimating long-distance dispersal. Oikos 103(2):261-273.

Naughton, G.P., Caudill, C.C., Keefer, M.L., Bjornn, T.C., Stuehrenberg, L.C., and Peery, C.A. 2005. Late-season mortality during migration of radio-tagged adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. Can. J. Fish. Aquat. Sci. 62(1):30-47.

Nelson, M.L., McMahon, T.E., and Thurow, R.F. 2002. Decline of the migratory form in bull charr, *Salvelinus confluentus*, and implications for conservation. Environ. Biol. Fish. 64(1-3):321-332.

Parker, R.R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Board Can. 28(10):1503-1510.

Pratt, K. L. 1992. A review of bull trout life history. *in* Howell, P.J. and D.V. Buchanan, editors. Proceedings of the Gearhart Mountain bull trout workshop. Oregon Chap. Am. Fish. Soc., Corvallis, Ore. pp. 5-9.

Rieman, B.E., and Dunham, J.B. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. Ecol. Fresh. Fish 9(1-2):51-64.

Rieman, B.E., and McIntyre, J.D. 1993. Demographic and habitat requirements for conservation of bull trout. USDA General Tech. Rep. INT-302.

Rieman, B.E., and McIntyre, J.D. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Trans. Am. Fish. Soc. 124(3):285-296.

Rieman, B.E., Lee, D.C., and Thurow, R.F. 1997. Distribution, status, and likely future trends of bull trout within the Columbia River and Klamath River basins. N. Am. J. Fish. Manage. 17:1111-1125.

Ripley, B. 2012. Tree: Classification and regression trees. R package version 1.0-3.2.

Schick, R.S., and Lindley, S.T. 2007. Directed connectivity among fish populations in a riverine network. J. Appl. Ecol. 44(6):1116-1126.

Schtickzelle, N., and Quinn, T.P. 2007. A metapopulation perspective for salmon and other anadromous fish. Fish and Fisheries. 8:297-314.

Selong, J.H., McMahon, T.E., Zale, A.V., and Barrows, F.T. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. Trans. Am. Fish. Soc. 130(6):1026-1037.

Shellberg, J.G., Bolton, S.M., and Montgomery, D.R. 2010. Hydrogeomorphic effects on bedload scour in bull char (Salvelinus confluentus) spawning habitat, western Washington, USA. Can. J. Fish. Aquat. Sci. 67(4):626-640.

Stacey, P.B., Johnson, V.A., and Taper, M. 1997. Migration within metapopulations: the impact upon local population dynamics. *In* Metapopulation biology: ecology, genetics, and evolution. *Edited by* I.A. Hanski and M.E. Gilpin. Academic Press, San Diego, Calif. pp. 267-291.

Stearns, S.C. 1989. Trade-offs in life-history evolution. Funct. Ecol. 3(3):259-268.

Warren, D.R., Robinson, J.M., Josephson, D.C., Sheldon, D.R., and Kraft, C.E. 2012. Elevated summer temperatures delay spawning and reduce redd construction for resident brook trout (*Salvelinus fontinalis*). Glob. Change Biol. 18(6):1804-1811.

Wenger, S.J., Isaak, D.J., Dunham, J.B., Fausch, K.D., Luce, C.H., Neville, H.M., Rieman, B.E., Young, M.K., Nagel, D.E., Horan, D.L., and Chandler, G.L. 2011. Role of climate and invasive species in structuring trout distributions in the interior Columbia River Basin, USA. Can. J. Fish. Aquat. Sci. 68(6):988-1008.

White, G., and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120-139.

White, G.C. 2000. Population viability analysis: data requirements and essential analyses. *In* Research techniques in animal ecology: controversies and consequences. *Edited by* L. Boitani and T.K. Fuller. Columbia University Press, New York. pp. 288-331.

White, G.C., Burnham, K.P., Barker, R.J., Thomson, D.L., Cooch, E.G., and Conroy, M.J. 2009. Evaluation of a bayesian MCMC random effects inference methodology for capture-mark-recapture data. *In* Modeling demographic processes in marked populations. *Edited by* G.P. Patil, T.G. Gregoire, A.B. Lawson and B.D. Nussbaum. Springer US, New York. pp. 1119-1127.

Wisdom, M.J., Mills, L.S., and Doak, D.F. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. Ecology 81(3):628-641.

Zuo, W., Moses, M.E., West, G.B., Hou, C., and Brown, J.H. 2012. A general model for effects of temperature on ectotherm ontogenetic growth and development. Proc. Royal Soc. B: Biol. Sci. 279(1734):1840-1846.

Table 9.1. Stage-specific total lengths (TL) and demographic parameters estimated from two bull trout populations. Survival rates, temporal variance (SD), and spawning probability were estimated from the South Fork Walla Walla River, Oregon (SFWWR). Transition rates (probability of growing from one stage to the next in one year) were estimated based on recapture data from the SFWWR and Mill Creek (MC) populations. For simplicity, low transition rates (<0.01 were omitted) and transition rates that spanned multiple stages were combined (see supplementary material Table B8.2).

Stage	TL (mm)	Survival	SD	Spawning probability	Transition probability (SFWWR/MC)
1	60 to 120	0.218	0.205[a]	NA	1.00/ND
2	120 to 180	0.264	0.205	ND	1.00/0.54*
3	180 to 240	0.382	0.097	0.05	0.88/0.83
4	240 to 300	0.384	0.165	0.10	0.70/ND
5	300 to 360	0.389	0.048	0.30	0.33*/0.83
6	360 to 420	0.444	0.076	0.33	0.20/0.76
7+	>420	0.471	0.189	0.70	NA

ND indicates no data
NA indicates a parameter that was not applicable to a particular life stage
[a]SD for stage-1 was assumed from stage-2 estimates
*indicates low sample size

Table 9.2. Lower-level vital rates included in population models for migratory, mixed, and resident bull trout life-history types. A parameter that was not applicable to a particular life stage is indicated by NA.

Parameter	Migratory	Mixed	Resident
m_2	NA	227	227
m_3	NA	450	450
m_4	NA	750	641
m_5	1128	1128	1059
m_6	1583	1583	NA
m_7	3184	2623	NA
B_2	NA	0.025	0.100
B_3	NA	0.100	0.330
B_4	NA	0.180	0.600
B_5	0.300	0.500	0.900
B_6	0.400	0.400	NA
B_7	0.900	0.900	NA
S_{egg}	0.43	0.43	0.43
S_0	0.284	0.284	0.284
S_1	0.218	0.218	0.284
S_2	0.264	0.264	0.218
S_3	0.384	0.384	0.264
S_4	0.389	0.389	0.389
S_5	0.444	0.444	NA
S_6	0.471	0.471	NA
γ_1	1.000	1.000	1.000
γ_2	1.000	0.800	0.180
γ_3	1.000	0.740	0.340
γ_4	0.850	0.600	0.200
γ_5	0.830	0.500	0.120
γ_6	0.750	0.700	NA

m_i = number of eggs per stage median total length

B_i = proportion of females attempting spawning

S_i = probability of survival for an individual in stage *i*

γ_i = probability of growing from stage *i* into *i* + 1

Table 9.3. Metrics used to assess population connectivity within the Walla Walla basin: (a) dispersal rates between populations based on the proportion of marked fish observed moving from one population to another, (b) dispersal rates estimated from a movement function developed from combined capture-mark-recapture movement data, and (c) migrants per generation based on genetic divergence between populations (pairwise F_{st} values). For (a) estimates describe rates of dispersers moving from each population in a column into the populations in rows, (b) dispersal is based on distance, so assumed equal in either direction, and (c) indication of genetic exchange assumed equal in either direction.

	(a) Recapture dispersal rate per 7 years			**(b) Dispersal function rate (applied annually in model)**			**(c) Migrants per generation (i.e. dispersers per 7 years)**		
	SFWWR	MC	TR	SFWWR	MC	TR	SFWWR	MC	TR
SFWWR		0.0052	0.0000						
MC	0.000		0.0098	0.002			3.580		
TR	0.000	0.000		0.0014	0.0015		3.440	2.380	

Table 9.4. Rule set used to define four categories of spawning habitat in the Walla Walla basin, Oregon. All spawning density data was based on bull trout redd censuses in the Walla Walla basin during the Columbia Plateau's bull trout Ecological Monitoring and Assessment Program assessment (EMAP); physical habitat attributes were downloaded from the Ecosystem Diagnosis and Treatment (EDT) analysis (Mobrand Biometrics 2004).

Habitat type	Rule set	Mean stream width (m)	Maximum density (redds·km^{-1})
No spawning	<700 m elevation Or gradient <0.01725 and >0.0745 Or max mean monthly temp >1.95 (rating)	NA	0
Low density spawning	Gradient <0.027 and >0.01725 And max mean monthly temp <1.95 and >1	13	6
High density spawning	Gradient >=0.027 and <0.0745 And min (low flow) width >4.5 m	9	64
Spawning tributary	Gradient >0.04 and <0.0745 And min (low flow) width <4.5 m and >0 m	1.5	19

Table 9.5. Isotherm shift rates (ISR), bull trout habitat, and spawner capacity estimated for current and future conditions in the Walla Walla basin. Future estimates are predicted for 2035 based on four rates of stream warming. (a) Isotherm shift rates (the rate at which a stream temperature threshold is expected to shift upstream, shown for a range of channel slopes. Spawning habitat predicted from the spawning capacity rule set for (b) entire spawning patches and (c) spawning survey index reaches only. (d) Maximum number of redds based on spawning habitat in redd survey index reaches.

(a) Isotherm shift rate (km·decade^{-1}) function in 2035 with stream warming rate (°C·decade^{-1}).

% Channel slope	Stream warming rate (°C·decade^{-1}) 0.1	0.15	0.2	0.3
0.5	4.2	6.3	8.3	12.5
1	2.1	3.1	4.2	6.3
2	1	1.6	2.1	3.1
3	0.7	1	1.4	2.1
5	0.42	0.63	0.83	1.25

(b) Spawning habitat (km) predicted from capacity function in 2035 with stream warming rate (°C·decade^{-1}).

Population	Current	0.1	0.15	0.2	0.3
SFWWR	45.1	40.7	38.5	36.4	32.0
MC	21.8	17.9	16.0	13.6	11.7
TR	43.7	34.2	29.4	21.1	10.5

(c) Spawning habitat (km) in redd survey index reaches function in 2035 with stream warming rate (°C·decade^{-1}).

Population	Current	0.1	0.15	0.2	0.3
SFWWR	11.9	11.9	11.9	11.9	11.9
MC	17.6	14.7	12.9	11.5	10.1
TR	22.0	17.6	15.5	9.9	6.1

(d) Estimated spawner capacity in index reaches (max. # redds) function in 2035 with stream warming rate (°C·decade^{-1}).

Population	Current	0.1	0.15	0.2	0.3
SFWWR	478	478	478	478	478
MC	395	383	370	337	288
TR	690	612	573	396	245

Table 9.6. Population growth rate (λ) for each life-history type based on changes to parameters in our base model, where λ = 0.931 (λ<1 indicates a declining population growth rate). Hypothetical mechanisms for changes in individual demographic parameters related to Management (M), climate (C), or both (CM) are shown.

Scenario	**Hypothesized mechanism**	**Change in parameter**	**Migratory λ**	**Mixed λ**
C 1	Increased winter scour and redd sedimentation due to higher winter flows	Decrease S_{egg} by 20%	0.903	0.893
M 2	Improved habitat in rearing areas due to management actions	Increase S_2 and S_3 by 10%	0.950	0.962
M 3	Improved passage through migratory corridor	Increase S for two largest stages by 10%	0.948	0.939
C 4	Higher growth rates due to increased water temperatures in spawning areas	Increase stage 1 growth rate by 10%	0.962	0.979
C 5	Lower growth rates for sub-adult stages resulting from increased water temperatures (above optimum)	Decrease stage 3 and 4 growth rate by 10%	0.922	0.913
C 6	Elevated water temperatures throughout the system	C4 and C5 combined	0.943	0.969
C 7	Elevated water temperatures throughout and increased winter flows	C1, C4, and C5 combined	0.928	0.947
CM 8	Elevated water temperatures, increased winter flows, improved passage	C1, C4, C5, and M3 combined	0.945	0.955
CM 9	Elevated water temperatures, increased winter flows, improved passage, and improved rearing habitat	C1, C4, C5, M2, and M3 combined	0.968	0.983

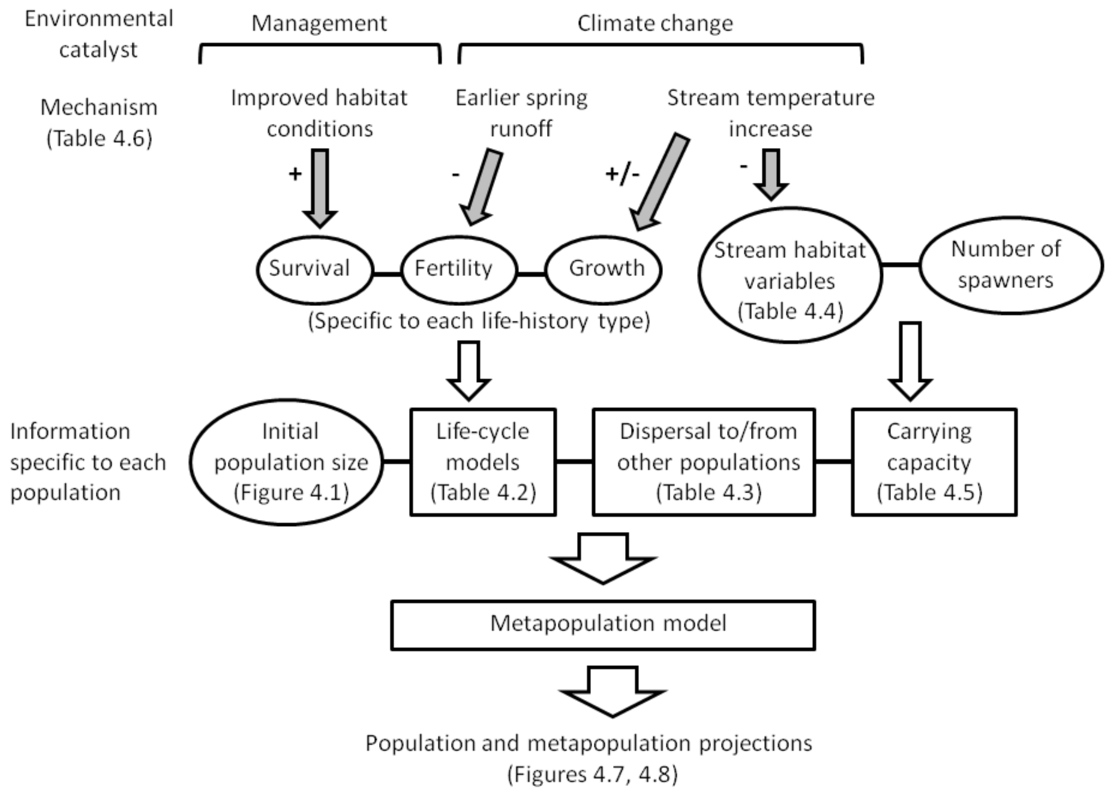

Figure 9.1. Schematic representation of components used in metapopulation model projections, with associated references to tables and figures where applicable. Model parameters that were based on empirical measurements are depicted with an oval, and components that describe a model are outlined with a rectangle. Model inputs are shown by an open arrow. Changes to model inputs based on hypothetical management and climate changes are shown with a gray arrow, and an increase (+) or decrease (-) in the response is shown next to the arrow.

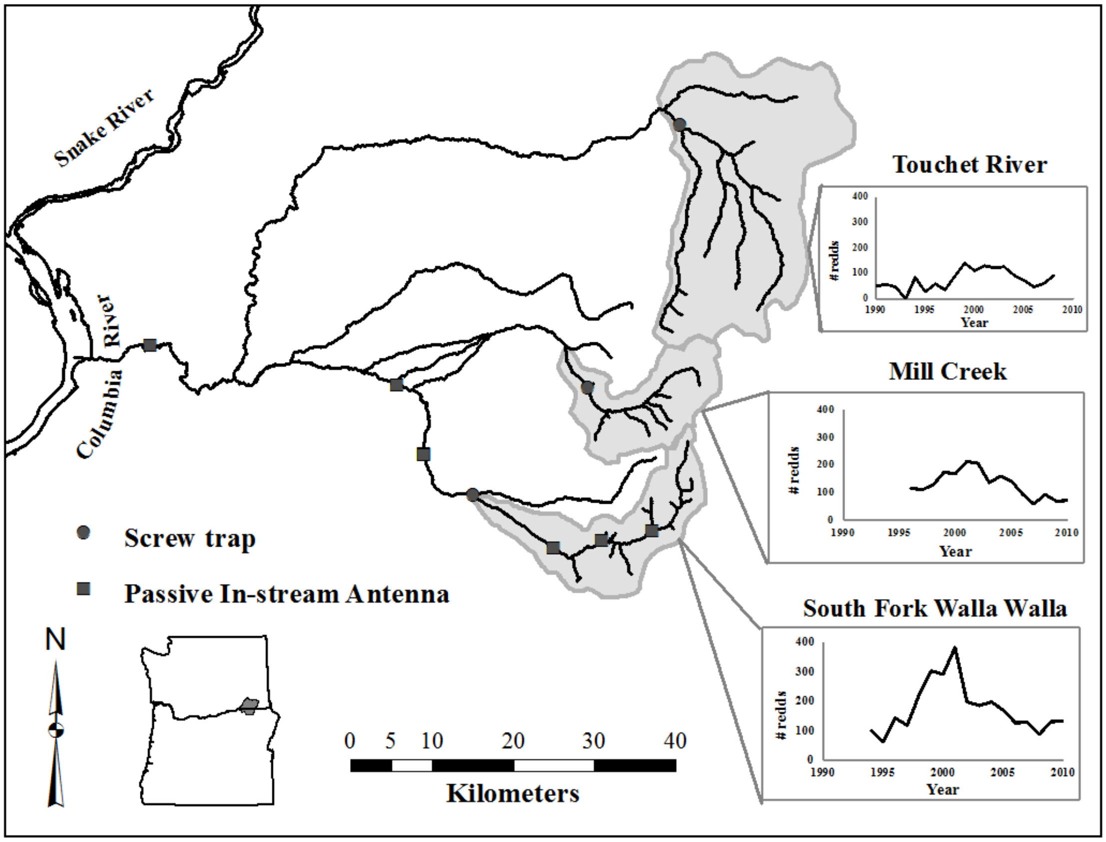

Figure 9.2. Three bull trout populations located within the Walla Walla River basin, Oregon and Washington: Touchet River, Mill Creek, and South Fork Walla Walla River. Watershed outlines depict spawning habitat patches, where spawning and juvenile rearing occurs, and bull trout migrate throughout the basin. Graphs show the number of redds counted in index reaches for each of the three populations from 1990 through 2010.

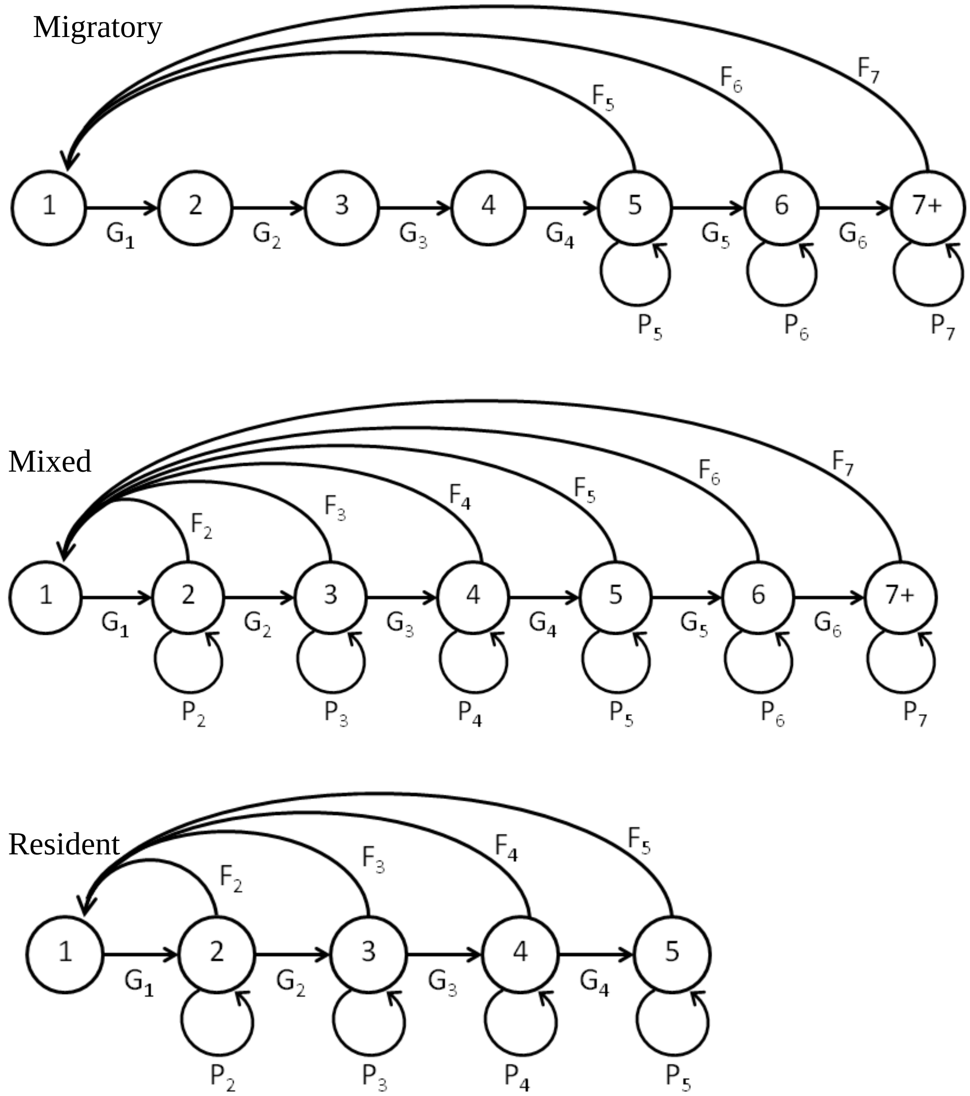

Figure 9.3. Life cycle diagrams describing migratory, mixed, and resident bull trout life-history types. G_i represents the probability of surviving in stage *i* and growing into the next stage, P_i is the probability of surviving and staying in the same stage, and F_i represents the fertility contribution of each stage, the total number of female eggs expected to live to stage 1. Life cycle element estimates are shown in Tables 9.1 and 9.2.

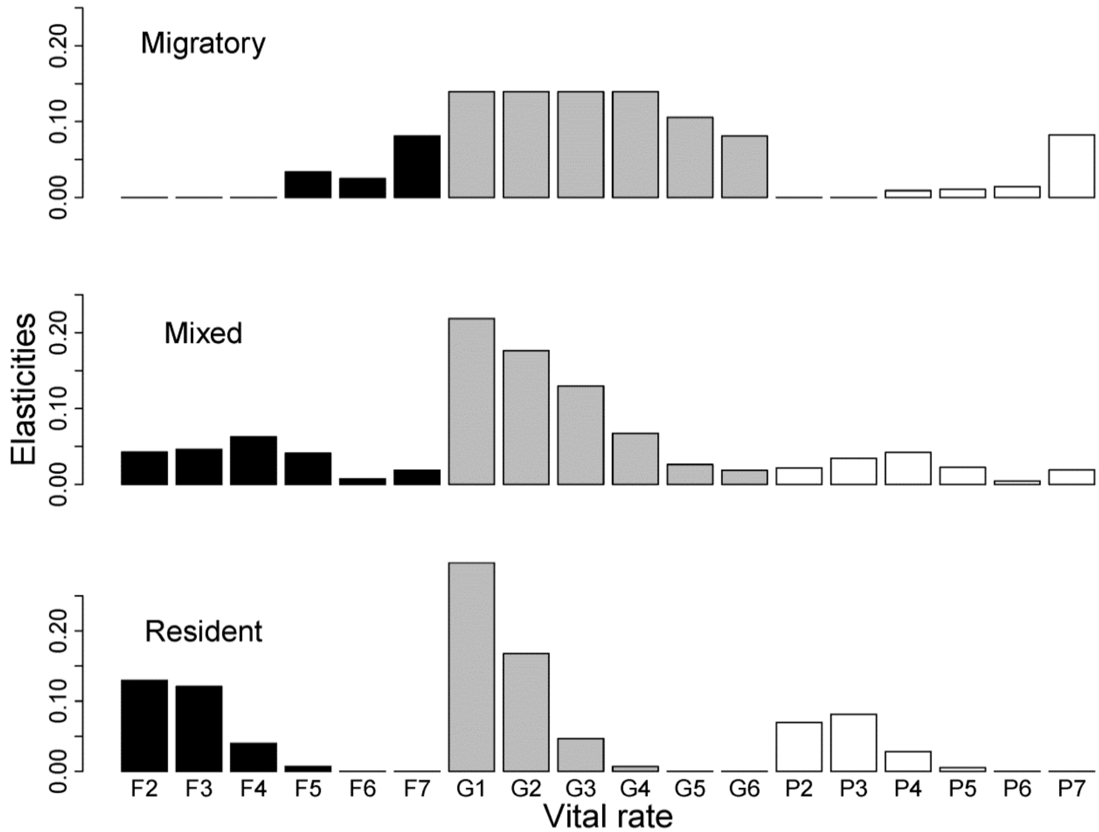

Figure 9.4. Elasticity values of stage-specific matrix elements for three different bull trout life-history types. Black bars represent elasticity values for fertility rates, gray bars represent elasticities associated with the probability that an individual survives and grows into the next stage, and open bars represent elasticities for the probability that an individual survives and remains in the current stage.

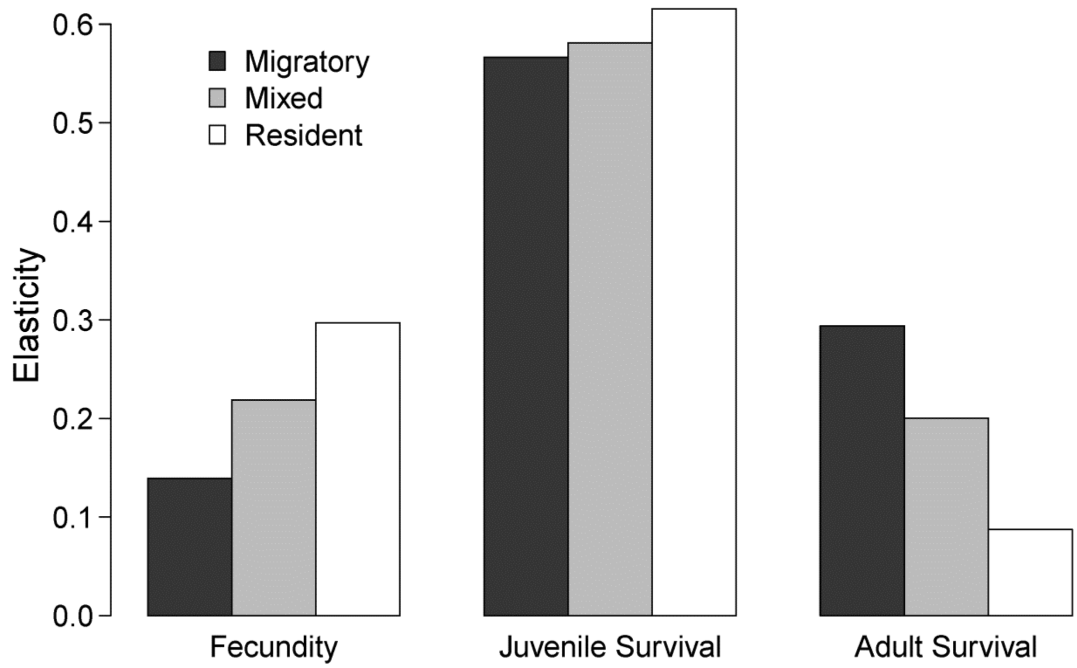

Figure 9.5. Elasticity values representing matrix elements for fertility, juvenile survival, and adult survival combined across life stages for three different bull trout life-history types. Elasticities for fertility are summed across all stages; juvenile survival represents the sum of G_1 through G_4 and P_2 through P_4 for migratory and mixed life-history types, and $G_1 + G_2 + P_2$ for the resident type; adult survival is the sum of all remaining matrix elements.

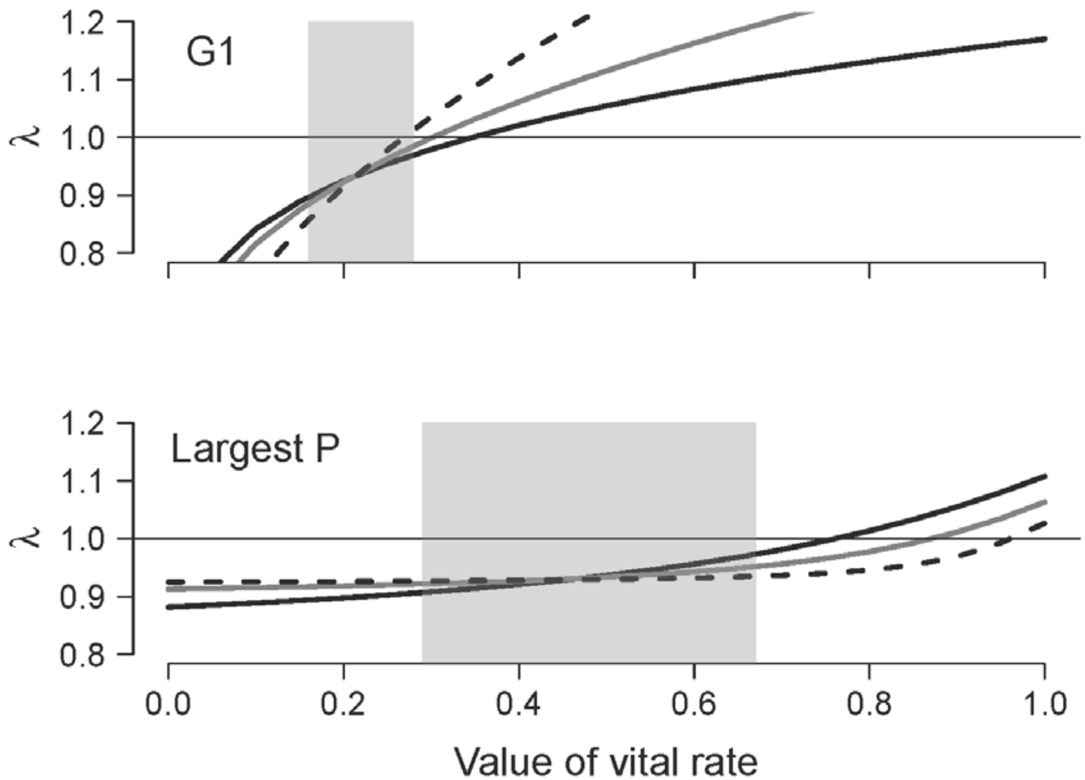

Figure 9.6. Response of population growth rate (λ) to changes in a single matrix element across a range of values while holding all other elements constant for the migratory (solid black line), mixed (gray line), and resident (dashed line) life-history types. Matrix elements are described in Figure 9.2; the largest value of P refers to P_7 for the migratory and mixed life-history types, and P_5 for the resident type. A horizontal reference line shows a reference value of $\lambda = 1$, and shaded areas represent the range of possible values for each vital rate based on 95% confidence intervals (for G1) or 95% credible intervals (for P).

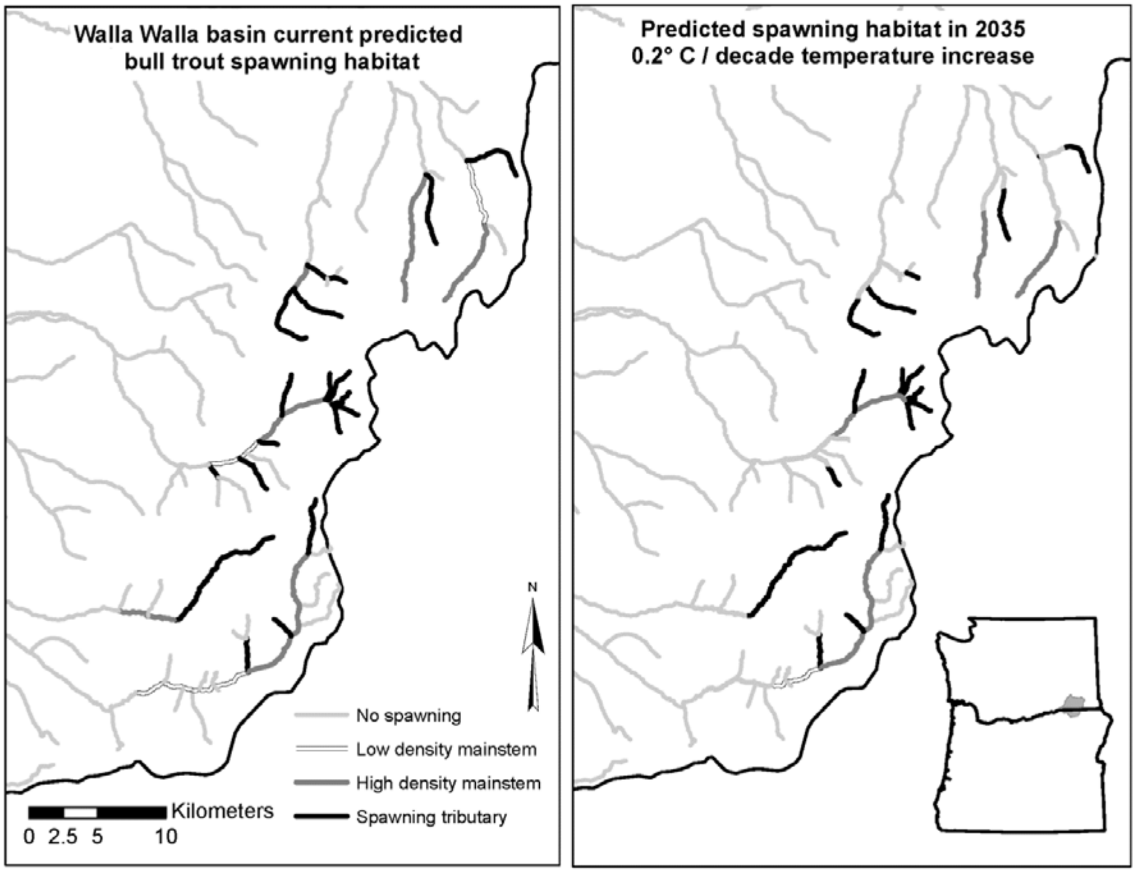

Figure 9.7. Three categories of suitable spawning habitat in the Walla Walla basin under current conditions (left panel), and predicted available spawning habitat in 25 years (2037) based on a 0.2 °C per decade increase in stream temperatures (right panel). Spawning habitat types were based on the rule set described in Table 9.5.

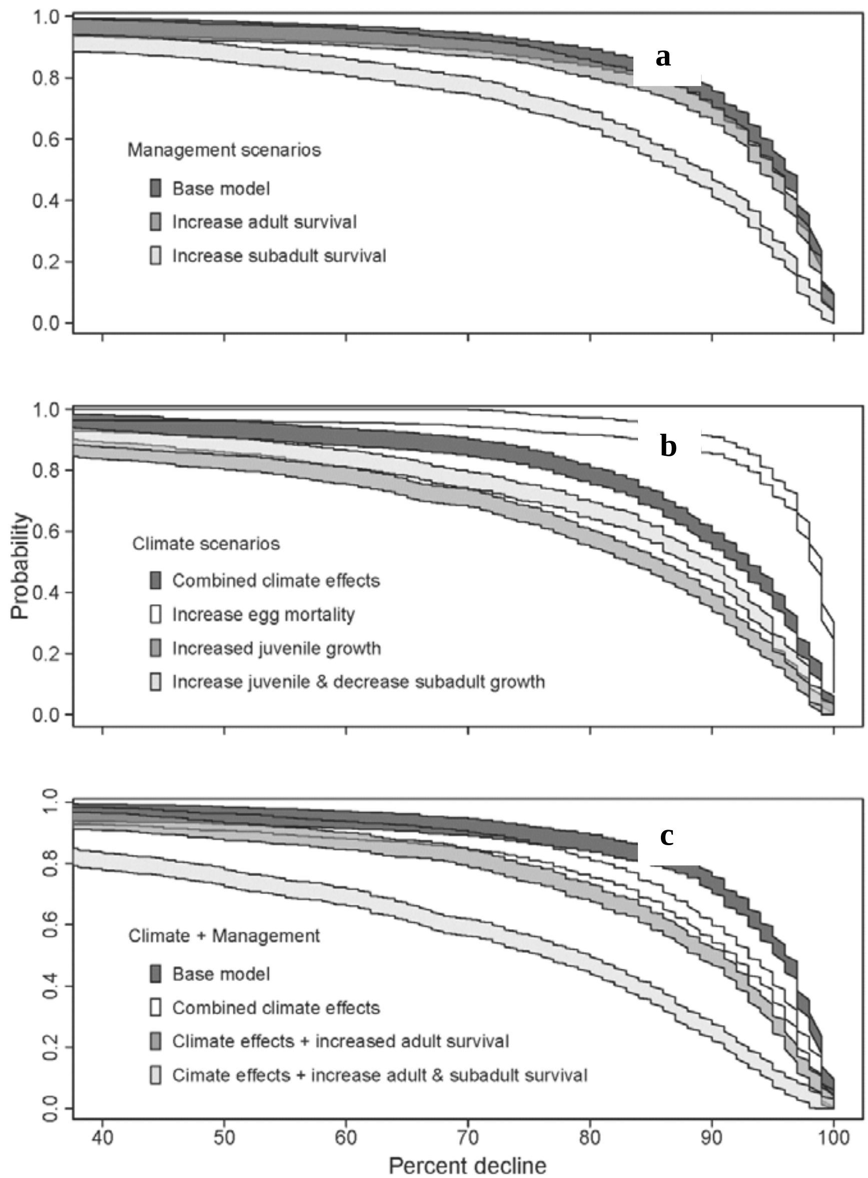

Figure 9.8. Effects of potential changes to vital rates resulting from changes in climate or management on the probability of the Walla Walla basin metapopulation declining by a percentage of the current population size in 25 years, assuming a baseline population growth rate of λ=0.931. The width of the band represents 95% confidence intervals.

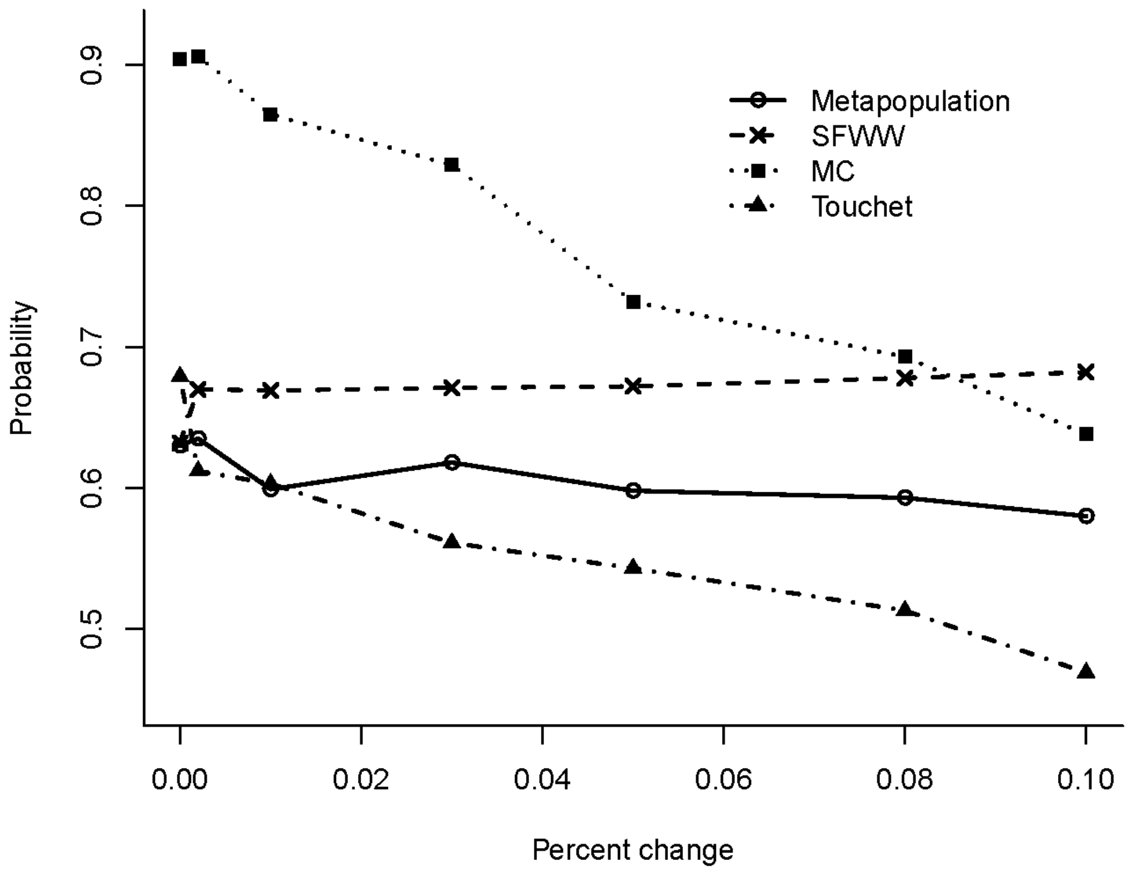

Figure 9.9. Effects of varying dispersal rates on the probability that a population will fall below 75% of its current population size in 25 years based on a scenario in which all three sub-populations were affected by climate-related changes in vital rates, and positive management actions were applied to the SFWWR and TR populations (λ = 0.983), but not to the MC population (λ = 0.928).

Appendix 8B

Bull Trout Growth, Spawning, Migrations, Fecundity, and Survival

Between 2002 and 2012, we sacrificed a total of 62 bull trout from the South Fork Walla Walla River (SFWWR), Oregon. We removed sagittal otoliths to estimate age, and used this data to develop a von Bertalanffy growth model to estimate age-at-length (Iseley and Grabowski 2007). Based on available data, the von Bertalanffy equation for the SFWWR bull trout population was

$$L_t = 1134(1 - e^{-0.07(t+0.02)}),$$

where L_t is the length of the fish at time (or age) t (Figure B8.1). We used this model, combined with growth estimates from mark-recapture data, to establish stages for bull trout that represented age classes (Table B8.1).

We counted eggs from 22 sacrificed mature females and used non-linear regression to develop a fecundity-to-length relationship (Figure B8.2). We assessed spawning probability based on the total number of marked individuals in each size class observed making a distinct spawning migration relative to the number of marked individuals in each size class detected during that year (Table B8.2).

We estimated stage transition probabilities based on the proportion of marked survivors from a given stage during one year that grew into another stage in the following year in SFWWR and Mill Creek (MC; Table B8.3a and B8.3b). We also evaluated the range of growth rates for different sizes of bull trout from each of the populations of interest (Figure B8.3)

We estimated survival rates for six stage of bull trout based on a Barker model implemented in Program MARK and analyzed with a random effects model in a Bayesian framework. We modeled survival as differing between years and among groups. We used minimally informative prior distributions on the mean (μ) and standard deviation (σ) of the hyperdistribution. We assumed a normal prior distribution on μ, with a mean of 0 and standard deviation (SD) of 100, and a gamma distribution prior for σ, with α = 1.001 and β = 0.0001. For all other parameters (not included in the hyperdistribution), we assumed a reasonably uninformative prior distribution of with a mean of 0 and SD of 1.75 (White et al. 2009). We ran 10 complete Monte Carlo Markov Chains, and after assessing convergence of the chains, we used a sample size of 10,000 from the posterior distribution of a single chain to calculate summary statistics. For the stage-specific survival parameters in the population models, we back-transformed estimates of μ and σ from the posterior probability distribution to get the mean estimate of survival and 95% credible intervals. These values represent the mean estimates of survival for each life stage over ten years and the associated temporal process variance, with sampling variance removed (Table B8.4).

Literature Cited

Iseley, J. J., and T. B. Grabowski. 2007. Age and growth. Pages 187-228 *in* C. S. Guy, and G. W. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

White, G. C., K. P. Burnham, R. J. Barker, D. L. Thomson, E. G. Cooch, and M. J. Conroy. 2009. Evaluation of a bayesian MCMC random effects inference methodology for capture-mark-recapture data. Pages 1119-1127 *in* G. P. Patil, T. G. Gregoire, A. B. Lawson, and B. D. Nussbaum, editors. Modeling demographic processes in marked populations, volume 3. Springer US, New York.

Table B8.1. Size classes for bull trout, given in total length (TL) and fork length (FL), and the median length in each size class. Size classes approximate ages, based on data from a von Bertalanffy growth model and observed growth estimated from individuals marked and recaptured in the South Fork Walla Walla River, Oregon.

Size class	TL (mm)	FL (mm)	Median TL (mm)
1	60 to 120	65 to 115	95
2	120 to 180	115 to 175	150
3	180 to 240	175 to 230	210
4	240 to 300	230 to 290	270
5	300 to 360	290 to 345	330
6	360 to 420	345 to 405	390
7+	>420	>405	500

Table B8.2. Total number of distinct spawning migrations of marked bull trout in each life stage per year relative to the total number of marked fish in each life stage that were detected in that same year. The proportion of observed spawning migrations relative to the total number of fish detected was used to establish a baseline estimate of spawning probability for population models.

	Observed spawning migrations				**Total marked fish detected**			
Year	stage4	stage5	stage6	stage7+	stage4	stage5	stage6	stage7+
2003	0	1	0	14	3	7	6	20
2004	0	1	0	15	16	10	4	32
2005	1	4	0	13	14	16	7	19
2006	0	5	4	12	12	11	10	17
2007	1	1	4	9	12	7	5	15
2008	2	1	3	10	9	2	5	10
2009	0	2	1	8	3	3	2	7
2010	2	1	0	6	18	4	2	8
2011	4	2	1	11	27	5	3	10
Total	10	18	13	98	114	65	44	138
Proportion	0.09	0.28	0.30	0.71				

Table B8.3. Number of recaptured individual bull trout from the (a) South Fork Walla Walla River and (b) Mill Creek populations that transitioned from one stage into another in the following year. Data shows for recaptures for all years between 2002 and 2011 combined. Size transition probabilities are shown in parentheses. For simplicity, some transition probabilities were combined in population models.

a.

Stage in year 2	Stage in year 1: 1	2	3	4	5	6	7
1	2 (0.05)	--	--	--	--	--	--
2	36 (0.95)	3 (0.08)	--	--	--	--	--
3	--	23 (0.64)	2 (0.12)	--	--	--	--
4	--	10 (0.28)	14 (0.88)	4 (0.30)	--	--	--
5	--	--	--	8 (0.62)	4 (0.67)	--	--
6	--	--	--	1 (0.08)	2 (0.33)	8 (0.8)	--
7	--	--	--		--	2 (0.2)	10 (1.0)
TOTAL	38	36	16	13	6	10	10

b.

Stage in year 2	Stage in year 1: 1	2	3	4	5	6	7
1	--	--	--	--	--	--	--
2	--	6 (0.46)	1 (0.17)	--	--	--	--
3	--	3 (0.23)	0 (0.00)	--	--	--	--
4	--	4 (0.31)	4 (0.66)	--	--	--	--
5	--	--	1 (0.17)	--	2 (0.11)	--	--
6	--	--	--	--	15 (0.83)	18 (0.24)	--
7	--	--	--	--	1 (0.06)	58 (0.76)	133 (1)
TOTAL	0	13	6	0	18	76	133

Table B8.4. Estimated mean (μ) and standard deviation (σ) of the hyperdistribution for survival rates. The mean and 95% credible intervals for μ and the mean of σ from the posterior distribution are reported.

Life stage	Survival (μ)	5% CI	95% CI	SD (σ)
Stage 2	0.264	0.154	0.403	0.205
Stage 3	0.382	0.258	0.539	0.097
Stage 4	0.384	0.194	0.608	0.165
Stage 5	0.389	0.311	0.527	0.048
Stage 6	0.444	0.318	0.586	0.076
Stage 7	0.471	0.293	0.666	0.189

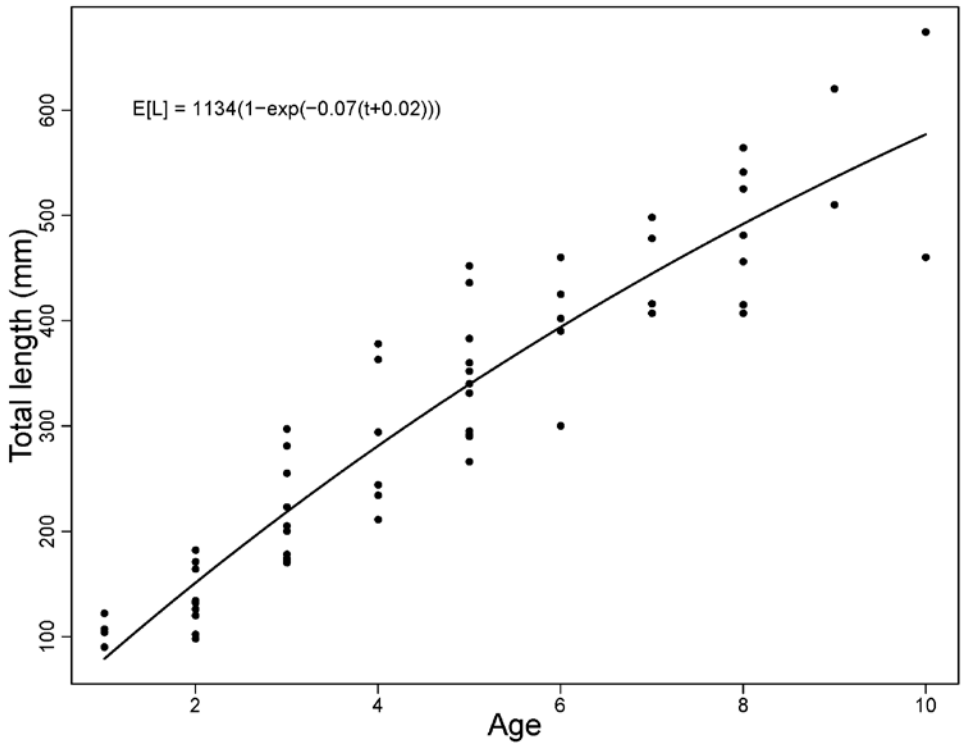

Figure B8.1. Von Bertalanffy growth curve based on aged otoliths removed from 62 sacrificed bull trout from the South Fork Walla Walla River, Oregon, between 2002 and 2011. The growth equation is shown on the graph.

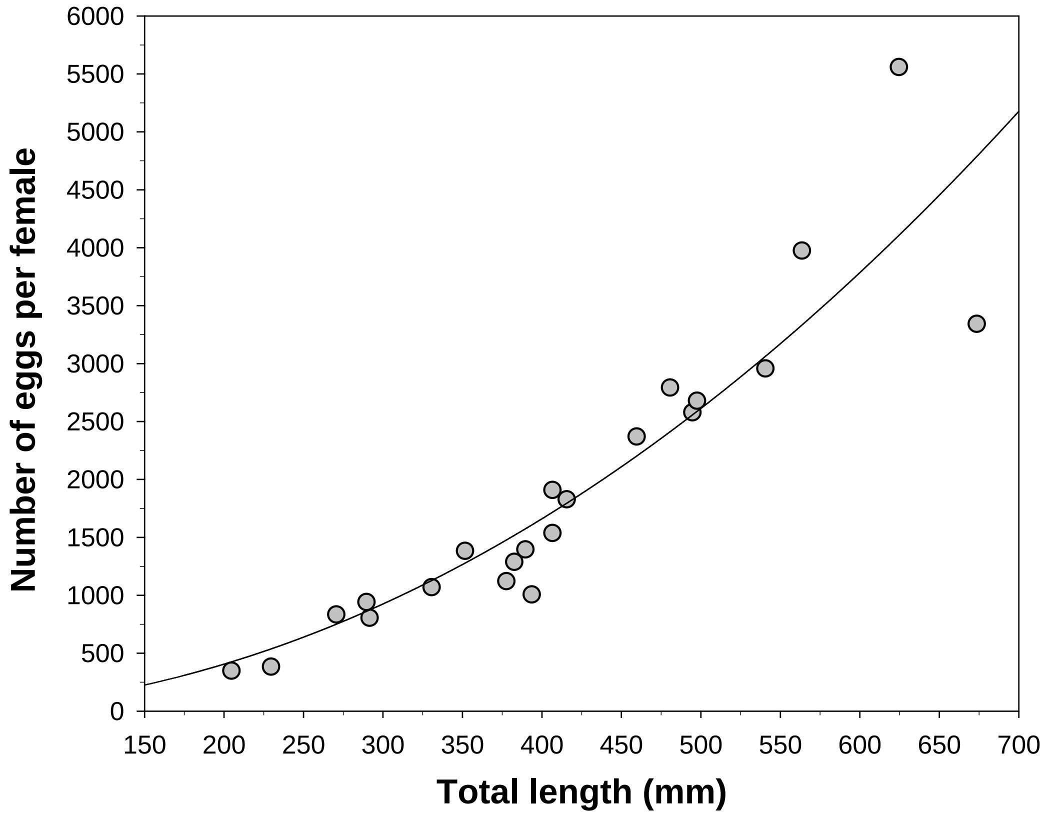

Figure B8.2. The total number of eggs from female bull trout of a given total length (mm). Data were from sacrificed or incidentally taken bull trout in the South Fork of the Walla Walla River, Oregon, between 2002 and 2011.

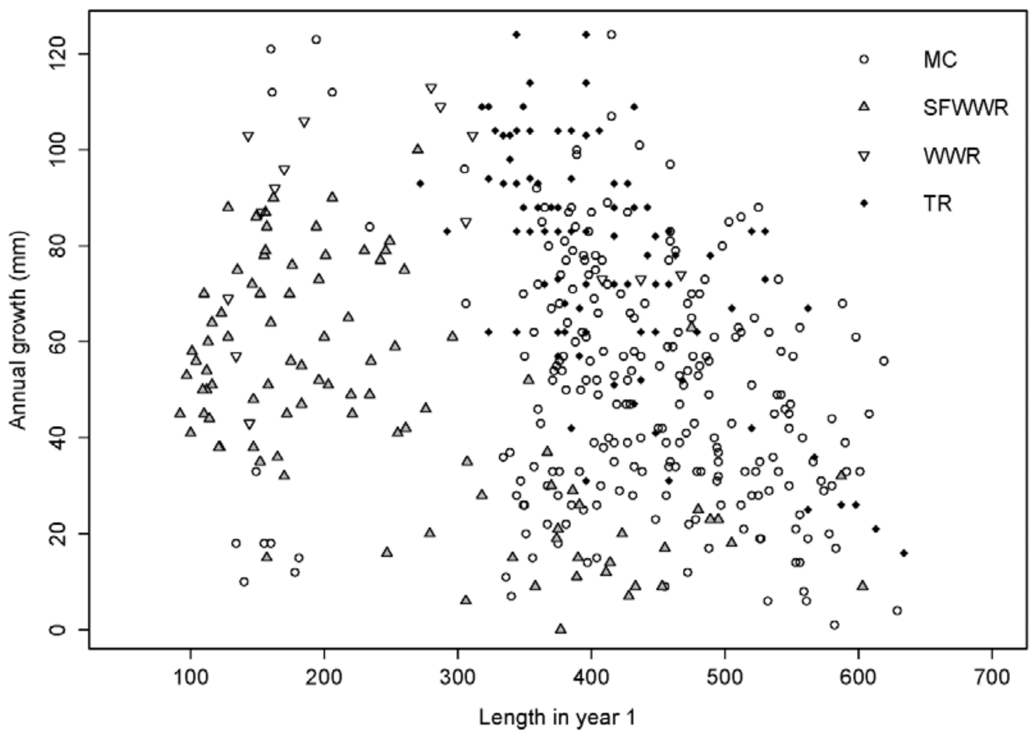

Figure B8.3. Annual growth rate (mm) for bull trout across a range of initial lengths from the mainstem Walla Walla River (WWR) and three tributary populations: Mill Creek (MC), South Fork Walla Walla River (SFWWR), and Touchet River (TR).

Appendix I - Walla Walla River Passive Instream Antenna Site Descriptions and Operations

authored by

Ryan Koch

U.S. Fish and Wildlife Service

Introduction

In 2002, the U.S. Fish and Wildlife Service (FWS) and Utah State University (USU) initiated a long term research project in the Walla Walla River (WWR) and tributaries to address critical knowledge gaps concerning bull trout ecology (Anglin et al. 2008a, 2008b; Anglin et al. 2009a, 2009b, 2010; Barrows et al. 2012a, 2012b, 2014). Since the beginning of this project, passive integrated transponder (PIT) technology has been the main tool used to gather information on bull trout. Passive instream antennas (PIA) have been installed throughout the basin since September of 2002 to collect data on bull trout (Figure I-1). Passive instream antenna sites were located in the South Fork Walla Walla River (SFWWR), Mill Creek, Yellowhawk Creek and the mainstem WWR (Figure I-2).

In order to interpret detection data, each array's operation status was evaluated to account for antenna down times throughout the duration of this study (Figure I-1). Since biological or physical detection efficiency was not calculated for each site on a continual basis, we estimated electromagnetic coverage at each array using a combination of antenna functionality (i.e., power outages and number of antennas functioning) and estimated percent flow monitored. For sites located at fish ladders or dams, both an upstream and downstream estimate of coverage was calculated. We produced monthly estimates of operational status for each PIA. Each PIA is unique in application and several critical assumptions were used to derive a monthly "efficiency" estimate. These unique site features are detailed in each PIA section. One critical assumption common to all PIA was that the average monthly estimates were based on bull trout tagged with 23 mm PIT tags. Several different models of PIT tags have been used in the basin to tag bull trout since 1998 and not all models are as detectable as 23 mm PIT tags, which are larger and have a greater read range especially at sites with pass over or flat plate antenna design types. The second assumption was if the PIA was on, the detection probability within the antenna's read range was 100%. Further, we did not have the ability to account for tag collisions, which occur when two PIT tags occur within the electromagnetic field of an antenna at the same time. The result of a tag collision is that neither tag is interrogated. In addition, we did not account for noise variations at individual antennas. Ambient noise at each PIA can fluctuate, and can affect the ability of an individual antenna to detect a PIT tag. In general, PIAs were built to detect 12 mm PIT tags throughout when the antenna was used in an upright, pass through orientation.

Walla Walla River Passive Instream Antenna Sites
(Ordered from upstream to downstream)

The Bear Creek PIA (WW2) was installed on the SFWWR near the confluence of Bear Creek, 21.4 km upstream from the confluence of North and South Forks of the Walla Walla River and SFWWR. The PIA was installed on October 16, 2002, and was operational for the duration of the study except for periods of down time related to power outages and damage caused by high flow events. The instream portion of the array consisted of two pass through antennas, approximately 4.5 m long by 1.4 m high that spanned the width of the river (Figure I-3). Array functionality at WW2 is summarized in Table I-1. Efficiency values were calculated by dividing the number of days when the array was on and functioning properly by the total days in each month. We assumed that all flows were covered by the antennas as long as both antennas were on and functioning properly. We estimated the percent flows covered in the event that only one antenna was functioning. Since the thalweg of the SFWWR passes through antenna 2 during most times of the year, we assumed that antenna 2 covered 75% of the flows and antenna 1 only covered 25% of the flows.

The Harris Park Bridge (WW1) PIA was installed on the SFWWR just below Harris County Park (rkm 12.8). The array has been operational since September 3, 2002, except for periods of down time related to power outages and damage caused by high flow events. The instream portion of the array consists of two pass through antennas, approximately 5.5 m long by 1.4 m high that span the width of the river. On October 4, 2006, three pass over antennas were installed downstream of the pass through antennas for directional information (Figure I-4). Large flow events in May 2008 and again in January 2009 damaged the array and only pass through antennas 1 and 2 were reinstalled. Array functionality at WW1 is summarized in Table I-2. Efficiency values were derived from dividing the number of days when the array was on and functioning properly by the total days in each month. We assumed that all flows were covered by the antennas as long as both antennas were on and functioning properly. We estimated that each antenna covered 50% percent of stream flow past the array. Pass over antennas were not used to calculate functionality as we assumed all flows were covered by pass through antennas.

The Nursery Bridge Dam (NBA) PIA is located on the mainstem WWR at Nursery Bridge Dam (rkm 74.3) in the town of Milton-Freewater, Oregon. The array has been operational since October 3, 2003, except for periods of down time related to power outages and damage to antennas caused by vandalism or high flows. Nursery Bridge Dam has three routes of downstream passage: east fish ladder, west fish ladder, and the spillway (Figure I-5). All upstream passage occurs through the east or west ladders as fish are not believed to be able to jump the spillway. A single antenna was originally installed in the east fish ladder. The west ladder antenna was installed April 15, 2004. The west ladder is shut down at the onset of summer low flows and all flows are directed through east ladder until fall or winter flows breach a manmade berm upstream. In July 2006, a second antenna was added to the east ladder to gain direction of fish movement. In an attempt to monitor the lower spillway notch additional antenna were installed from 2007-2009 to determine downstream passage over the spillway; however, none remained intact during high flow events.

Functionality of the array at NBA is summarized in Table I-3 (downstream) and Table I-4 (upstream). Data from the WDOE/WWBWC Pepper Bridge stream gage (ID: 32A120/S108; rkm 66.3) were used to estimate flows at Nursery Bridge Dam. We estimated that the east ladder passes 60 cfs and the west ladder (when in operation) passes 40 cfs. These rough flow estimates were based on USACOE Operational Guidelines for Nursery Bridge Fishway and personal communication with ODFW fish passage biologists. All flows over 100 cfs were assumed unmonitored and passed over the spillway. The downstream monthly efficiency value was derived by first calculating the percent flows passing through each ladder and then dividing the resulting value by the percentage of days per month each ladder antenna was functional. We did not attempt to include the lower spillway notch monitoring into this analysis as it was impossible to estimate flows around the multiple antenna configurations used. Upstream passage was assumed to be 100% when at least one antenna was functioning in each ladder. Upstream coverage is not related to flows as it is assumed that all fish must pass through one of the ladders during upstream movements.

The Burlingame Diversion Dam (BGM) PIA is located on the mainstem WWR at rkm 60.6 (Figure I-6) near the Oregon/Washington border. The site started monitoring for PIT tag detections beginning on January 24, 2007. The diversion facility has three routes of downstream passage: spillway, fish ladder, and canal. Pass through antennas monitor the fish ladder and canal. Tagged fish could pass undetected by going over the spillway. Additionally, a “passage notch” was opened on the spillway during adequate flows which was partially monitored from February 2007 to June 2010. Upstream passage occurred through the ladder and at times, the spillway passage notch. The fish ladder and canal entrance had two antennas each to provide insight into the direction of movement. Canal antennas measure approximately 6.4 meters long by 1.2 meters high and were installed just below the headgate. Fish ladder antennas measure approximately 0.9 meter long and 2.4 meters high and were attached to the upstream side of two weirs inside the fish ladder. A pass through antenna was also installed on the fish bypass channel in August 2008 to infer residence time of tagged fish in the canal. The canal was watered at the beginning of March, dewatered when instream flows drop below 18 cfs (usually in July), and watered again around October 1. Operation of the canal continued until irrigation delivery requirements were fulfilled, usually into December.

Array functionality at BGM is summarized in Table I-5. Flow data from the WDOE Beet RD gage station (ID: 32A105) were used to estimate percent flows monitored. We also used flow data measured going into the canal provided by Gardena Farms Irrigation District #13. We assumed that all flows through the ladder and into the canal were 100% covered when the PIA was operational. The monthly average was derived by first calculating the percent flows passing through the ladder and canal (when operating) and then dividing the resulting value by the percentage of days per month the array was functional. We did not account for detections at the passage notch as there was no record of operation and no way to discern direction. Upstream passage was not calculated because of the unknown operation of the passage notch. All tagged fish passing through the fish ladder would likely be detected as long as the PIA was on and no tag collisions occurred.

The Lowden Diversion Dam (LWD) PIA was located on the mainstem of the WWR at rkm 51 (Figure I-7). The diversion facility consisted of a blow up spillway that was unmonitored and a fish ladder. The PIA was installed in the ladder on November 29, 2007 and consisted of a single pass through antenna. Most flows, outside of summer low flows, spill over the dam. Array functionality at LWD is summarized in Table I-6 and consists of the percentage of days per month the site operated. This summary does not take into account flows at the array as a percentage flow estimate for the fish ladder was not calculated.

The Oasis Road Bridge (ORB) PIA was located on the mainstem of the WWR at rkm 10.1. The first antenna was installed April 15, 2005 and the additional five antennas were operational by August 2005. The array consisted of 6 total antennas which span the width of the river (Figure I-8). Two pass-over antennas were secured to the north and south shorelines. There are four hybrid pass through/over antennas attached to bedrock substrate and monitored the low flow width of the river.

The temporal performance of the ORB PIA was determined by calculating the monthly proportion of the water column monitored by the PIA. The monthly proportion of water column monitored was calculated by averaging all daily proportions. Each daily proportion of water column monitored was estimated from information on the daily area monitored by the array, the daily cross sectional area of the stream at the array, the functional status of each antenna (e.g., operational, not operational, not present), percent area monitored by each antenna, and water stage height.

The average daily stage data at USGS gage #14018500 (WWR near Touchet) was used to represent stage height at the ORB PIA. The stream gage is located 15 km upstream from the array. There are no major tributaries between the gage and the PIA, and observations suggested that stage heights at ORB responded similarly to stage heights at the USGS gage over a range of streamflows. Observations suggested that the river came into contact with bank antennas 1 and 6 (Figure I-8) when the USGS gage height was approximately 0.9 m, and flows exceeded the height of all of the antennas when the USGS gage height exceeded approximately 1.6 m. We used stream width and stage height to calculate the total cross sectional area of the river. River cross sectional area was compared to the cross sectional area of the PIA to determine the proportion of the river monitored by the PIA. Since gaps exist between several antennas, those areas were not included in calculations of the area monitored. Although river width typically varied with stage height, when flows were at or near a minimum (h_{min}) and stage height was $\leq$ 0.9 m we assumed the width of the river was equal to 13.3 m (W_4) (Figure I-9). When stage height was > 0.9 m, we assumed the width of the river was equal to 18.0 m (W_5). The following calculations were conducted to estimate the monthly proportion of the river cross section monitored by the PIA:

1) Area monitored by each antenna;
2) Area monitored by the array each day;
3) Total river cross sectional area each day;
4) Daily proportion of the river cross sectional area monitored;
5) Average the daily proportion of the river cross sectional area monitored for monthly estimates.

1) The area monitored by each antenna was calculated using the following equations;

$$A_{1,6} = (F\ x\ P\ x\ E\ x\ I\ x\ (h_d - h_{min}))$$
$$A_{2-5} = (F\ x\ P\ x\ E\ x\ h_d)$$

where,

$A_{1,6} = the\ area\ monitored\ by\ antennas\ 1\ and\ 6,$
$A_{2-5} = the\ area\ monitored\ by\ antennas\ 2, 3, 4\ and\ 5,$

$F \begin{cases} = 1\ if\ the\ antenna\ is\ functional \\ = 0\ otherwise \end{cases},$

$P = percent\ area\ monitored\ by\ each\ antenna\ based\ on\ monthly\ measurements,$
$E = electromagnetic\ field\ width,$

$I \begin{cases} = 1\ if\ h_d > 0.9 \\ = 0\ otherwise \end{cases},$

$h_d \begin{cases} = h_d\ if\ h_d < 1.6 \\ = 1.6\ otherwise \end{cases},$

$h_{min} = 0.9$

2) The area monitored ($Area\ Monitored_d$) each day was then calculated using the following equation;

$$Area\ Monitored_d = A_1 + A_2 + A_3 + A_4 + A_5 + A_6$$

3) The total river cross sectional area at the array ($Total\ Area_d$) each day was calculated using the following equation;

$$Total\ Area_d = [h_d(W_4)] + I(W_5 - W_4) \times (h_d - h_{min})$$

where,

$h_d = daily\ river\ stage\ height,$
$h_{min} = 0.9,$
$W_4 = 13.3,$
$W_5 = 18.0,$

$$I\begin{cases} = 1\ if\ h_d > 0.9 \\ = 0\ otherwise \end{cases}$$

4) The daily proportion of river cross section monitored was calculated using the following equation;

$$Daily\ proportion\ of\ cross\ section\ monitored = \frac{Area\ Monitored_d}{Total\ Area_d}$$

5) The mean monthly proportion of river cross section monitored was calculated by averaging the daily proportion of cross section monitored.

Mill Creek Passive Instream Antenna Sites
(Ordered from upstream to downstream)

The Mill Creek Intake Dam (MCI) PIA was located at the City of Walla Walla water intake dam (rkm 41). The site was installed on June 28, 2011. The MCI site consisted of a ladder and spillway (Figure I-10). Only the fish ladder was monitored with two pass through antennas (1.6 meters tall by 0.8 meters wide) located near the top and bottom of the structure.
The MCI PIA experienced no down time from date of original installation through 2011. Since only the fish ladder was monitored, all PIT tagged fish migrating upstream were assumed to have been detected. Downstream detection efficiency was not calculated for this site.

The Kiwanis Camp Bridge (KCB) PIA was originally installed at Kiwanis Camp Bridge (rkm 35) on April 15, 2005, but noise interference issues forced biologists to move the PIA approximately 170 meters upstream to a private bridge crossing on May 11, 2005. The PIA originally consisted of five pass through antennas (approximately 3.1 meters long by 1.2 meters high) that spanned the width of the creek (Figure I-11). In 2007, as the pass through antennas failed, they were replaced with pass over antennas (same length as pass through antennas) in an attempt to circumvent damage during high flow events. This site was decommissioned on March 31, 2011.

Site functionality at KCB was summarized in Table I-8. Daily average flow data from the USGS gage #14013000 (Mill Creek near Walla Walla, WA, rkm 33.8) was used to estimate the percent flows monitored by the array. The monthly average was derived by first calculating the percent of flows monitored passing through or over the antennas and then dividing that result by the percentage of days per month each antenna was functional. Pass through antennas used during the first three years of operation were assumed to have monitored 100% of flows while functioning. Pass over antennas used starting in 2007 were assumed to have monitored 0.46 meters (equivalent to 263 cfs) of the water column.

The Bennington Lake Diversion Dam (MCD) PIA is located near upper end (rkm 18.5) of the Mill Creek Flood Control Project near the City of Walla Walla. The dam is a flood control structure that diverts water into Bennington Lake under flood conditions (flows >2500 (cfs)). Bennington Lake Diversion Dam has three routes of downstream fish passage: a fish ladder, low flow outlet (LFO), and spillway (Figures I-12, I-13). Upstream fish passage is assumed to be possible only via the fish ladder since the spillway is impassable and a combination of high water velocity and head pressure at the radial gate in the LFO likely forms a barrier. The fish ladder is designed for flows up to 42 cfs. The LFO is opened when flows exceed 42 cfs and remain below approximately 400 cfs. When instream flows exceed 400 cfs for an extended period, both the ladder and LFO are closed and all water passes over the spillway.

The Bennington Lake Diversion Dam was monitored for detections within the fish ladder and the LFO. The ladder had two antennas originally installed on February 25, 2005. Monitoring the LFO with PIT antennas began in 2005, but the antenna designs were reliable (able to withstand high flows) until an experimental flat plate antenna was mounted to the floor on August 11, 2008. Two additional flat plate antennas were installed within the LFO on February 18, 2009 to provide additional detection capabilities. High water velocities in the LFO may result in tagged fish passing downstream undetected even under relatively low flows. The spillway and the Bennington Lake diversion canal (non-flood flows usually ran through fish screen) are not monitored for PIT detections. Array functionality at MCD is summarized in Tables I-9 (downstream) and Table I-10 (upstream). Flow data from the USGS gage #14013700 (Five Mile Road near Walla Walla, WA) was used to estimate the percent flows monitored by the array. The downstream monthly value was calculated as percent flows passing each antenna divided by the percentage of days per month each antenna was functional. Upstream passage was assumed to be 100% when at least one ladder antenna was functioning.

The Mill Creek Division Dam (MCD2) PIA was located downstream from MCD and was part of the first division works that diverts water into Yellowhawk Creek at rkm 16.9. The Mill Creek Division Dam has two routes of passage; a fish ladder and spillway consisting of four arm gates. The gates are opened for spill when flows are predicted to remain above 400 cfs for extended periods. It is assumed that upstream passage is not possible when the gates are down and all upstream passage occurs through the fish ladder during non-spill operations (flows <400 cfs).

The Mill Creek Division Dam was monitored for detections with antennas in the ladder and spillway. The ladder was monitored for detections beginning February 14, 2007 with a single pass through antenna. On November 20, 2008, a second antenna was installed to provide direction of fish passage. Experimental flat plate antennas were mounted on the spillway on August 12, 2010, but soon started leaking and provided minimal detection capability. The spillway antennas were removed on May 15, 2012.

Passive instream antenna functionality at MCD2 was summarized in Tables I-11 (downstream) and I-12 (upstream). Flow data from the USGS gage #14015000 (Mill Creek at Walla Walla, WA) was used to estimate the percent flows monitored by the array. The monthly value was derived by calculating the percent flows passing each antenna, then dividing the resulting value by the percentage of days per month each antenna was functional.

Yellowhawk Creek is a distributary of Mill Creek that historically was operated to divert flows away from downtown Walla Walla during periods of flooding. Currently, flows are maintained through a radial gate at less than 70 cfs to prevent flooding of residential properties and to provide irrigation water (COE 2007). During low flow periods (summer and fall), a majority of Mill Creek instream flows are diverted down Yellowhawk Creek. Upper Yellowhawk Creek

(YHC) is monitored with a single pass through antenna (4.6 meters long by 0.9 meters high) that spans the entire channel width (Figure I-14). The YHC passive instream antenna was installed on December 12, 2006, approximately 50 meters downstream from the radial gate. Array functionality at YHC is summarized in Table I-13. This summary does not incorporate flows at the PIA since all flows was monitored by the antenna as long as it was functioning. Middle Yellowhawk Creek (YHC2) is monitored with a single pass through antenna (3.0 meters long by 0.6 meters high) (Figure I-15). The YHC2 passive instream antenna was installed on August 8, 2007 at rkm 8. A weir was constructed to force fish through the antenna. Functionality at YHC2 is summarized in Table I-14. This summary also does not take into account flows at the array as all flows were monitored by the antenna as long as it was functioning.

Literature Cited

Anglin, D.R., D.G. Gallion, M. Barrows, C. Newlon, R. Koch. 2008. Current Status of Bull Trout Abundance, Connectivity, and Habitat Conditions in the Walla Walla Basin 2007 Update.

Anglin, D.R., D.G. Gallion, M. Barrows, C. Newlon, P. Sankovich, T.J. Kisaka, and H. Schaller. 2008. Bull Trout Distribution, Movements and Habitat Use in the Walla Walla and Umatilla River Basins 2004 Annual Progress Report.

Anglin, D.R., D.G. Gallion, M. Barrows, R. Koch, and C. Newlon. 2009. Monitoring the Use of the Mainstem Columbia River by Bull Trout from the Walla Walla Basin. Final Report for 2007 prepared for the U.S. Army Corps of Engineers, Walla Walla, WA.

Anglin, D.R., D.G. Gallion, M. Barrows, R. Koch, and C. Newlon. 2009. Monitoring the Use of the Mainstem Columbia River by Bull Trout from the Walla Walla Basin. Final Report for 2008 prepared for the U.S. Army Corps of Engineers, Walla Walla, WA.

Anglin, D.R., D.G. Gallion, M. Barrows, R. Koch, and C. Newlon. 2010. Monitoring the Use of the Mainstem Columbia River by Bull Trout from the Walla Walla Basin. Final Report for 2009 prepared for the U.S. Army Corps of Engineers, Walla Walla, WA.

Barrows, M.G., R. Koch, D.R. Anglin and S.L. Haeseker. 2012a. Use of the Mainstem Columbia River by Walla Walla Basin Bull Trout. 2010 Annual Report to the U.S. Army Corps of Engineers, Walla Walla District. Project BT-W-10-2.

Barrows, M.G., R. Koch, D.R. Anglin and S.L. Haeseker. 2012b. Use of the Mainstem Columbia River by Walla Walla Basin Bull Trout. 2011 Annual Report to the U.S. Army Corps of Engineers, Walla Walla District. Project BT-W-10-2.

Barrows, M.G., R. Koch, D.R. Anglin and S.L. Haeseker. 2014. Use of the Mainstem Columbia River by Walla Walla Basin Bull Trout. 2012 Annual Report to the U.S. Army Corps of Engineers, Walla Walla District. Project BT-W-10-2.

Budy, P., R. Al-Chokhachy, and G.P. Thiede. 2003. Bull trout population assessment and life-history characteristics in association with habitat quality and land use in the Walla Walla River Basin: a template for recovery planning. 2002 Annual Progress Report to US Fish and Wildlife Service, Vancouver, Washington. 41 pp.

Budy, P., R. Al-Chokhachy, and G.P. Thiede. 2004. Bull trout population assessment and life-history characteristics in association with habitat quality and land use: a template for recovery planning. 2003 Annual Progress Report to US Fish and Wildlife Service, Vancouver, Washington. 70 pp.

U.S. Army Corps of Engineers (ACOE) - Walla Walla District. 2007. Fish Passage Plan for Mill Creek Project. Walla Walla, WA.

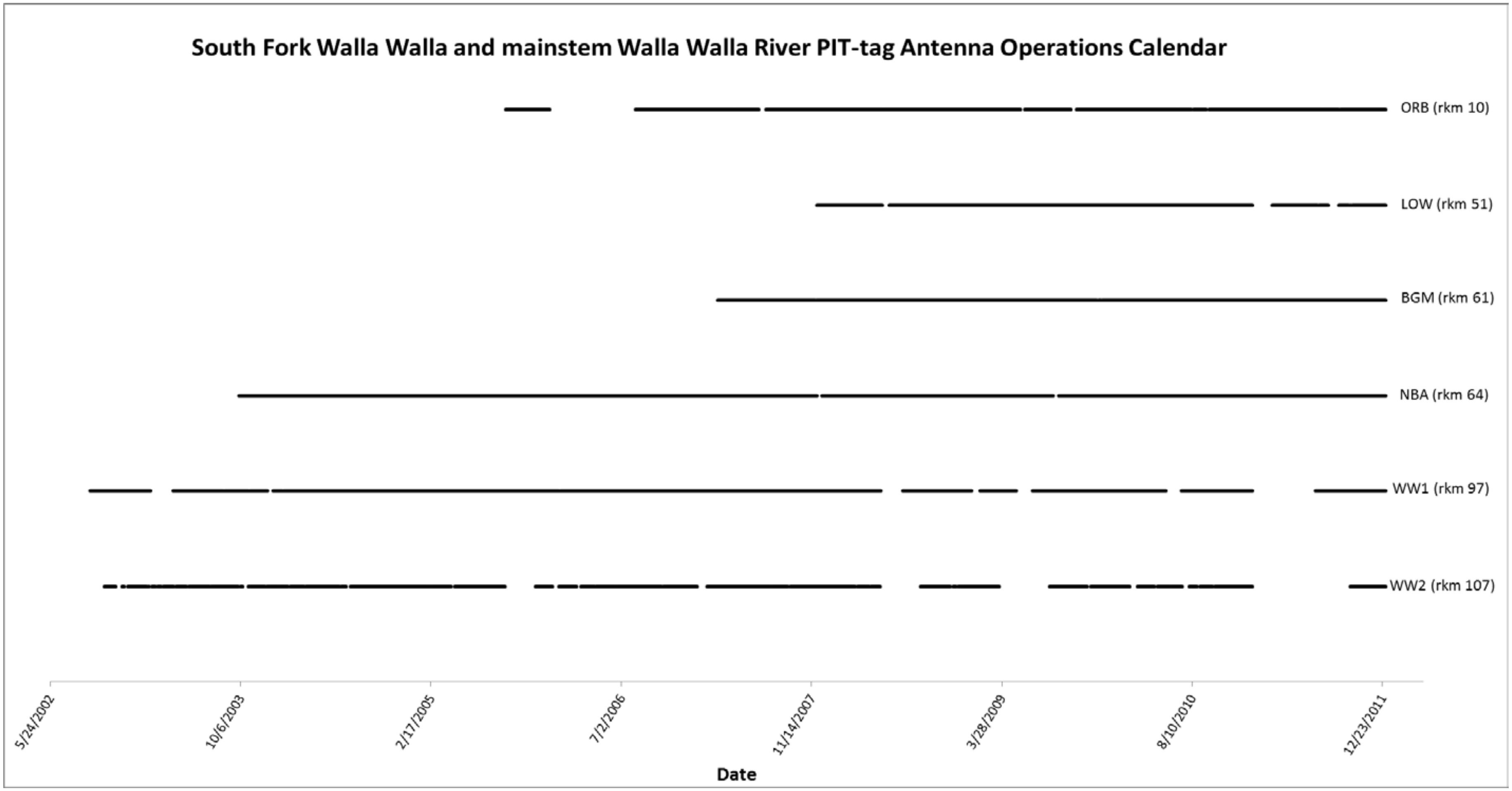

Figure I-1. Time line showing each PIA and operations since installation.

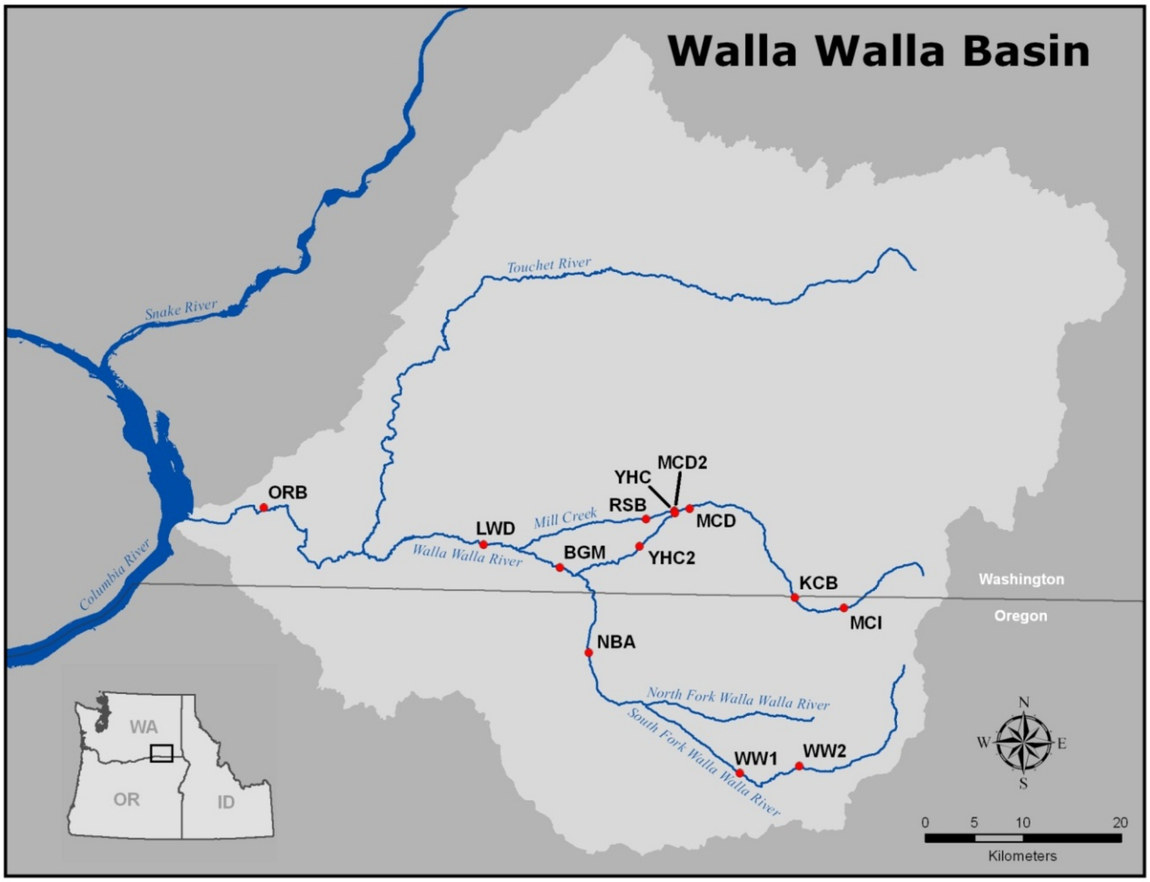

Figure I-2. Passive instream antennas located throughout the Walla Walla River and main tributaries.

Figure I-3. Bear Creek (WW2) PIA spanning the South Fork Walla Walla River. Antenna 1 and 2 are located on the left and right, respectively.

Table I-1. Average monthly percent flows covered by electromagnetic field based on operational status of the Bear Creek passive instream antenna (WW2).

	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
January	na	10	50	50	25	40	100	100	100	48
February	na	10	50	50	25	60	100	100	100	0
March	na	10	50	50	0	100	93	75	40	0
April	na	10	50	50	0	100	87	5	100	0
May	na	10	50	50	50	100	50	5	90	0
June	na	100	50	50	100	87	0	5	100	0
July	na	100	35	50	100	100	0	5	45	0
August	na	100	100	50	100	100	13	95	100	0
September	na	100	100	0	100	87	100	75	100	94
October	25	75	100	0	94	100	100	85	97	100
November	25	10	100	40	100	100	80	75	90	94
December	25	10	100	100	100	100	94	100	100	22

Figure I-4. Harris Park Bridge (WW1) PIA showing pass through antennas (upstream) and pass over antennas (downstream).

Table I-2. Average monthly percent flows covered by electromagnetic field based on operational status of the Harris Park Bridge (WW1) PIA.

	2002	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**
January	na	10	90	100	45	100	94	30	100	50
February	na	0	100	100	50	100	100	50	100	0
March	na	0	100	100	50	100	100	50	100	0
April	na	10	100	100	50	100	100	50	100	0
May	na	50	94	94	50	100	50	10	75	0
June	na	100	50	100	50	100	0	50	0	3
July	na	100	50	90	50	100	70	100	58	100
August	na	100	100	100	50	100	100	100	100	100
September	25	100	100	100	50	100	100	100	100	100
October	50	100	100	100	50	100	100	100	100	100
November	50	50	100	100	75	100	88	100	100	100
December	50	25	100	88	100	100	100	100	100	100

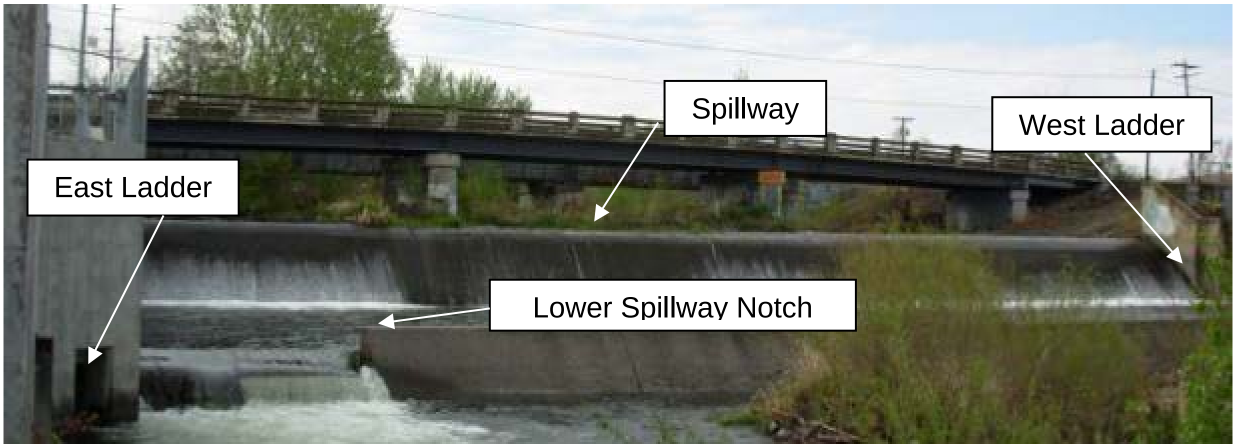

Figure I-5. Nursery Bridge Dam showing from left to right: east fish ladder, lower spillway notch, spillway, and west fish ladder from downstream view.

Table I-3. Average monthly percent flows covered by electromagnetic field based on operational status of array at the Nursery Bridge Dam (NBA) PIA.

	2003	2004	2005	2006	2007	2008	2009	2010	2011
January	na	50	71	36	62	56	39	52	30
February	na	34	87	49	43	19	54	51	40
March	na	35	89	46	33	54	31	73	29
April	na	37	59	23	53	81	18	56	25
May	na	24	78	40	87	18	18	39	22
June	na	61	100	79	100	39	78	54	36
July	na	100	100	100	100	100	100	100	100
August	na	84	100	100	100	100	100	100	100
September	na	100	100	100	100	100	100	100	100
October	50	87	100	100	100	100	100	100	100
November	0	91	100	70	60	96	100	95	100
December	25	65	79	37	47	75	81	46	94

Table I-4. Average monthly probability of upstream detection based on operational status of array at the Nursery Bridge Dam (NBA) PIA.

	2003	2004	2005	2006	2007	2008	2009	2010	2011
January	na	100	100	100	100	100	100	100	100
February	na	100	100	100	100	36	100	100	100
March	na	100	100	100	100	85	100	100	100
April	na	100	100	100	100	100	100	100	100
May	na	100	100	100	100	84	100	100	100
June	na	100	100	100	100	100	100	100	100
July	na	100	100	100	100	100	100	100	100
August	na	84	100	100	100	100	100	100	100
September	na	100	100	100	100	100	100	100	100
October	50	87	100	100	100	100	100	100	100
November	0	100	100	100	60	100	100	100	100
December	50	100	100	100	68	100	100	100	100

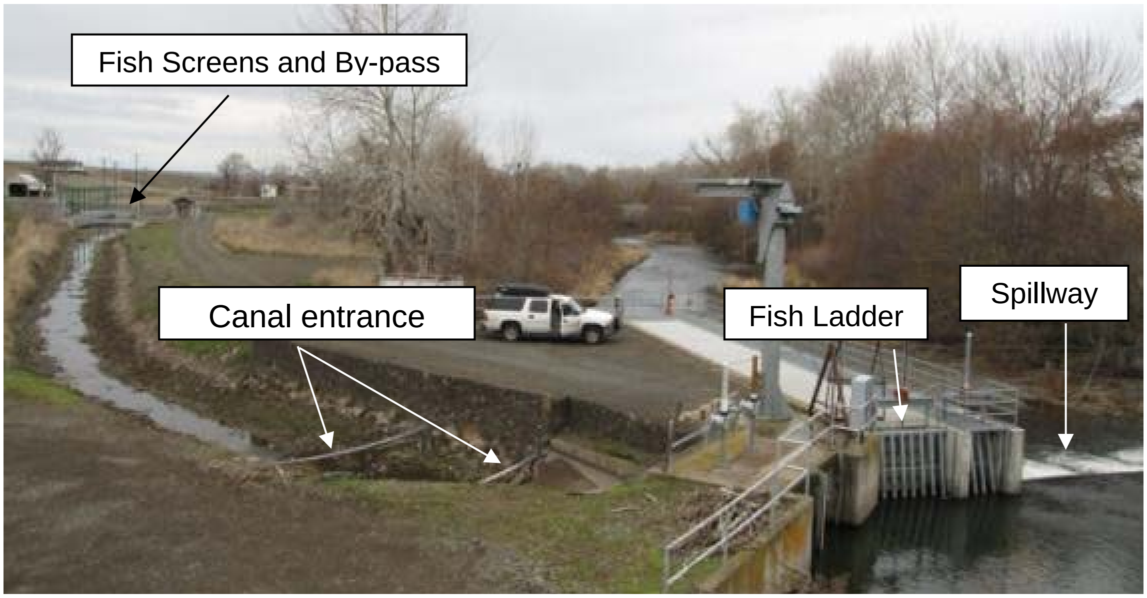

Figure I-6. Burlingame Dam diversion facility with canal dewatered.

Table I-5. Average monthly percent flows covered by electromagnetic field based on operational status of array at Burlingame Diversion Dam (BGM) PIA.

	2007	2008	2009	2010	2011
January	6	25	10	17	8
February	8	17	15	16	10
March	16	43	21	68	21
April	47	65	19	59	30
May	82	17	17	34	26
June	100	36	75	43	31
July	100	100	100	94	100
August	100	100	100	98	100
September	63	57	57	72	72
October	100	100	100	100	100
November	100	96	100	73	88
December	59	48	48	23	48

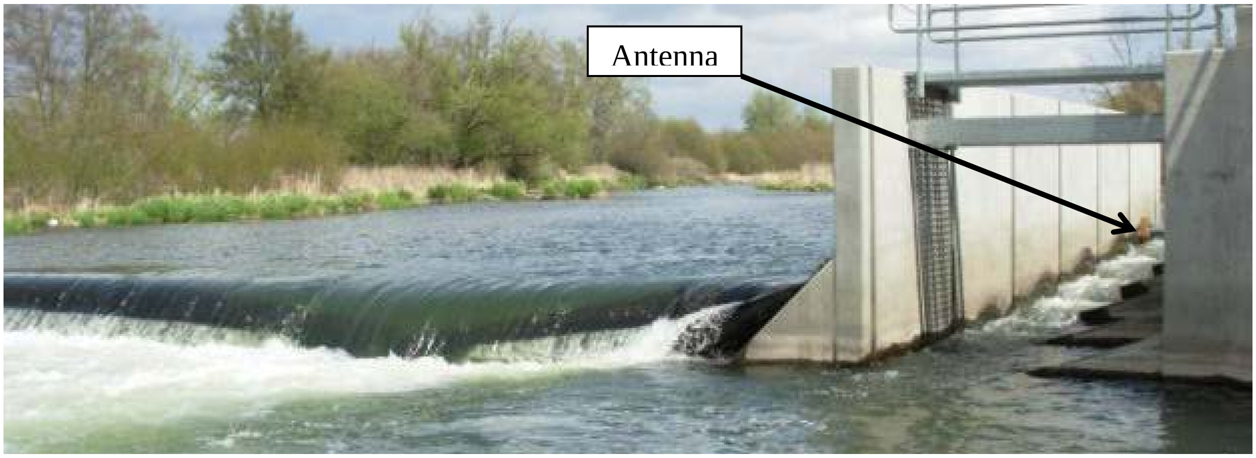

Figure I-7. Lowden Diversion Dam and fish ladder.

Table I-6. Monthly percent of operational days for the Lowden Diversion Dam (LWD) fish ladder.

	2007	**2008**	**2009**	**2010**	**2011**
January	na	100	100	100	52
February	na	100	100	100	0
March	na	100	100	100	74
April	na	100	100	100	100
May	na	58	100	100	97
June	na	83	100	100	100
July	na	100	100	100	100
August	na	100	100	100	19
September	na	100	100	100	97
October	na	100	100	100	97
November	3	100	100	100	100
December	100	100	100	100	100

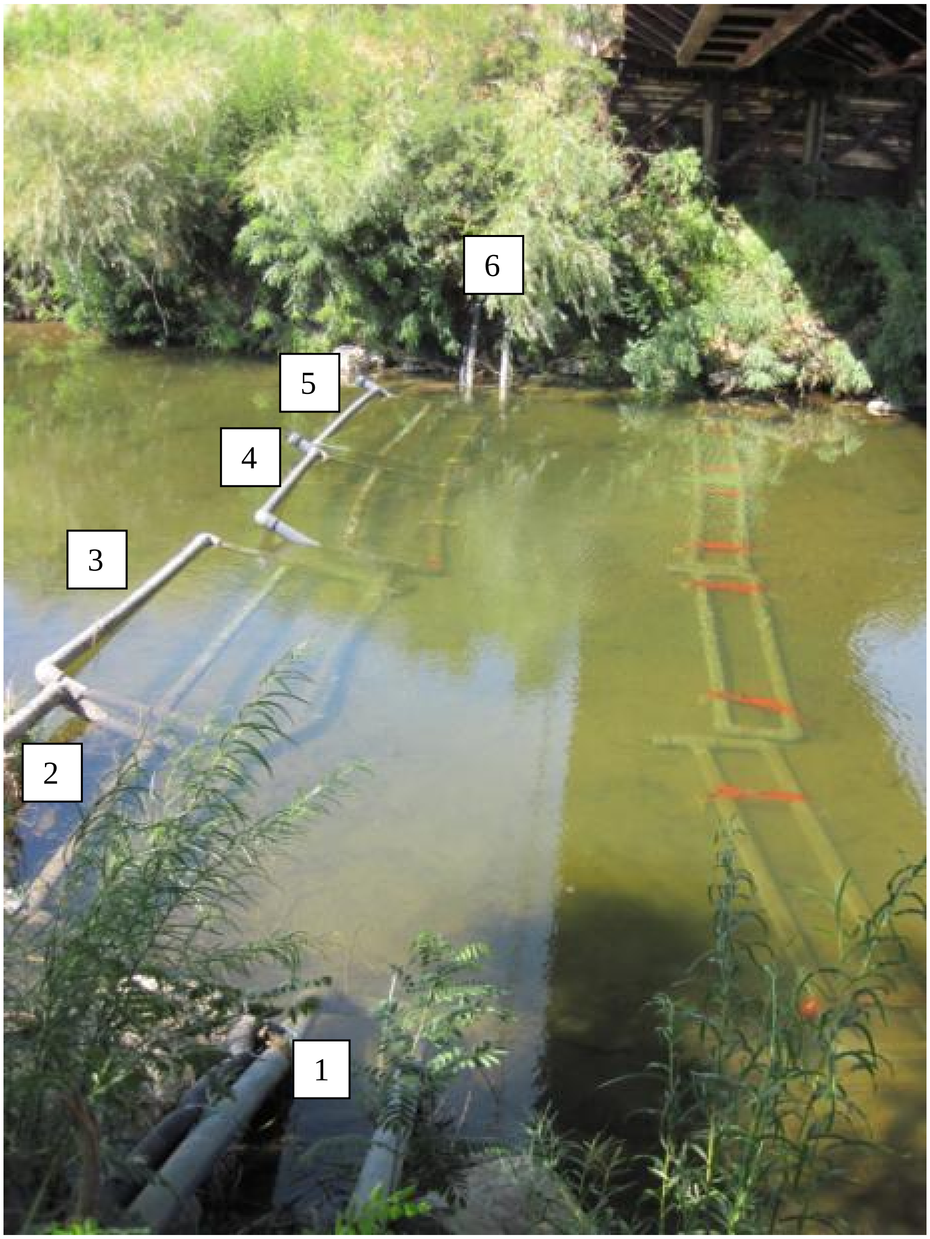

Figure I-8. The Oasis Road Bridge (ORB) PIA during low summer flows September 2011. Antenna 1 and 6 are pass overs located on the north and south shoreline. Antennas 2 - 5 are hybrid pass through/pass overs. Four additional pass over antennas were installed directly upstream to serve as backups in the case of hybrid failure.

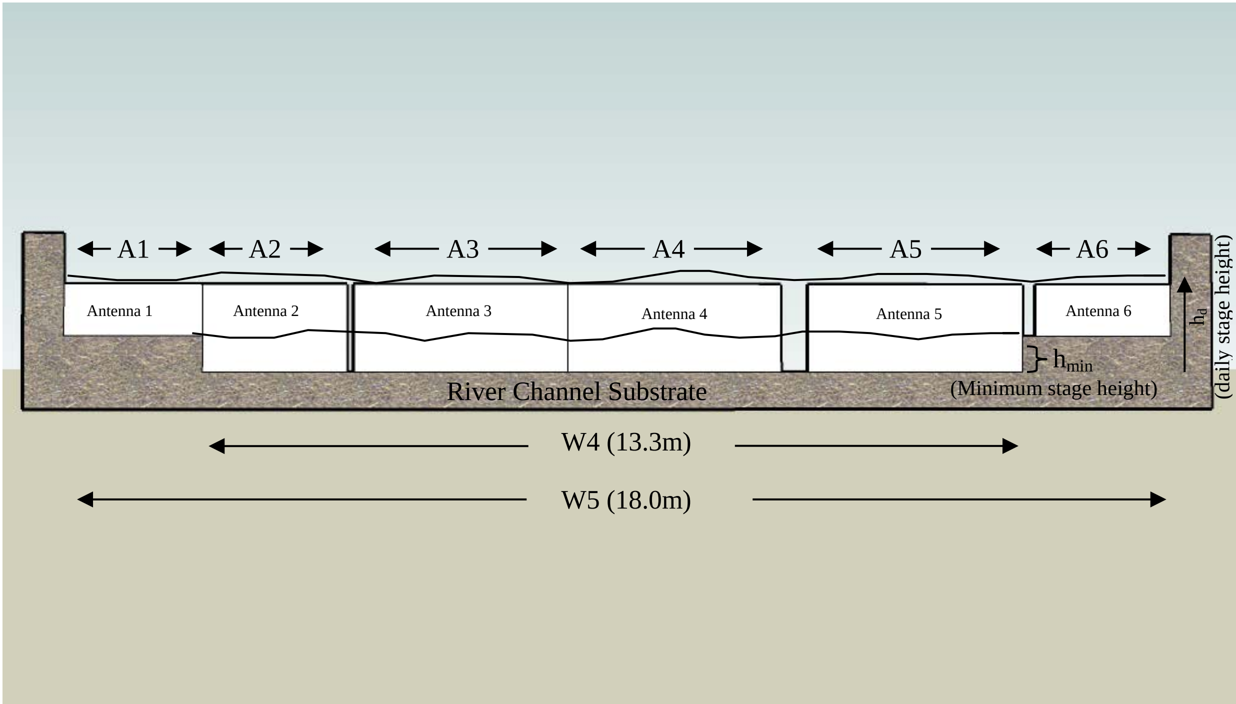

Figure I-9. Cross-sectional diagram of the six antennas at the Oasis Road Bridge (ORB) passive instream antenna.

Table I-7. Average monthly percent of the water column covered at the Oasis Road Bridge (ORB) passive instream antenna.

	2005	2006	2007	2008	2009	2010	2011
January	na	2	47	95	28	87	42
February	na	5	68	81	35	91	18
March	na	5	56	86	28	92	14
April	22	6	75	81	16	91	14
May	19	10	99	77	14	89	14
June	53	11	96	89	28	81	10
July	67	74	48	99	27	97	27
August	95	93	96	99	25	97	81
September	74	99	98	99	22	97	98
October	77	99	99	99	73	98	98
November	98	84	99	93	95	96	97
December	86	54	97	80	92	86	95

Figure I-10. Mill Creek Intake Dam (MCI) and fish ladder.

Figure I-11. The Kiwanis Camp Bridge (KCB) passive instream antenna showing pass over antenna configuration (A) and original pass through antenna configuration (B).

Table I-8. Average monthly percent flows covered by electromagnetic field based on operational status at the Kiwanis Camp Bridge (KCB).

	2005	2006	2007	2008	2009	2010	2011
January	na	100	72	100	24	93	54
February	na	100	93	99	25	75	25
March	na	97	96	81	57	90	23
April	97	89	100	82	72	100	na
May	65	100	100	80	83	100	na
June	100	100	100	86	100	92	na
July	100	100	100	100	100	100	na
August	81	100	100	100	100	100	na
September	100	100	100	100	100	100	na
October	100	100	100	100	100	100	na
November	100	62	100	98	100	100	na
December	100	71	99	97	100	94	na

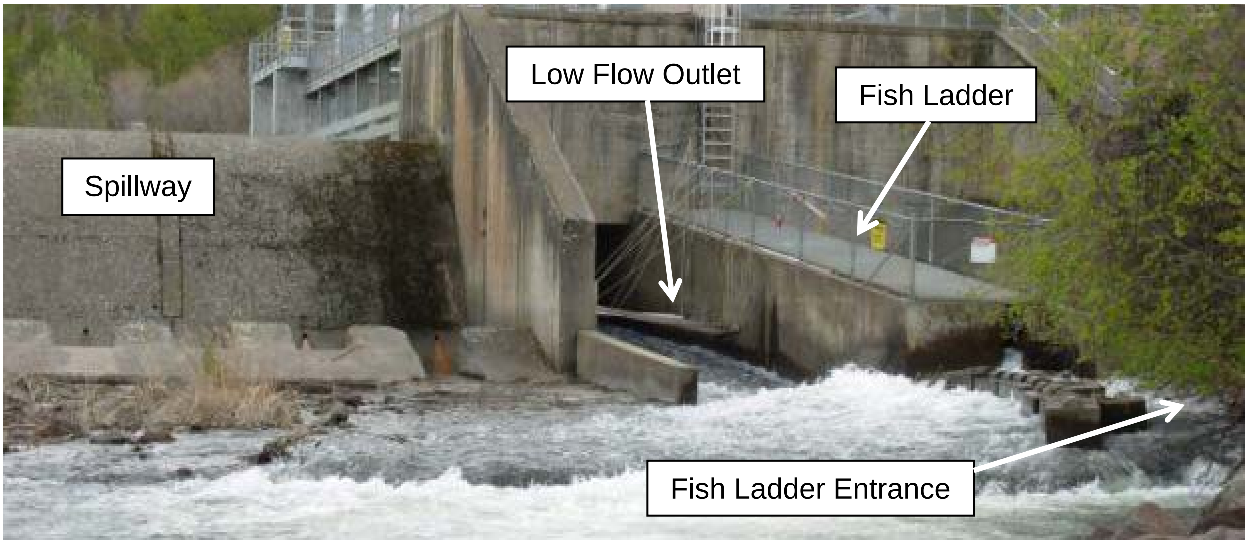

Figure I-12. Downstream view of the south side of Bennington Lake Diversion Dam (MCD).

Figure I-13. Low flow outlet showing the original flat plate antenna (A) and two additional flat plates installed just downstream (B).

Table I-9. Average monthly percent flows covered by electromagnetic field based on operational status the Bennington Lake Diversion Dam (MCD) passive instream antenna.

	2005	2006	2007	2008	2009	2010	2011
January	na	17	48	78	40	53	28
February	12	56	51	54	73	68	52
March	86	31	31	35	24	87	18
April	96	15	59	44	11	52	22
May	97	43	95	25	22	49	28
June	99	76	100	44	73	64	51
July	100	100	87	100	100	100	100
August	100	100	100	100	52	100	100
September	100	100	59	100	100	100	100
October	99	100	100	100	99	83	100
November	91	47	98	87	92	96	97
December	71	71	78	73	82	46	89

Table I-10. Average monthly probability of upstream detection based on operational status at the Bennington Lake Diversion Dam (MCD) passive instream antenna.

	2005	2006	2007	2008	2009	2010	2011
January	na	81	94	100	71	97	84
February	14	100	100	100	100	100	100
March	97	97	100	96	90	100	77
April	100	77	100	97	47	100	73
May	100	100	100	87	90	100	94
June	100	100	100	90	100	70	97
July	100	100	87	100	100	100	100
August	100	100	100	100	52	100	100
September	100	100	100	100	100	100	100
October	100	100	100	100	100	77	100
November	100	93	100	97	100	83	100
December	87	90	100	94	100	84	94

Table I-11. Average monthly percent flows covered by electromagnetic field based on operational status of array at Mill Creek Division Dam (MCD2) passive instream antenna.

	2007	2008	2009	2010	2011
January	0	13	8	12	24
February	4	11	15	16	58
March	8	7	6	24	22
April	16	9	3	10	19
May	63	5	6	11	31
June	100	9	34	26	47
July	100	83	100	100	96
August	65	100	98	100	100
September	16	100	100	99	100
October	100	98	65	95	99
November	66	31	39	87	88
December	19	17	28	47	77

Table I-12. Average monthly probability of upstream detection based on operational status of the Mill Creek Division Dam (MCD2) passive instream antenna.

	2007	2008	2009	2010	2011
January	0	100	78	100	85
February	54	100	100	100	100
March	100	100	90	100	94
April	100	97	54	100	62
May	100	97	100	100	100
June	100	93	100	90	100
July	100	100	100	100	100
August	100	100	100	100	100
September	100	100	100	100	100
October	100	100	100	100	100
November	100	100	100	100	100
December	100	100	100	91	91

Figure I-14. Downstream view of the upper Yellowhawk Creek (YHC) passive instream antenna.

Table I-13. Monthly percent of days that the Yellowhawk Creek (YHC) passive instream antenna was operating.

	2006	2007	2008	2009	2010	2011
January	na	100	100	100	100	100
February	na	100	100	100	100	100
March	na	100	100	100	100	100
April	na	100	100	100	100	100
May	na	100	100	100	100	100
June	na	100	100	100	100	100
July	na	100	100	100	100	100
August	na	100	100	100	100	100
September	na	100	100	100	100	100
October	na	100	100	100	100	100
November	na	100	100	100	100	100
December	61	100	100	100	100	100


Figure I-15. View of the middle Yellowhawk Creek (YHC2) passive instream antenna.

Table I-14. Monthly percent of days that the Middle Yellowhawk Creek (YHC2) passive instream antenna was operating.

	2007	2008	2009	2010	2011
January	na	97	32	100	100
February	na	100	100	100	100
March	na	100	100	100	100
April	na	100	07	100	100
May	na	100	81	100	100
June	na	100	100	100	100
July	na	100	100	100	100
August	90	100	100	100	100
September	100	100	100	100	100
October	100	100	100	100	100
November	100	100	100	100	100
December	100	100	100	100	100

Appendix II - Sampling and Tagging Methodologies

authored by

Ryan Koch

U.S. Fish and Wildlife Service

Bull Trout Sampling

South Fork Walla Walla River

Sampling for bull trout in the South Fork Walla Walla River (above Harris Park) began in 2002 (Budy et al. 2004; 2005; 2006; 2007; 2008; 2009; 2010; 2011). Multiple sampling techniques were used to capture bull trout including electroshocking down to a seine, angling, electroshocking with dip nets and trap netting. Electroshocking down to a seine was the most prominent fish sampling method used for all years. All captured bull trout were weighed (nearest 0.1 g) and measured (nearest mm total length, TL, and fork length, FL). These measurements were used to determine length-to-weight regressions and calculate condition. Scales were taken from all tagged bull trout prior to release. Gonads, otoliths, stomach contents, and tissue samples were taken from a small subsample of sacrificed adults to estimate fecundity, sex ratio, age, and diet. Tissue samples may be used for future stable isotope analysis. Bull trout < 70 mm (age-0) were not marked, but were immediately measured for TL and weight and then returned to the stream to avoid predation by larger bull trout in the holding tanks. Bull trout previously passive integrated transponder (PIT) or Floy tagged (recaptures) had the tag numbers recorded, and were then measured, weighed, and released.

Walla Walla River

Sampling for bull trout in the mainstem Walla Walla River (rkm 51-81) started in 2004 (Anglin et al. 2008a, 2008b, 2009a, 2009b, 2010; Barrows et al. 2012a, 2012b, 2014). Multiple sampling techniques were used to capture bull trout including angling, screw trapping, beach seine, fyke and dip netting. Starting in 2007, angling became the most utilized sampling method. Each captured bull trout was anesthetized in a bath containing 40 mg/l of tricaine methanesulfonate (MS-222) buffered with sodium bicarbonate at a concentration of 80 mg/l and measured for FL (in mm). For the 2011 sampling season, bull trout were weighed to the nearest gram. Bull trout previously PIT or Floy tagged (recaptures) had the tag numbers recorded, and were then measured, weighed, and released.

Bull Trout Tagging

South Fork Walla Walla River

Prior to tagging, bull trout larger than 120 mm were anesthetized until they exhibited little response to stimuli. A 23 mm PIT tag was subsequently placed into a surgical incision on the ventral side of the fish, anterior to the pelvic fins. In addition, an external T-bar anchor tag (Floy tag), unique to year and stream, was placed adjacent to the dorsal fin on fish > 120 mm TL. The Floy tag was used for population estimates using mark and resight techniques. Subsequently, fish were placed in a flow-through recovery container within the channel, and monitored until full equilibrium was restored. All fish were returned to slow-water habitat near individual capture locations. Beginning 2007, in addition to tagging bull trout >120 mm, we marked smaller bull trout (70-119 mm TL) with 8 or 12 mm PIT tags. Adipose fins from bull trout (70-119 mm) were also removed for identification and genetic analyses. For the 2009 sampling year and beyond, the use of 8mm PIT tags was discontinued and the tagging size for bull trout tagged with 23 mm PIT and Floy tags was increased to 170 mm TL.

Walla Walla River

Each captured bull trout was anesthetized and scanned for the presence of a PIT tag. Bull trout less than 170 mm (FL) comprised less than 5% of sampled fish in the mainstem Walla Walla. Therefore, most fish sampled were tagged with 23 mm PIT tags. Bull trout smaller than 170, usually were tagged with 12 mm PIT tags. After anesthetization, tags were inserted into a 3-4 mm abdominal incision made just under the skin with a scalpel slightly off the mid-line and anterior to the pelvic girdle. A cocktail straw was used to push the tag approximately 5mm past the incision and potentially reduce the chance of tag loss. Individuals were released into nearby sheltered areas after equilibrium was restored.

Literature Cited

Anglin, D.R., D.G. Gallion, M. Barrows, C. Newlon, R. Koch. 2008. Current Status of Bull Trout Abundance, Connectivity, and Habitat Conditions in the Walla Walla Basin 2007 Update.

Anglin, D.R., D.G. Gallion, M. Barrows, C. Newlon, P. Sankovich, T.J. Kisaka, and H. Schaller. 2008. Bull Trout Distribution, Movements and Habitat Use in the Walla Walla and Umatilla River Basins 2004 Annual Progress Report.

Anglin, D.R., D.G. Gallion, M. Barrows, R. Koch, and C. Newlon. 2009. Monitoring the Use of the Mainstem Columbia River by Bull Trout from the Walla Walla Basin. Final Report for 2007 prepared for the U.S. Army Corps of Engineers, Walla Walla, Wa.

Anglin, D.R., D.G. Gallion, M. Barrows, R. Koch, and C. Newlon. 2009. Monitoring the Use of the Mainstem Columbia River by Bull Trout from the Walla Walla Basin. Final Report for 2008 prepared for the U.S. Army Corps of Engineers, Walla Walla, Wa.

Anglin, D.R., D.G. Gallion, M. Barrows, R. Koch, and C. Newlon. 2010. Monitoring the Use of the Mainstem Columbia River by Bull Trout from the Walla Walla Basin. Final Report for 2009 prepared for the U.S. Army Corps of Engineers, Walla Walla, WA.

Barrows, M.G., R. Koch, D.R. Anglin and S.L. Haeseker. 2012a. Use of the Mainstem Columbia River by Walla Walla Basin Bull Trout. 2010 Annual Report to the U.S. Army Corps of Engineers, Walla Walla District. Project BT-W-10-2.

Barrows, M.G., R. Koch, D.R. Anglin and S.L. Haeseker. 2012b. Use of the Mainstem Columbia River by Walla Walla Basin Bull Trout. 2011 Annual Report to the U.S. Army Corps of Engineers, Walla Walla District. Project BT-W-10-2.

Barrows, M.G., R. Koch, D.R. Anglin and S.L. Haeseker. 2014. Use of the Mainstem Columbia River by Walla Walla Basin Bull Trout. 2012 Annual Report to the U.S. Army Corps of Engineers, Walla Walla District. Project BT-W-10-2.

Brown, R.S., S.J. Cooke, W.G. Anderson, and R.S. McKinley. 1999. Evidence to Challenge the “2% Rule” for biotelemetry. North American Journal of Fisheries Management 19:867-871.

Budy, P., R. Al-Chokhachy, and G.P. Thiede. 2003. Bull trout population assessment and life-history characteristics in association with habitat quality and land use in the Walla Walla River Basin: a template for recovery planning. 2002 Annual Progress Report to US Fish and Wildlife Service, Vancouver, Washington. 41 pp.

Budy, P., R. Al-Chokhachy, and G.P. Thiede. 2004. Bull trout population assessment and life-history characteristics in association with habitat quality and land use: a template for recovery planning. 2003 Annual Progress Report to US Fish and Wildlife Service, Vancouver, Washington. 70 pp.

Budy, P., R. Al-Chokhachy, K. Homel, and G.P. Thiede. 2005. Bull trout population assessment in northeastern Oregon: a template for recovery planning. 2004 Annual Progress Report to US Fish and Wildlife Service. UTCFWRU 2005(3):1-93.

Budy, P., R. Al-Chokhachy, K. Homel, and G.P. Thiede. 2006. Bull trout population assessment in northeastern Oregon: a template for recovery planning. 2005 Annual Progress Report to U.S. Fish and Wildlife Service. UTCFWRU 2006(6):1-102.

Budy, P., R. Al-Chokhachy, and G.P. Thiede. 2007. Bull trout population assessment in northeastern Oregon: a template for recovery planning. 2006 Annual Progress Report to US Fish and Wildlife Service. UTCFWRU 2007(1):1-83.

Budy, P., P.D. MacKinnon, T. Bowerman, and G.P. Thiede. 2008. Bull trout population assessment in northeastern Oregon: a template for recovery planning. 2007 Annual Progress Report to US Fish and Wildlife Service. UTCFWRU 2008(6):1-62.

Budy, P., P.D. MacKinnon, T. Bowerman, and G.P. Thiede. 2009. Bull trout population assessment in northeastern Oregon: a template for recovery planning. 2008 Annual Progress Report to US Fish and Wildlife Service. UTCFWRU 2009(1):1-57.

Budy, P., T. Bowerman, and G.P. Thiede. 2010. Bull trout population assessment in northeastern Oregon: a template for recovery planning. 2009 Annual Progress Report to US Fish and Wildlife Service. UTCFWRU 2010(3):1-48.

Budy, P., L. B. Tennant, T. Bowerman, and G.P. Thiede. 2011. Bull trout population assessment in northeastern Oregon: a template for recovery planning. 2010 Annual Progress Report to US Fish and Wildlife Service. UTCFWRU 2011(5):1-90.

Winter, J. 1996. Advances in underwater biotelemetry. Pages 555-590 in B. R. Murphy and D. W. Willis, editors. Fisheries Techniques, Second Edition. American Fisheries Society. Bethesda, Maryland.

Appendix III - Low Flow Passage Barrier Assessment of the Walla Walla River

authored by

Ryan Koch

U.S. Fish and Wildlife Service

Introduction

Dating back to the 1880s, surface water in the Walla Walla River (WWR) has been over-appropriated resulting in dewatering during periods of low streamflow (summer and fall) and high irrigation demand (Siemann and Martin 2007). Columbia River populations of bull trout, including those in the Walla Walla Core Area were listed as threatened under the ESA in 1998. The listing of bull trout led to a Civil Penalty Settlement Agreement between the U.S. Fish and Wildlife Service (FWS), the Walla Walla River Irrigation District, Hudson Bay District Improvement Company, and Gardena Farms Irrigation District #13 regarding take of bull trout due to inadequate surface flows brought on by irrigation withdrawals. Thus, seasonal dewatering of the WWR below Milton-Freewater, OR (Figure III-1), ended in 2000 with an agreement to leave 13 cfs in river below Nursery Bridge Dam. The amount of water left in river was raised to 18 cfs in 2001, to better facilitate fish passage, and further increased to 25 cfs in 2002. Fish salvages conducted by the Confederated Tribes of the Umatilla Indian Reservation biologists below Nursery Bridge Dam captured numerous species including 108 bull trout in 1999 (Schwartz et al. 2005). Fish salvages in 2000 and 2001 captured only 10 and 14 bull trout respectively, possibly indicating that restored flows improved upstream passage for bull trout.

Evaluation of restored flows below Nursery Bridge Dam in 2002 demonstrated seepage loss by the time flows reached Tumalum Bridge (Anglin et al. 2003; Figure III-1). During snorkel surveys in August 2007, the FWS observed diminished flows and the potential for low flow passage barriers below Tumalum Bridge. Low flow passage barriers occur when streamflow decreases such that the water depth over riffles is insufficient for fish to pass over. The concern was that the 25 cfs passed at Nursery Bridge Dam was being lost due to processes such as hyporheic exchange and that surface flows downstream of Tumalum Bridge were inadequate for fish passage. Consequently, surveys were conducted during 2007 to quantify low flow passage barriers. Based on the results of the 2007 barrier surveys, a 2009 study was initiated to measure the relationship between surface flows and the occurrence of barriers. The relationship between flows and barriers was then applied to ten years of flow data from the Washington Department of Ecology (WDOE) Pepper Bridge stream flow monitoring station (32A120) to model periodicity of barriers within the study reach. Bull trout movement data were supplemented with fish tagged within the study reach.

Methods

2007 Low Flow Barrier Survey

Surveys were conducted on September 12-13, 2007 to determine the number and location of barriers resulting from low stream flows. To evaluate passage conditions for adult bull trout, a minimum water depth criterion of 0.6 ft was employed. This criterion has been established for both steelhead and large resident trout (Reiser and Bjorrn 1979; Thompson 1972). Beginning at Cemetery Bridge (rkm 76) and ending at Burlingame Diversion Dam (rkm 61; Figure III-1), survey crews walked downstream and surveyed each potential passage barrier, which usually occurred at riffles. A riffle would qualify as a barrier if the minimum thalweg depth of 0.6 ft was not maintained across one fifth the wetted width of the river along a cross section traversing the riffle. A GPS point and photo were taken at each qualifying barrier. Sampling methods were adjusted to assess passage conditions for sub-adult bull trout by utilizing a depth criterion of 0.4 ft. Approximately every fifth barrier was sub-sampled to derive a ratio of sub-adult barriers to total barriers.

2009 Low Flow Barrier Survey

The primary objective of the 2009 barrier survey was to identify the minimum streamflow (cfs) that provides passage and connectivity for migrating adult and sub-adult bull trout. Surveys took place on June 23, 24 and July 15. We used the same depth criterion from Thompson (1972) to identify barriers. Surveys took place from Tumalum Bridge (rkm 70.4) downstream to Pepper Bridge (rkm 66.3). In addition, flows were manually measured near Nursery Bridge Dam (rkm 74.3), Tumalum Bridge, a site near the Boch property (rkm 67.1), and Pepper Bridge, to evaluate spatial variability in flow. The range of flows assessed included the agreement flow of 25 cfs and at least 2 additional flows that were incrementally greater than 25 cfs that would adequately describe the range of passage conditions in this stretch of the river. Regression was used to identify a linear relationship between flow (cfs) and the number of passage barriers for adult and sub-adult bull trout. The minimum streamflow required to provide passage was the model predicted cfs value that would result in no passage barriers.

10 Year Periodicity

To assess the temporal and seasonal prevalence of barriers between Nursery Bridge Dam and Pepper Bridge, the predicted minimum stream flow to prevent barriers was examined in relation to Pepper Bridge gage streamflow records for the 10 year period from 2002 to 2011. A periodicity table was constructed to display the prevalence of low flow barriers to evaluate the adequacy of the Settlement Agreement flows for bull trout.

Snorkel Surveys

Snorkel surveys were conducted to assess the distribution and number of bull trout potentially impacted by low flow barriers in the reach below Tumalum Bridge from 2007 through 2010. Snorkel surveys coincided with a multi-year study (2007 through 2009) investigating ground water inflows and hyporheic exchange utilizing fiber optic techniques (Collier 2008). The FWS provided salmonid observation data for use in the analysis. The snorkel survey area (fiber optic study area) was approximately 2000 m long and started near Mauer Lane at the upstream end and ended just south of the Oregon and Washington state line. All pool habitats were surveyed within the study reach. During 2007, three surveys took place on June 20, July 18, and August 16. The 2008 snorkel surveys took place on August 27 and September 10. In 2009, snorkel surveys occurred on June 25, before the onset of summer base flows, July 15 and August 12. Surveys in 2010 were completed on June 28, July 12, and August 9. Temperatures were recorded at each pool snorkeled and recorded on loggers placed near the study area. In 2009, sub-adult bull trout were captured and PIT-tagged to monitor potential movement out of the study area. Detections of these tagged individuals at Burlingame Diversion Dam (downstream of study site) or Nursery Bridge Dam (upstream) could lend insight to the movement of sub-adult bull trout during summer low flows.

Results

2007 Barrier Survey

A total of 92 low flow passage barriers were identified (Figure III-1 and Table III-1). Eighty-four were located between Tumalum Bridge and Burlingame Diversion Dam, seven between Nursery

Bridge Dam and Tumalum Bridge, and one (Smith Dam) between Cemetery Bridge and Nursery Bridge Dam. Smith Dam, the farthest upstream barrier, was removed in 2012.

Of the 92 passage barriers, 17 were evaluated further and designated as either adult or sub-adult/adult barriers (Table III-1). Eleven were determined to be adult barriers while six were classified as barriers for both sub-adults and adults. Most barriers were located between Tumalum Bridge and the confluence of Yellowhawk Creek.

Tag detections at Passive Instream Antennas (PIA) indicated the latest spring detection for a bull trout exhibiting an adult movement pattern upstream past Burlingame Diversion Dam (May 31) to Nursery Bridge Dam (June 4) closely coincided with the onset of summer low streamflows. Mean daily flows measured at Pepper Bridge decreased sharply in late May and averaged approximately 21.5 cfs during June through October and did not increase again until November. Although both adult and sub-adult bull trout were first detected during October passing Burlingame Diversion Dam, the majority of downstream movement between Nursery Bridge Dam and Burlingame Diversion Dam occurred during November and December after streamflows increased.

2009 Barrier Survey

Barrier surveys took place at three different flows during 2009 (Table III-2). The number of barriers for adults ranged from 5 (2 sub-adult) to 66 (49 sub-adult) for the flows sampled. Manually measured flows taken below Nursery Bridge Dam and at Pepper Bridge were similar to established gage readings at both sites (WWBWC 2009). The current settlement agreement flows of approximately 25 cfs bypassed at Nursery Bridge Dam result in 8.01 cfs at Pepper Bridge with the lowest measured flows near the Boch property (rkm 67.1) at 4.46 cfs. The model predicted that 40.6 cfs (measured at Pepper Bridge gage) was the flow at which sub-adult barriers ceased to exist. Adult barriers were estimated to be eliminated at 42.3 cfs (Figure III-2).

10 Year Periodicity

Periodicity of barriers was estimated for 2002 – 2011 (Figure III-3). Because barriers occurred at similar flows for adult and sub-adult bull trout (42.3 cfs and 40.6 cfs respectively), periodicity was determined to be the similar for both life stages based on percent of days per month that barriers were present. For the ten years analyzed, low flow barriers began appearing in May and June with the exception of 2005 (March). Barriers were most prevalent July through October. The number of barriers generally decreased in November and there were few or none in December. Overall, 2005 was a relatively low flow year and barriers were present during nine months.

Snorkel Survey

Snorkel surveys took place during 2007 through 2010 (Table III-3). No bull trout were observed in the study area during the 2007 snorkel surveys. However, two sub-adult bull trout were located during exploratory snorkeling above and below the study area, one near the OR/WA Stateline, and the other near Tumalum Bridge. Snorkel surveys during 2008 took place later in the year (August, September) and two bull trout were located in each survey. Snorkel surveys during 2009 were initiated before summer base flows and 45 bull trout were observed during the June survey. During subsequent 2009 surveys in July and August, numbers of bull trout observed declined to 13 and 2 respectively. Bull trout were observed at a higher frequency in the upstream section of the survey (Figure III-4). During 2010 snorkel surveys 13, 16, and 5 sub-adult bull trout were observed in June, July, and August respectively. No adult bull trout were observed during any snorkel surveys. Water temperatures measured during June through August surveys were well above the EPA limits of 16 °C set for bull trout.

After observing several bull trout during the June 2009 survey, subsequent efforts were made to capture and tag these fish to potentially determine their fates. Hook and line sampling on July 26 resulted in only one fish being captured and PIT-tagged. A second capture effort using a beach seine was conducted on July 7 and resulted in six sub-adults being captured and PIT-tagged. A third and final seining effort was made on July 16 which resulted in six fish being captured; five of these individuals received a tag and the other was a recapture tagged on July 7. Of the 13 sub-adult bull trout tagged in the study section, three were detected at the Nursery Bridge Dam PIA approximately 4 km upstream from their release site (Table III-4). The remaining 10 bull trout were never detected at any PIA location. Based on its detection history, one bull trout (3D9.1C2C688A45) was detected passing upstream the following spring, suggesting that this individual oversummered and overwintered below Nursery Bridge Dam.

Discussion

The barrier and snorkel surveys conducted by the FWS focused on a relatively short section of the WWR below Tumalum Bridge. This area was of interest because of other ongoing research (fiber optic study) and PIT detection data indicated that this reach was near the downstream extent of sub-adult bull trout spring/summer distribution. Low surface flows within this reach were also a concern for adult bull trout returning from the lower river to spawn. While our studies were limited to a relatively small section of river, it is likely that areas in the lower WWR could be even more detrimental to bull trout passage because of even lower surface flows. Low surface flows and a wider river channel likely result in a larger number of low flow barriers and thus more adverse impacts on bull trout returning from the lower river. Long range migrants tend to be larger and more fecund than short range migrants or residents because they reside in more productive winter habitat. Thus, the potential loss of these large fluvial spawners has an overall negative impact on bull trout populations. While our evaluation of barriers was focused on potential impacts to bull trout, artificial low flows undoubtedly affect steelhead and spring Chinook salmon migration, foraging, and habitat needs in a similarly deleterious manner.

2007 Barrier Survey

Barrier survey results in 2007 suggest that settlement agreement flows may not be suitable for sub-adult and adult bull trout passage below Nursery Bridge Dam during times of low flows and irrigation withdrawals. Experiencing numerous barriers during migration likely leaves bull trout vulnerable to predation, injury and exhaustion. Also, some barriers can be complete blockages that trap fish. Adults may not be able to carry out spawning, and sub-adults may be forced to compete for resources with species more tolerant of higher water temperatures. During the warmest parts of the summer, bull trout in this river section would be exposed to water temperatures that limit growth and migration. EPA guidelines recommend 7DADM temperatures of 16°C as an upper optimal temperature threshold for bull trout migration and 8 - 12°C (7DADM) for bull trout juvenile rearing (USEPA 2003). Bull trout were observed inhabiting pools with temperatures exceeding 20°C, which is well over the EPA guidelines.

2009 Barrier Survey

Discharge measurements throughout the survey section displayed a loss of surface flows in a downstream direction with a slight increase at Pepper Bridge. The area below Tumalum Bridge is an area of high deposition of gravel and cobbles as the river gradient becomes nearly flat. The magnitude of surface flow loss seems to be more pronounced at summer base flows. Reasons for this could include lowering of the water table due to well withdrawals, interchange with subsurface flows (shallow aquifer), or late season surface withdrawals in this section of river. Surveys at different flow levels led to the development of estimated minimum flows to eliminate barriers for adult and sub-adult bull trout.

10 Year Periodicity

Low flow barriers could impact bull trout during several critical periods in their life histories. Adults can be limited in their upstream and downstream migrations to and from spawning grounds resulting in failure to spawn or outright loss to the population. Sub-adults are also limited by barriers during upstream and downstream migration, affecting their ability to forage and escape inhospitable conditions. Both life stages are more vulnerable to predation by mammalian and avian species when forced to navigate barriers brought on by low surface flows. Years when drought conditions are present could result in substantial losses of bull trout. The Walla Walla Watershed Management Partnership developed criteria in their Critical Low Flow Plan for the WWR to be implemented during periods of drought (WWWMP 2012).

Snorkel Survey

Snorkel surveys were initially conducted to enumerate fish during the fiber optic monitoring study. The fiber optic cable was usually placed instream well after base flows were achieved. Snorkeling after the onset of summer base flows and elevated temperatures potentially limited our ability to observe bull trout in the study area. Surveys in 2009 were adjusted to begin before base flows and a relatively large number of sub-adult bull trout were observed. This result led to a tagging effort in order to monitor movements of these sub-adults. Out of 13 bull trout PIT tagged, three were subsequently detected moving upstream to Nursery Bridge Dam. Two of these fish were detected within a relatively short time after tagging. The first sub-adult tagged was detected four days later and before the onset of summer base flows. A second sub-adult was tagged after the onset of base flows but was detected at Nursery Bridge Dam shortly after a slight increase in flows on July 13 (Figure III-5). These two detections may indicate that sub-adult bull trout are attempting to move upstream when conditions allow, likely to escape warm temperatures and limited habitat. Further, movement after a relatively small increase in flows indicates that pulsing water after summer low flows have materialized may be an effective management action to allow bull trout to escape non ideal habitat conditions.

Low stream flows and the resulting barriers likely make bull trout an easier target for predators. In 2009, observations of attempted avian predation (bill marks on each side of fish), were made during snorkeling and PIT-tagging efforts and frequency increased from earlier to later sampling sessions. Bill marks were observed on 17% of bull trout from the July 7 tagging effort, but were detected on 50% of bull trout on the July 16 effort. The increased percentage of bull trout with bill marks in later surveys indicates that fish in this area are experiencing increased attacks. As flows drop, fish are concentrated into less available habitat leaving them more vulnerable to predators. Bull trout migrating upstream are likely exposed to increased predation as they attempt to pass low flow barriers or they become easier targets when trapped in small pools. While bill marks suggest attempted predation, direct evidence of bull trout mortality from avian predators has been observed during other PIT-tagging efforts in the WWR. Several tags implanted into bull trout have been recovered on avian breeding colonies on the Columbia River (Barrows et al. 2012). Evaluation of PIT detection histories suggests that some bull trout are being harvested by avian predators within or near the study reach.

Literature Cited

Anglin, D. R., D.G. Gallion and T.J. Kisaka. 2003. Evaluation of the Effect of Increased Instream Flows during 2002 and Implications for Bull Trout in the Upper Walla Walla River. U.S. Fish and Wildlife Service, Columbia River Fisheries Program Office, Vancouver, WA.

Barrows, M.G., D.R. Anglin, R. Koch, J.J. Skalicky. 2012. Use of the Mainstem Columbia River by Walla Walla Basin Bull Trout. 2010-11 Annual Report Prepared for the U.S. Army Corps of Engineers, Walla Walla District, Walla Walla, WA. Contract #: W68SBV12861437.

Collier, M.W. 2008. Demonstration of Fiber Optic Distributed Temperature Sensing to Differentiate Cold Water Refuge between Ground Water Inflows and Hyporheic Exchange. Master Thesis, Oregon State University, Corvallis, OR. 107 p.

Reiser, D.W., and T.C. Bjornn. 1979. Influence of forest and rangeland management on anadromous fish habitat in western North America: habitat requirements of anadromous salmonids. USDA: Forest Service Technical Report. PNW-6. Pacific Northwest Forest and Range Experiment Station, Portland, OR. 53 pp.

Schwartz, J.D.M., P. Kissner, M. Lambert, B. Mahoney and C.R. Contor. 2005. The Walla Walla Basin Natural Production Monitoring and Evaluation Project. Progress report for 2003 prepared for Bonneville Power Administration, Portland, OR.

Siemann, D., and S. Martin. 2007. Managing Many Waters: An Assessment of Capacities for Implementing Water and Fish Improvements in the Walla Walla Basin. The William D. Ruckelshaus Center. Washington State University and University of Washington.

U.S. Environmental Protection Agency (USEPA). 2003. EPA Region 10 Guidance for Pacific Northwest State and Tribal Temperature Water Quality Standards. EPA 910-B-03-002. Region 10 Office of Water, Seattle, WA.

Thompson, K. E. 1972. Determining streamflows for fish life. Pages 31–50 in Proceedings of the Instream Flow Requirement Workshop. Pacific Northwest River Basins Commission, Portland, Oregon.

Walla Walla Basin Watershed Council (WWBWC). 2009. Flow Restoration: Water in the Walla Walla River. From website: http://www.wwbwc.org.

Walla Walla Watershed Management Partnership (WWWMP). 2012. Critical Flow Plan for the Walla Walla Basin. From website: http://www.wallawallawatershed.org.

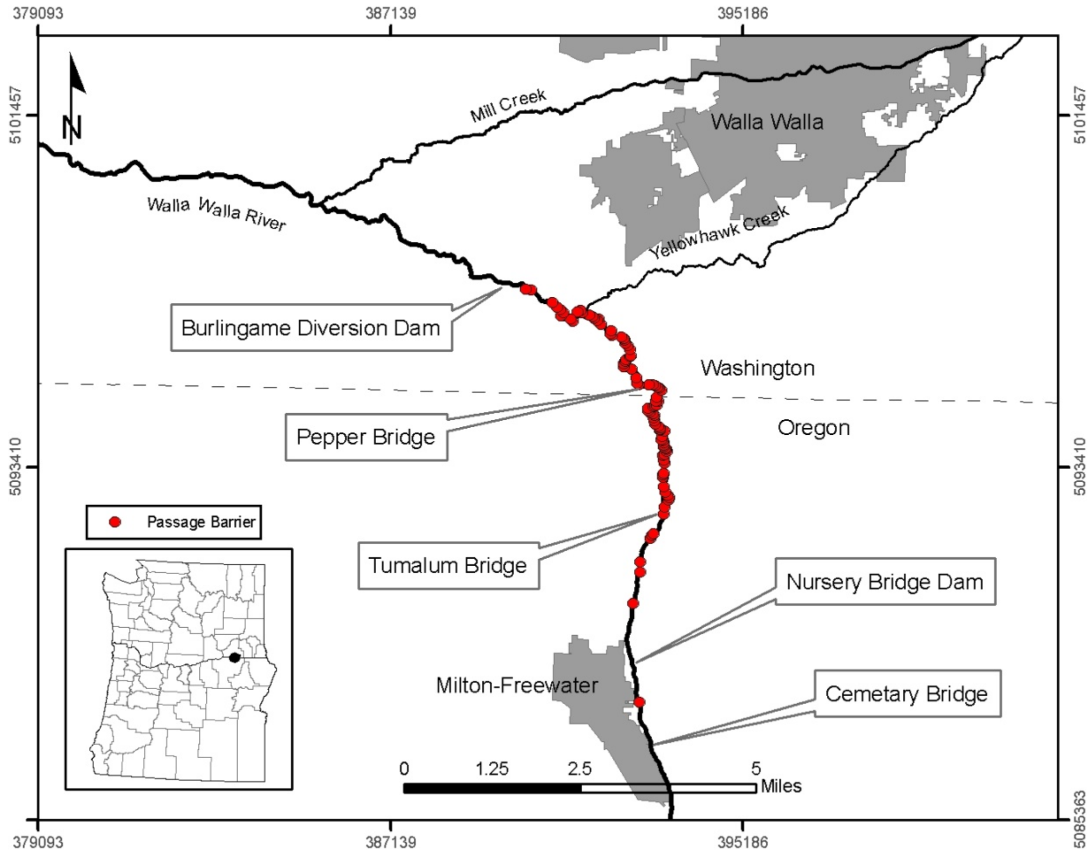

Figure III-1. Location of physical passage barriers identified during surveys on September 12 and 13, 2007.

Table III-1. Number of physical passage barriers identified, evaluated and designated as adult and sub-adult/adult barriers in the Walla Walla River between Cemetery Bridge and Burlingame Dam in 2007.

Reach Description	Total Barriers	Evaluated Barriers	Adult Only	Sub-adult/Adult
Cemetery Bridge to Nursery Bridge Dam	1	1	1	0
Nursery Bridge Dam to Tumalum Bridge	7	7	5	2
Tumalum Bridge to Burlingame Dam	84	9	5	4
Total	**92**	**17**	**11**	**6**

Table III-2. Manually measured surface flows and corresponding barrier counts for three surveys conducted during 2009.

Survey Date	RKM 74.3 flow(cfs)	RKM 70.4 flow(cfs)	RKM 67.1 flow(cfs)	RKM 66.3 flow(cfs)	Sub-adult Passage Barriers	Adult Passage Barriers
6/23/2009	65.26	49.34	39.48	42.83	2	5
6/24/2009	51.44	37.60	33.65	34.21	4	9
7/15/2009	23.59	8.03	4.46	8.01	49	66

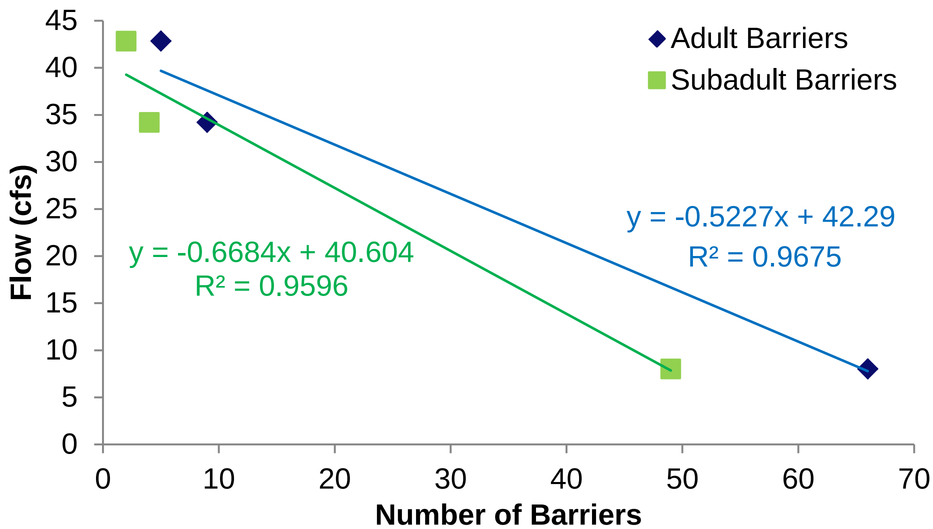

Figure III-2. Relationship between incidence of adult and sub-adult barriers and flow.

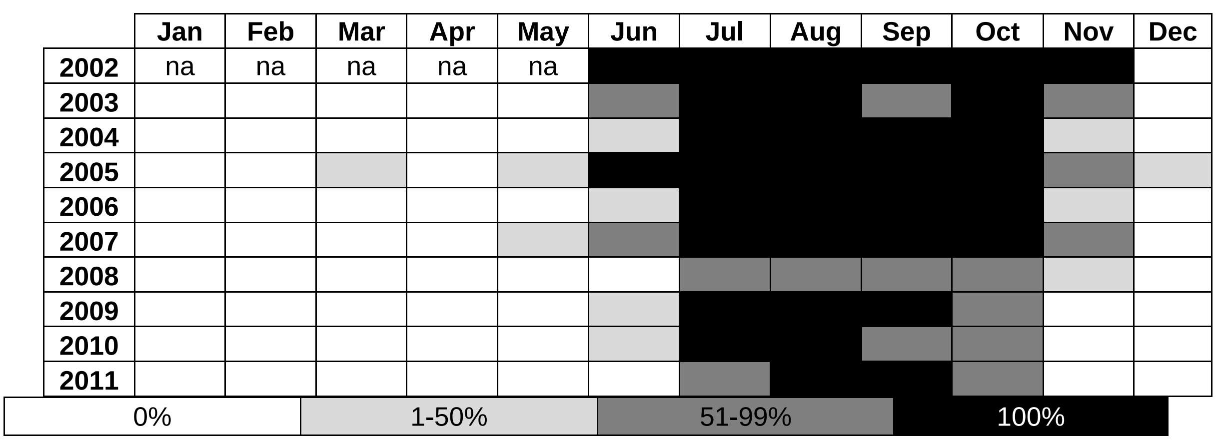

Figure III-3. Periodicity of barriers, 2002-2011, from Nursery Bridge Dam to Pepper Bridge. Each cell represents the percent of days per month that adult and sub-adult barriers were present. White cells indicate the absence of barriers. Light grey cells indicate presence of barriers from 1-50% of days per month. Dark grey cells indicate presence of barriers 51-99% of days per month. Black cells indicate presence of barriers 100% of days per month. Incidence of barriers is based on daily average flow as measured at the WDOE gage at Pepper Bridge.

Table III-3. Number of sub-adult bull trout enumerated during snorkel surveys and average temperature for each survey. Temperatures were measured at each pool snorkeled.

	2007		2008		2009		2010	
	Number of Bull Trout	Mean Temp (°C)	Number of Bull Trout	Mean Temp (°C)	Number of Bull Trout	Mean Temp (°C)	Number of Bull Trout	Mean Temp (°C)
June	0	18.3	na	na	45	19.1	13	20.7
July	0	19.2	na	na	13	19.9	16	21.2
August	0	18.8	2	18.6	2	20.0	5	21.7
September	na	na	2	14.3	na	na	na	na

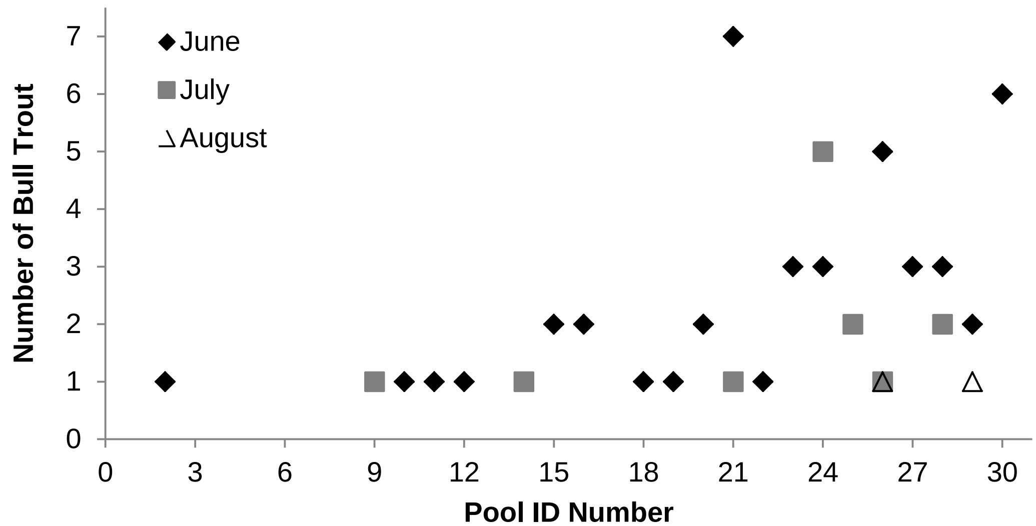

Figure III-4. Distribution of bull trout observed during 2009 snorkel surveys. Pool ID number starts at the downstream end of the survey.

Table III-4. Tagging and detection information for sub-adult bull trout PIT tagged in the snorkel survey study reach and detected at Nursery Bridge Dam.

PIT Tag ID	Tagging Date	Detection Date
3D9.1C2C68795F	6/26/2009	6/30/2009
3D9.1C2C6CADF4	7/7/2009	7/16/2009
3D9.1C2C688A45	7/7/2009	5/28/2010

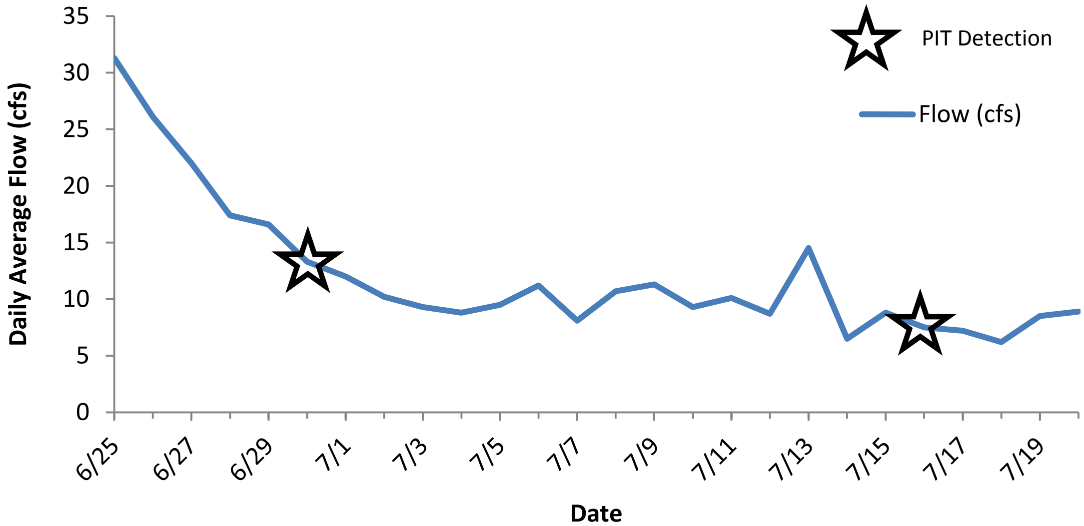

Figure III-5. Daily average flow measured at the WDOE Pepper Bridge gage and PIT detections of bull trout at Nursery Bridge Dam during 2009.

Appendix IV – Summer Microhabitat Use of Fluvial Bull Trout in Eastern Oregon Streams

authored by

Robert Al-Chokhachy
Phaedra Budy

Utah State University

North American Journal of Fisheries Management 27:1068–1081, 2007
American Fisheries Society 2007
DOI: 10.1577/M06-154.1

[Article]

Summer Microhabitat Use of Fluvial Bull Trout in Eastern Oregon Streams

ROBERT AL-CHOKHACHY* AND PHAEDRA BUDY

U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit, Department of Watershed Sciences, Utah State University, Logan, Utah 84322-5290, USA

Abstract.—The management and recovery of populations of bull trout *Salvelinus confluentus* requires a comprehensive understanding of habitat use across different systems, life stages, and life history forms. To address these needs, we collected microhabitat use and availability data in three fluvial populations of bull trout in eastern Oregon. We evaluated diel differences in microhabitat use, the consistency of microhabitat use across systems and size-classes based on preference, and our ability to predict bull trout microhabitat use. Diel comparisons suggested bull trout continue to use deeper microhabitats with cover but shift into significantly slower habitats during nighttime periods; however, we observed no discrete differences in substrate use patterns across diel periods. Across life stages, we found that both juvenile and adult bull trout used slow-velocity microhabitats with cover, but the use of specific types varied. Both logistic regression and habitat preference analyses suggested that adult bull trout used deeper habitats than juveniles. Habitat preference analyses suggested that bull trout habitat use was consistent across all three systems, as chi-square tests rejected the null hypotheses that microhabitats were used in proportion to those available ($P < 0.0001$). Validation analyses indicated that the logistic regression models (juvenile and adult) were effective at predicting bull trout absence across all tests (specificity values = 100%); however, our ability to accurately predict bull trout absence was limited (sensitivity values = 0% across all tests). Our results highlight the limitations of the models used to predict microhabitat use for fish species like bull trout, which occur at naturally low densities. However, our results also demonstrate that bull trout microhabitat use patterns are generally consistent across systems, a pattern that parallels observations at both similar and larger scales and across life history forms. Thus, our results, in combination with previous bull trout habitat studies, provide managers with benchmarks for restoration in highly degraded systems.

The management and recovery of imperiled species requires an explicit understanding of the habitat attributes that can ensure population persistence across multiple life stages (Garshelis 2000). To quantify species–habitat relationships, fisheries managers have increasingly relied on physical habitat models to aid in making complex decisions (Rosenfeld 2003). In particular, these approaches attempt to link an animal's habitat requirements with its presence or absence (e.g., Guay et al. 2000), density data (e.g., Horan et al. 2000), or individual-based information (e.g., Railsback and Harvey 2002). Ultimately, a thorough evaluation of a species–habitat relationship must include both local and large-scale processes (Imhof et al. 1996; Fausch et al. 2002).

Microhabitat suitability–type models, which describe species habitat relationships at small spatial scales (i.e., 1 m^2), have been used extensively as tools to estimate and predict the amount of suitable and unsuitable habitat under changing flow regimes (e.g., Bovee 1982). In these models, fish are assumed to select microhabitats based on the quality of multiple physical factors, including water velocity, depth, substrate, and cover (Bovee 1996; Rosenfeld 2003). However, the validity of these models has been challenged or criticized with respect to the analytical approach used (Vadas and Orth 2001), the criteria used to designate habitat (Thomas and Bovee 1993), misleading use of terminology (e.g., suitability versus preference; Rosenfeld 2003), and the disconnection between this approach and individual fitness (Garshelis 2000; Rosenfeld 2003).

Despite the many controversies associated with microhabitat models, they are widely applied and can offer insight into species-specific habitat needs for fish (Heggenes 2002; Maki-Petays et al. 2002) or guilds of fishes (Freeman et al. 1997). At small spatial scales (e.g., reach), microhabitat relationships may be more appropriate for understanding fish–habitat relationships as compared with channel–unit (e.g., pools and riffles) relationships, where habitat use patterns may be obscured by the arbitrary designation of individual habitat units (Baxter 2002). Ultimately, the incorporation of microhabitat relationships into a hierarchical arrangement of a species' habitat requirements, from riverscapes down to microhabitats (see Fausch et al.

* Corresponding author: robertal@cc.usu.edu

Received May 31, 2006; accepted January 22, 2007
Published online August 27, 2007

2002), may provide the most biologically relevant information for understanding and managing the habitat of riverine fishes; however, assembling this information can be difficult for many systems when one considers the costs, logistics, and effort.

The bull trout *Salvelinus confluentus* is a species of char native to the Pacific Northwest that has experienced significant declines due to habitat fragmentation and loss (Rieman et al. 1997; Ripley et al. 2005), the introduction of nonnative fishes (Leary et al. 1993), and barriers to migration (Rieman and McIntyre 1995). These declines ultimately led to their listing as "of special concern" in Canada since 1995 and "threatened" under the Endangered Species Act (ESA) in the United States in 1998. Previous research and monitoring have demonstrated that bull trout require cold water temperatures (Selong et al. 2001; Dunham et al. 2003) and are often associated with complex habitats (Rieman and McIntyre 1993; Muhlfeld and Marotz 2005) that provide cover and impediments in streamflows (Fausch and Northcote 1992). However, much of our knowledge of bull trout habitat use has occurred at large spatial scales (e.g., patch and watershed scale; Rieman and McIntyre 1995; Rieman et al. 1997; e.g., reach and stream scale; Watson and Hillman 1997). At smaller scales (e.g., pool–riffle) bull trout are consistently associated with complex habitats (Rich et al. 2003; Muhlfeld and Marotz 2005), yet the habitat type (pool–riffle) does not appear to be important (Watson and Hillman 1997; Rich et al. 2003). This regular use of different habitat types suggests that particular features within these units (i.e., cover) may be more important than specific habitat types, and identifying the quality of these habitat factors may help guide future restoration efforts. While microhabitat studies for parr and juvenile bull trout exist (Baxter 1997; Sexauer and James 1997; Polacek and James 2003), we are unaware of any comprehensive and validated microhabitat studies for both juvenile and adult bull trout. Thus, further evaluation of bull trout habitat use at these life stages, in combination with previous studies, will provide a more complete picture of the consistency of bull trout habitat use across their complex life cycle.

We evaluated the summer microhabitat use of fluvial bull trout populations in eastern Oregon. Based on microhabitat use and availability data, our objectives were to evaluate (1) patterns of microhabitat use for juvenile and adult fluvial bull trout, (2) consistencies in microhabitat use across juvenile and adult life stages, (3) the consistency of fluvial bull trout microhabitat use across streams in eastern Oregon, and (4) the effectiveness of using predictive models for bull trout presence or absence at the microhabitat scale. We used a combination of microhabitat preference curves, chi-square analyses for transferability of preferences, and logistic regression techniques to provide a comprehensive understanding of the patterns of bull trout microhabitat use in these systems. This greater understanding of bull trout habitat use can be used in combination with population and demographic data to guide recovery and restoration efforts, designate critical habitat, and allow for robust land and water management decisions for this imperiled species (e.g., Al-Chokhachy 2006).

Methods

Study Sites and Sampling Design

Sampling occurred in the headwaters of three streams in northeastern Oregon during the months of June, July, and August in 2003 and 2004 (Figure 1). Each stream originates in the Blue Mountains at the eastern boundary of the arid steppe of the Columbia River basin; these streams receive over 100 cm of precipitation annually. The hillslopes of this region are dominated by coniferous forests, riparian areas containing a mixture of deciduous and coniferous vegetation. With maximum elevations near 1,800 m, the climate throughout the Blue Mountains is characterized by hot, dry summers and cold, wet winters.

The South Fork Walla Walla (SFWW) and the North Fork Umatilla (NFUM) rivers are tributaries of the Columbia River and occur in Umatilla National Forest; the SFWW and the NFUM study areas are approximately 21 and 8 km in length, respectively. The South Fork Wenaha (SFWEN) River, located in the Wenaha-Tucannon National Forest, is a tributary of the Grand Ronde River and is approximately 11 km long. Within each watershed, there are few or no forest management activities. The SFWEN and NFUM sites occurred in wilderness areas, while only recreational activities are allowed in the SFWW; as such, the study areas within these streams are relatively unaltered with no water diversions or artificial barriers to movement.

Fluvial bull trout populations, including both resident and migratory life history forms, are present within each system (Ratliff and Howell 1992; Al-Chokhachy et al. 2005). The SFWW and SFWEN are larger streams (average width = 10 and 8 m, respectively), while the NFUM is the smallest of the three streams (average width = 6 m). All three study areas occur at relatively low elevations (610–1,000 m) but are largely driven by cold, groundwater sources; maximum summer water temperatures within each study area do not exceed 16°C (Baxter 2002; Budy et al. 2004), the reported upper limit for bull trout (Selong et al. 2001). Finally, brook trout *S. fontinalis* are absent from these systems, offering an opportunity to better

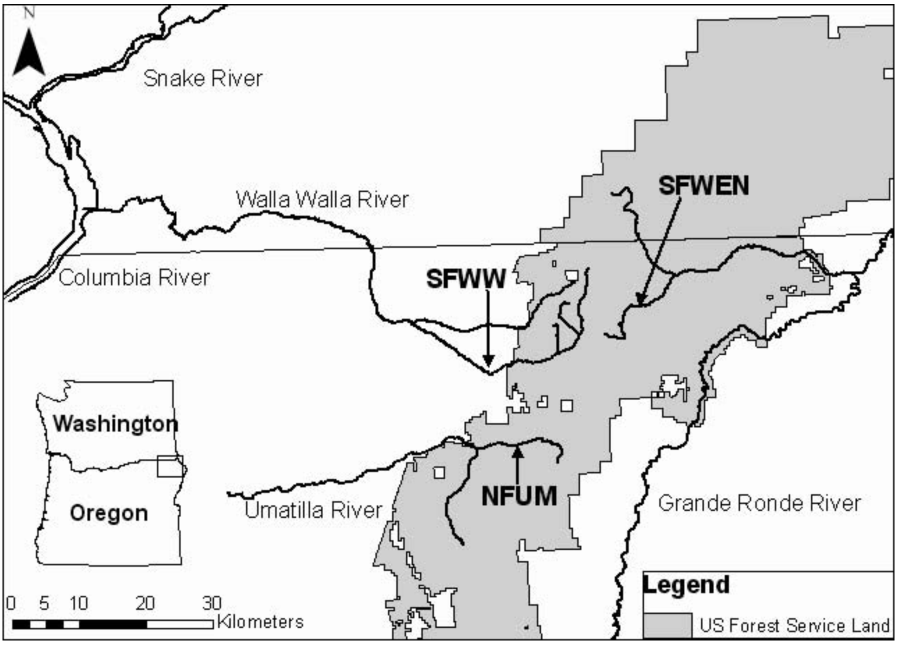

FIGURE 1.—A regional map of northeastern Oregon and southeastern Washington. Microhabitat use and availability data were collected on the South Fork Walla Walla (SFWW), North Fork Umatilla (NFUM), and the South Fork Wenaha (SFWEN) rivers.

understand patterns of bull trout microhabitat use in the absence of other potential limiting factors such as nonnative species.

We systematically selected reaches (approximately 150–200 m in length) with a random start and sampled each reach within the three study areas. We used a systematic sampling design to achieve spatial balance in sampling throughout each site and quantify the range of habitat conditions available (Stevens and Olsen 2004). This approach also enabled us to quantify the habitat use patterns of multiple age-classes, including both the small resident bull trout found primarily in the headwater reaches and larger adult bull trout found throughout each area. The majority of our sampling occurred in the SFWW (the largest study site; 15 reaches), relatively equal sampling efforts being conducted in the smaller NFUM and SFWEN study sites (six reaches in each system).

Habitat Use

We performed snorkel surveys to quantify habitat use and completed all surveys prior to habitat availability measurements to minimize disturbances to fish. We conducted the majority of our surveys during daylight hours, which occurred between 2 h after sunrise and 2 h before sunset. However, research has suggested that night surveys may be more appropriate for bull trout within the Columbia River basin (Bonneau et al. 1995; Thurow et al. 2006), and diel shifts have been identified in adfluvial populations (Muhlfeld et al. 2003) and for juvenile resident and fluvial bull trout (Sexauer and James 1997; Thurow 1997). Therefore, we conducted both day and night surveys in four reaches in the SFWW to evaluate differences in diel microhabitat use for fluvial juvenile and adult bull trout.

To quantify bull trout microhabitat use, we used snorkeling techniques, whereby snorkelers began at the downstream end of each reach and progressed upstream in a zigzagged pattern to cover the entire channel (e.g., Thurow 1994). We used handheld halogen lanterns to locate fish during nighttime surveys and marked the locations of undisturbed bull trout, both day and nighttime surveys, with either painted rocks or large metal washers (e.g., Guay et al. 2000). Snorkelers also estimated both the length and focal elevation of each observed fish, which were reported to a third person on the streambank. To estimate the appropriate depth for focal water velocity measurements, we categorized fish focal elevation into four categories, including bottom one-fourth, one-fourth to one-half depth, one-half to three-quarters depth, and three-quarters to water surface. Since few age-0 bull trout have been observed in previous snorkeling surveys (Budy et al. 2004), our analyses were restricted to fish 70 mm and greater.

At each marked focal position, we measured water depth, bottom and average water column velocities, cover and cover type, and dominant substrate. We classified any cover type found within 1 m of the original focal position of the fish as cover and further delineated cover into six categories: vegetation, large woody debris (LWD), undercut bank, boulder (substrate >125 mm), turbulence, and depth. We considered undercuts and boulders cover if the undercut area was at least 5 cm deep, 10 cm long, and 5 cm high (Kershner et al. 2004). We classified pieces of wood that were at least 1 m in length and 10 cm in diameter as LWD cover (Kershner et al. 2004). We assumed that overhanging vegetation provided a source of cover and was classified as present when it occurred within 1 m of the water surface (e.g., Thurow 1997) and protruded from the bank at least 0.5 m. Since both turbulence and increasing depth are considered to be surrogates for physical cover for instream fishes (Cunjak 1996), we classified turbulence as cover when it prevented the observer from accurately viewing the stream substrate with a Plexiglas viewer, and arbitrarily classified depth as cover when greater than 0.7 m. Next, we quantified water depth and measured water velocity at the fish focal position with a calibrated stadia rod and an electromagnetic flowmeter. We measured average water column velocity at 60% of the total water depth (measured from the water surface) and bottom water velocity at approximately 2 cm above the substrate to prevent measurements within the substrate. Finally, we examined substrate within 1 m^2 of the focal position with a Plexiglas viewer for purposes of classification. We recorded the dominant substrate according to Geist et al. (2000) within a 1-m^2 area; substrate was classified as one of the following: 1 (0–6 mm), 2 (7–25 mm), 3 (26–50 mm), 4 (51–75 mm), 5 (76–125 mm), or 6 (125 mm).

Habitat Availability

Within each reach, we used systematically spaced transects (10-m intervals between each transect) to measure habitat availability. At each transect, we sampled 10 equidistant points perpendicular to the thalweg flow, intervals between each sampling point based on the wetted width at the transect location. To account for available near-bank habitat, which may be underrepresented owing to the intervals between each sampling point (i.e., undercut banks), we also sampled two additional points at 10 cm off each of the wetted stream boundaries. For habitat use locations, we measured water depth, bottom and average water column velocity, cover type, and dominant substrate within 1 m^2 at each point.

Data Analysis

We used a one-way analysis of variance to test for diel differences in microhabitat use with respect to depth, bottom water velocity, and substrate within the SFWW. For cover, a categorical variable, we used chi-square analyses to test observed microhabitat use against the null hypothesis that cover was used in similar proportions across diel periods.

Habitat preference.—We used habitat use and availability data to calculate bull trout habitat preference values for the range of available habitat types (e.g., Maki-Petays et al. 2002). We calculated habitat preference for each microhabitat variable as the percent of used habitat/percent available habitat according to Baltz (1990). We scaled the preference values from 0 to 1 by dividing each habitat preference value by the highest preference value observed for each factor. For this calculation, we grouped depth (cm) and velocity (m/s), both continuous variables, into six intervals: 0–20, 21–40, 41–60, 61–80, 81–100, and 100. We calculated habitat preferences for cover and substrate for each category of the respective variable. Within each stream, we calculated preference values for all observed bull trout In the SFWW, where fish density and sample size was the greatest, we compared preference values for bull trout smaller than 220 mm (to represent juvenile, not sexually mature fish; Al-Chokhachy 2006) and bull trout 220 mm or larger (to represent both resident and migratory adult fish; Al-Chokhachy et al. 2005). For other streams, with lower fish densities, we did not delineate observations into size-classes to avoid artificially inflating preference values as a result of low sample sizes.

We used the distribution of bull trout habitat use data to classify available habitat data in the SFWW (e.g., Thomas and Bovee 1993). We selected this approach because it simultaneously considers the quality of multiple habitat factors and does not assume that fish select microhabitats factors independently of others (Vadas and Orth 2001). We classified the central 50% and 95% of the frequency distributions from microhabitat use data (depth, velocity, and substrate) in the SFWW as "optimal" and "useable" habitat, respectively, and anything outside of the 95% central distribution as "unsuitable." We then used these cutoffs to classify bull trout microhabitat use and availability data for each factor (e.g., depth, velocity) in the NFUM and SFWEN into three categories as optimal, useable, and unsuitable. We assumed that bull trout equally valued the different cover types and grouped all categories as "cover" (versus no cover). For preference classification, we used the optimal classification for the cover category (cover or no cover) that had the higher frequency of use and useable classification for the category with the lower frequency. Within this framework, we used a composite index of the microhabitat characteristics of each microhabitat cell (1 m^2), where cells were classified as optimum if all habitat characteristics were optimum (as defined above); useable if all characteristics were optimum, useable, or both; and unsuitable if any of the measured characteristics were considered unsuitable. For the SFWW data set, we used a chi-square test to test observed habitat use data against the null hypothesis that bull trout microhabitat use was used in similar proportions to available microhabitat.

We evaluated the consistency of bull trout microhabitat use by testing the transferability of habitat preference curves across systems. We used the SFWW data set as the base model, as previous research indicated the SFWW contained large populations of juvenile (<220-mm) and adult (≥220-mm) bull trout. This allowed us to reduce the occurrence of type II errors associated with low densities of bull trout. We conducted separate tests of transferability of the SFWW preference criteria against the NFUM and SFWEN data. Within each system, we classified use and availability data as either optimum, useable, or unsuitable based on the central 50% and 95% of the SFWW frequency distributions. Unlike Thomas and Bovee (1993), we used a two-tailed chi-square test to determine the transferability of the model (Maki-Petays et al. 2002). With this approach, we tested the null hypotheses that composite optimum, useable, and unsuitable cells were used in the same proportion as available in all three systems based on the distribution of microhabitat use from the SFWW. We considered the model transferable if the null hypothesis for each test was rejected at $\alpha = 0.05$. Although the chi-square test lacks power in some tests (Williams et al. 1999), it can provide additional supporting evidence for consistent habitat preferences across streams (Freeman et al. 1999) when used in combination with additional analytical measures (see below).

Logistic regression.—We also evaluated the influence of microhabitat factors on bull trout presence using logistic regression (threshold cutoff value = 0.50). As in the habitat preference analyses, we used the SFWW data set as the base model and completed separate analyses for both juveniles (<220 mm; hereafter, $\text{logistic}_{\text{juv}}$) and adult (≥220 mm; hereafter, $\text{logistic}_{\text{ad}}$) bull trout. In each model, we modeled depth, substrate, and water velocity as continuous variables and treated cover as a dummy variable whereby we assumed that all cover types were equally valued by bull trout ("yes" if any cover was present and "no" otherwise). Because of the potential effects of density on habitat selection (Hayes et al. 1996), we also included average bull trout density at the reach level (from the snorkeling surveys) for each system as an explanatory variable.

Prior to the final analyses, we checked the models for multicollinearity among explanatory variables. Next, we used two separate approaches to assess the logistic models. First, we reported the max-rescaled R^2 values, which provide a measure of model fit (range 0–1, where higher values suggest greater model fit; Peng and Nichols 2003). Next, we used receiver operating characteristic (ROC) plots as a measure of model accuracy. We calculated area under the ROC curve (AUR), which provides an assessment of model accuracy independent of the probability threshold (Fielding and Bell 1997; Manel et al. 2001). With this approach, AUR values ranging from 0.50 to 0.70 suggest low accuracy, values from 0.70 to 0.90 indicate moderate accuracy, and values greater than 0.90 suggest high accuracy (Manel et al. 2001).

We validated the logistic regression models from the SFWW both internally and externally. Internally, we used 10%-fold cross validation techniques ($n = 10$), where 10% of the data (both use and availability) were randomly withheld from the data set, and we used the remaining data to refit the logistic model (Olden et al. 2002). We used the logistic parameters from each cross validation model to predict the presence or absence of bull trout and evaluated the model by comparing the presence or absence predictions with actual field observations in the SFWW. The probability of presence or absence was calculated as

$$P(Y_i = 1) = \frac{e^{g(x)}}{1 + e^{g(x)}}, \qquad (1)$$

where Y_i is the response variable, P is the probability of presence, e is the base of natural logarithms, and $g(x)$ is a linear model of the explanatory variables. We evaluated the predictive success of each model (both internal and external validation) by calculating the sensitivity, percent of correctly classified presences, and specificity values (percent of correctly classified absences; threshold cutoff value = 0.50).

We validated the logistic models from the SFWW (both $\text{logistic}_{\text{juv}}$ and $\text{logistic}_{\text{ad}}$) externally with both the NFUM and the SFWEN data. For each validation exercise, we used field data (use and availability) from each system to predict bull trout presence or absence and evaluated the model by comparing the presence or absence predictions to actual field observations using equation (1). As in the internal validation, we evaluated the transferability of the model by calculating sensitivity and specificity values for each system.

TABLE 1.—Mean and SD values (parentheses) for microhabitat use and availability data for bull trout in the North Fork Umatilla, South Fork Wenaha, and the South Fork Walla Walla rivers. Cover types were combined into a binary variable (yes/no), and cover is reported as the percent of cells, either used or available, that contained cover. Microhabitat use data is reported by fish size category (<220 mm or ≥220 mm). Sample size (n) varies by analysis.

River and habitat status	Depth (m)	Substrate (size-class)	Average velocity (m/s)	Bottom velocity (m/s)	Percent of cells with cover	n	Average density/100 m^2
North Fork Umatilla River							0.0126 (0.0118)
Available habitat	0.17 (0.14)	4.49 (1.57)	0.42 (0.29)	0.27 (0.25)	18	419	
Habitate use by fish <220 mm[a]	0.35 (0.18)	4.43 (1.73)	0.19 (0.16)	0.10 (0.10)	91	23	
South Fork Wenaha River							0.0106 (0.0078)
Available habitat	0.23 (0.14)	4.36 (1.57)	0.58 (0.38)	0.30 (0.26)	41	527	
Habitat use by fish <220 mm	0.37 (0.12)	2.28 (1.6)	0.22 (0.19)	0.08 (0.08)	100	18	
Habitat use by fish ≥220 mm	0.44 (0.21)	4.50 (1.58)	0.44 (0.30)	0.17 (0.17)	90	10	
South Fork Walla Walla River							0.0081 (0.0053)
Available habitat	0.33 (0.28)	4.60 (1.40)	0.59 (0.47)	0.28 (0.28)	21	1722	
Habitat use by fish <220 mm	0.39 (0.21)	4.70 (1.62)	0.24 (0.23)	0.12 (0.14)	75	44	
Habitat use by fish ≥220 mm	0.53 (0.29)	4.17 (1.56)	0.24 (0.24)	0.12 (0.13)	73	29	
Habitat use by all fish	0.48 (0.37)	4.50 (1.59)	0.24 (0.23)	0.12 (0.13)	74	73	

[a] No bull trout ≥220 mm were observed in this river.

We conducted all logistic regression analyses with SAS software (Proc Logistic; SAS Institute 2000) and assessed statistical significance at $\alpha = 0.05$. We reported all parameter estimates and test statistics for each variable. Cross validation of logistic models included both significant and nonsignificant parameters.

Results

In all three rivers, bull trout used deep, slow-water habitats with cover (Table 1). The use of substrate size-classes appeared relatively consistent across systems, the exception being the SFWEN, where bull trout smaller than 220 mm used smaller substrate sizes. The majority of bull trout observed in snorkeling surveys were on or associated with the stream bottom. Specifically, 88% of the observed bull trout occupied the bottom one-fourth of the water column in the SFWW (the remaining 12% were within the one-fourth to one-half portion of the water column) and 100% of the observed bull trout did so in the NFUM and the SFWEN. Therefore, while we collected both average and bottom water column velocity measurements, we used bottom water velocity in all subsequent analyses.

During the nighttime, bull trout continued to use deeper, slow-water habitats with cover ($F_{1,36} = 2.5$, $P = 0.12$; Table 2); however, bull trout used shallower and significantly lower-velocity habitats during the nighttime ($F_{1,36} = 4.0$; $P = 0.05$) as compared with the daytime. We did not find any evidence of diel shifts in substrate use ($F_{1,36} = 0.7$; $P = 0.4$) or the use of cover ($P = 0.58$; df $= 1$).

Habitat Preference

Habitat preference analyses suggested similar use patterns across the three systems, particularly for depth and water velocity (Figure 2). Bull trout consistently used habitats with cover; however, the use and preference values for particular cover types varied substantially across systems. For bottom water column velocity and depth, bull trout used slower water velocities and deeper habitat. Finally, habitat preference values suggested that bull trout more frequently used smaller substrate and that the preference values for larger substrate-classes varied across systems. Substrate preference values were consistently the highest for all size-classes in the NFUM (except for substrate class 2, where no observations were recorded), and consistently the lowest for larger size-classes in the SFWEN.

The SFWW had the largest sample size of observed

TABLE 2.—Summary statistics, including means and SDs (parentheses) and results from diel microhabitat comparisons for the South Fork Walla Walla River (day: $n = 19$; night: $n = 19$).

Parameter	Day	Night	Test statistic[a]	P-value
Depth (m)	0.49 (0.29)	0.36 (0.19)	2.47	0.12
Substrate	4.42 (1.12)	4.05 (1.51)	0.73	0.4
Bottom velocity (m/s)	0.12 (0.12)	0.06 (0.05)	4.04	0.05
Percent of cells with cover	0.68	0.84	0.58	0.55

[a] An F-statistic is reported for depth, substrate, and bottom velocity; a χ^2 value is reported for the percent of cells with cover.

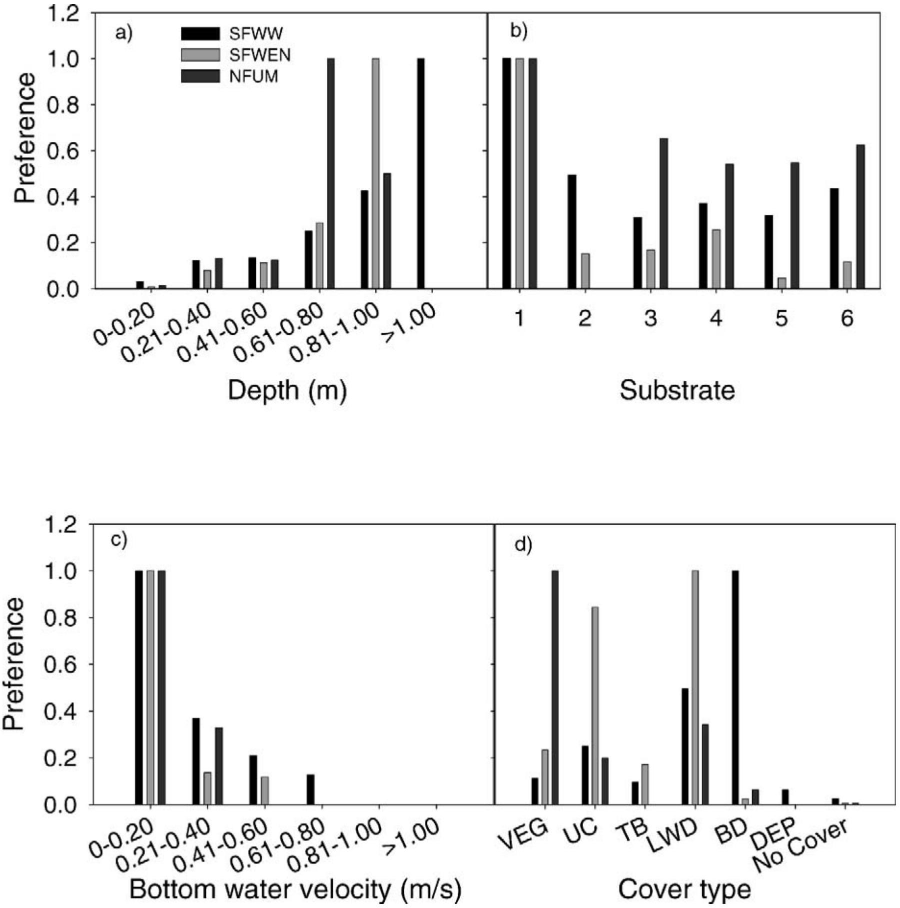

FIGURE 2.—Habitat preferences of bull trout with respect to **(a)** depth, **(b)** substrate size (1: 0–6 mm; 2: 7–25 mm; 3: 26–50 mm; 4: 51–75 mm; 5: 76–125 mm; and 6: >125 mm), **(c)** bottom water velocity, and **(d)** cover for the South Fork Walla Walla (SFWW; black), South Fork Wenaha (SFWEN; tan), and North Fork Umatilla (NFUM; gray) rivers. Individual cover types include vegetation (VEG), undercuts (UC), turbulence (TB), large woody debris (LWD), boulder (BD; >125 mm), water depth (DEP; >0.70 m), and no cover.

bull trout (n = 73) across the three systems we evaluated, and therefore we compared habitat preference values separately for small (<220-mm) and large (≥220-mm) bull trout in this system (Figure 3). Similar to the general patterns observed across systems, both size-groups used habitat with greater depths, smaller substrate, lower bottom water velocities, and cover. However, these results also suggest that compared with smaller bull trout, larger bull trout more frequently used deeper habitats and typically used LWD as cover, while smaller bull trout used boulders as cover.

Based on the chi-square transferability analyses, habitat preferences measured in the SFWW transferred reasonably well to both the NFUM and the SFWEN. All three chi-square tests were significant ($P < 0.0001$; df = 2), rejecting the null hypotheses that composite (optimum, usable, and unsuitable) microhabitats were used in similar proportion to available microhabitats. In each of the systems, bull trout used optimal and usable habitats at a significantly greater proportion than was available and used unsuitable habitats substantially less (Figure 4). While these results do indicate similar patterns across systems, we acknowledge that there may be a higher probability of both type I and type II errors due to the relatively small sample sizes in both the SFWEN and NFUM (Thomas and Bovee 1993).

Logistic Regression

Preliminary diagnostics demonstrated no multicollinearity among the explanatory variables; therefore, we ran the logistic models with depth, substrate, bottom water velocity, cover, and fish density as explanatory

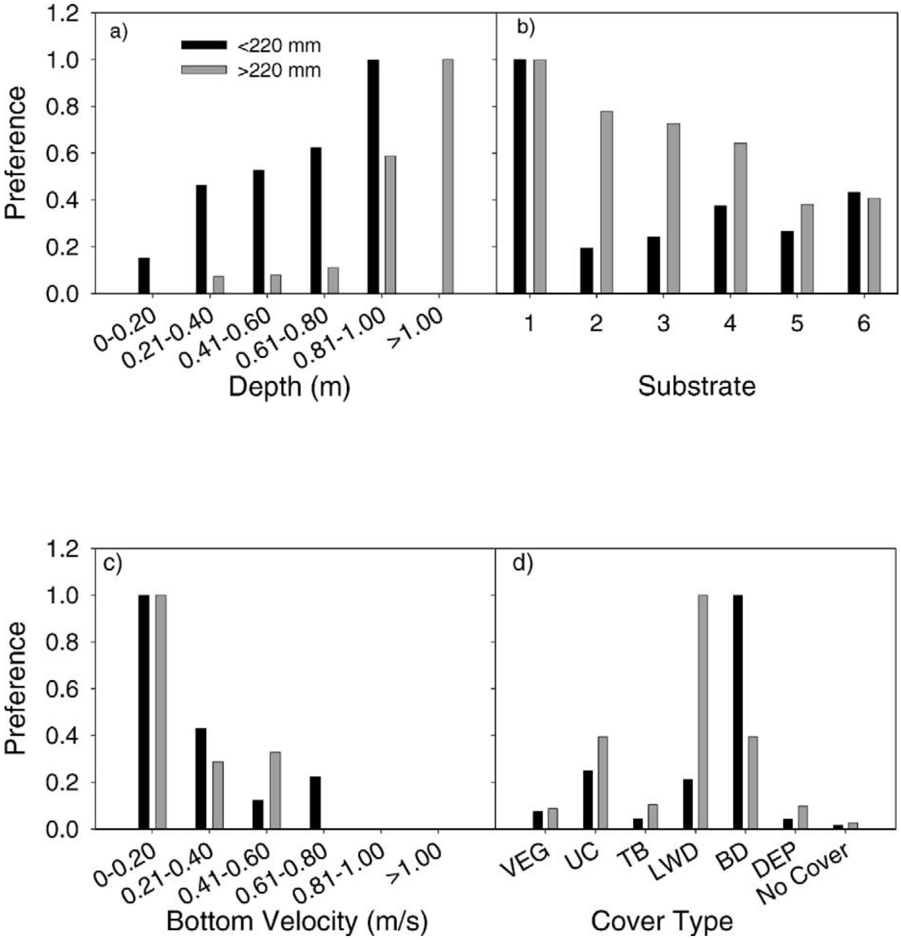

FIGURE 3.—Habitat preferences of different size-classes of bull trout in the South Fork Walla Walla River. See Figure 2 for other details.

variables. The $\text{logistic}_{\text{juv}}$ model resulted in a reasonable fit with a max-rescaled R^2 of 0.177 ($P < 0.0001$; df = 5) and moderate accuracy (AUR = 0.755). Only bottom water velocity and cover were significant variables for predicting the presence or absence of juvenile bull trout at the microhabitat scale, while substrate, water depth, and density were insignificant (Table 3). The $\text{logistic}_{\text{ad}}$ model demonstrated a similar fit, with a max-rescaled R^2 of 0.211 ($P < 0.001$; df = 5) and similar accuracy (AUR = 0.761). However, in addition to bottom water velocity and cover, which were significant in the $\text{logistic}_{\text{juv}}$ model, water depth and substrate were significant in predicting adult bull trout presence or absence (Table 3).

For the logistic models ($\text{logistic}_{\text{juv}}$ and $\text{logistic}_{\text{ad}}$), internal and external validation suggested that depth, bottom velocity, substrate, and cover accurately predict bull trout absence at the microhabitat level. These variables were less effective, however, at predicting bull trout presence. Sensitivity values for both the $\text{logistic}_{\text{juv}}$ and $\text{logistic}_{\text{ad}}$ models were 0% for both internal and external validation, which suggested the logistic model could not accurately predict bull trout presence at the microhabitat scale. However, specificity values for the SFWW, SFWEN, and NFUM were all 100%, indicating that depth, bottom velocity, substrate, and cover can be used to predict bull trout absence.

Discussion

Habitat Use

Our evaluation of microhabitat use by three fluvial bull trout populations in northeastern Oregon indicated that both juveniles and adults use slow-velocity habitats with cover. In addition, adult bull trout consistently used deeper habitat across systems. These results suggest that throughout their life cycle, bull

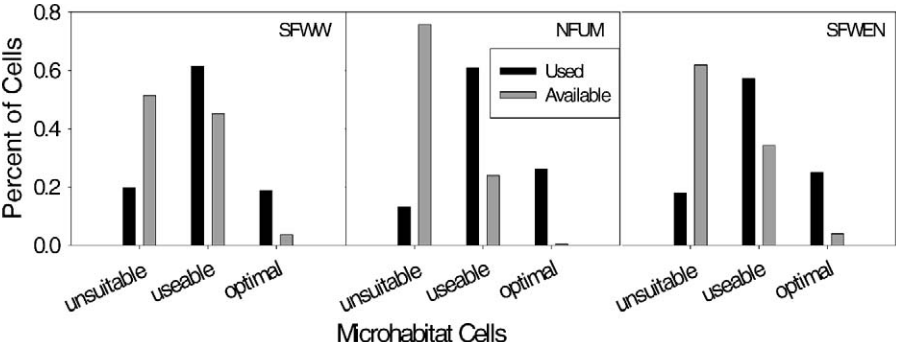

FIGURE 4.—Proportions of optimal, useable, and unsuitable habitat using transferability criteria from the South Fork Walla Walla River (SFWW) for the North Fork Umatilla (NFUM) and South Fork Wenaha (SFWEN) rivers.

trout in these headwater systems generally use complex habitats and generally avoid habitats which are both energetically costly and may increase their mortality through exposure to predators. Furthermore, the shift to use of deeper-water habitats by adult bull trout suggests that for successful habitat restoration and management of systems the ontogenetic differences in habitat use within systems must be considered. The corroboration of our results with previous research at different scales (Rieman and McIntyre 1993; Rich et al. 2003), seasons (Jakober 1995; Muhlfeld et al. 2003), and life stages (Baxter and McPhail 1997; Sexauer and James 1997) further suggests the importance of these habitat factors in determining bull trout habitat use.

Our results demonstrated that cover is an extremely important component of juvenile and adult bull trout habitat use; however, the use of specific cover types may vary substantially across systems and size-classes. Consistent with Sexauer and James (1997), we found that juvenile fluvial bull trout in the SFWW predominantly used boulders as a source of cover. However, this pattern was not consistent in the NFUM, the smallest of three systems we compared; in this stream, similar size-classes (<220 mm) of bull trout primarily used vegetation as a source of cover. Similarly, we found that adult bull trout used a variety of cover types, a result supported by research at larger spatial scales (Rieman and McIntyre 1993; Watson and Hillman 1997; Muhlfeld and Marotz 2005). As such, bull trout appear to use different sources of cover across different systems (e.g., LWD, undercut banks, and riparian vegetation, here), indicating the availability of cover may be more important than any specific cover type. The use of cover also appears to be consistent across seasons as illustrated in fall and winter surveys of juvenile, fluvial (Jakober 1995) and subadult, adfluvial (Muhlfeld et al. 2003) bull trout. Across life stages, life history forms, and seasons, bull trout appear to be using habitats with cover, a behavior that corresponds to their cryptic nature (Thurow et al. 2006) and that presumably occurs to avoid exposure to potential avian and terrestrial predators.

TABLE 3.—Parameter estimates, SEs, odds ratio estimates, and *P*-values for explanatory variables from logistic regression analysis for juvenile (<220 mm) and adult ($\geq$220 mm) bull trout.

Variable	Parameter estimate	SE	Odds ratio estimate	*P*-value
Juveniles				
Intercept	−4.084	0.672		<0.0001
Depth (m)	0.725	0.598	2.065	0.225
Substrate	0.070	0.109	1.073	0.521
Bottom velocity (m/s)	−3.395	1.077	0.034	0.001
Cover	2.038	0.362	7.677	<0.0001
Density (fish/100 m^2)	−53.5973	45.451	<0.001	0.207
Adults				
Intercept	−3.524	0.707		<0.0001
Depth (m)	2.926	0.697	18.643	<0.0001
Substrate	−0.269	0.128	0.764	0.354
Bottom velocity (m/s)	−3.381	1.352	0.034	0.0124
Cover	1.606	0.444	4.983	0.0003
Density (fish/100 m^2)	−73.391	51.025	<0.001	0.1503

At the microhabitat scale, we found that water depth was a significant factor for predicting adult bull trout microhabitat use. Although preference data suggested juvenile bull trout used deeper habitats than available, depth was not a significant factor in predicting summer bull trout microhabitat use in logistic regression analyses, an observation consistent with research from the eastern Cascades in Washington (Sexauer and James 1997). While we found no comparable results for adult fluvial bull trout, use of deep habitats has been observed for subadult, adfluvial bull trout of similar sizes during summer (Muhlfeld and Marotz 2005) and winter (Muhlfeld et al. 2003) seasons in Montana streams. At intermediate spatial scales (e.g., channel unit), bull trout occurrence was positively associated with increased water depth in both Oregon and Washington streams (Banish 2003) and in central Idaho (Zurstadt 2000). With increased body size, adult bull trout, which are too large to use the interstitial spaces of substrate (e.g., Thurow 1997), may shift to deeper habitats to minimize water surface protrusion and avoid avian and terrestrial predators.

Across size-classes and systems, bull trout consistently used slow-water habitats. The use of low-velocity areas appears to be a regular pattern across life stages, including juvenile (Sexauer and James 1997; Thurow 1997), subadult (Muhlfeld et al. 2003; Muhlfeld and Marotz 2005), and adult bull trout (Jakober 1995; Banish 2003), as well as across life history forms, including resident (Zurstadt 2000), fluvial (Jakober 1995), and adfluvial (Muhlfeld et al. 2005). Our results are supported by recent physiological work by Mesa et al. (2004) demonstrating that bull trout have low critical swimming velocities relative to other salmonids. Bioenergetically, this would suggest bull trout should use slower water habitats to achieve maximum energy efficiency. The consistent use of slower habitats with cover and general morphology of bull trout (e.g., large head; Markle 1992) reflects their basic biology as an ambush predator; across their range, large juvenile and adults are considered to be largely piscivorous (Fraley and Shepard 1989; Rieman and McIntyre 1993; Clarke et al. 2005).

We also found bull trout were generally associated with fine substrate sizes. In particular, habitat preference values were highest for small sediment sizes, and substrate (negative parameter value) was a significant factor in predicting adult bull trout presence or absence in logistic regression analyses. Our results are in contrast to previous work where large substrate was found to be an important factor for juvenile bull trout, which commonly use the interstitial spaces between particles as sources of cover (Jakober 1995; Thurow 1997; Zurstadt 2000). However, for our study, the negative relationship with substrate size must be viewed with caution. We underestimated the importance of large substrate at the microhabitat scale due to inherent difficulties in quantifying the availability of interstitial microhabitats within the substrate (i.e., accurately measuring velocity) and detecting juvenile bull trout use of these habitats with snorkel surveys (Thurow et al. 2006). In addition, our research was conducted in unmanaged, high-quality watersheds that generally do not experience excessive fine sediment loading, a detrimental factor for several life stages (e.g., Suttle et al. 2004). Finally, we found bull trout used deeper, slow-velocity habitats, which act as deposition areas for fine sediment; thus, the use of deeper, slow-velocity habitats may artificially inflate the importance of fine sediment.

Our analyses of diel microhabitat use in the SFWW suggest that bull trout use slower velocity habitats at night, a pattern that is consistent with previous research evaluating diel habitat use patterns (Thurow 1997; Muhlfeld et al. 2003). Similar to Jakober (1995) and Sexauer and James (1997), we also found that most bull trout continued to use sources of cover during both day and night periods, which suggests that bull trout may be avoiding predators (e.g., mink *Mustela vison*) during both daytime and nighttime periods. While Muhlfeld et al. (2003) found that most adfluvial bull trout shifted away from daytime cover sources to near channel margin habitat at night (presumably to forage), these channel banks may still provide an indirect source of cover from terrestrial predators. Finally, unlike Thurow (1997) and Muhlfeld et al. (2003), we did not find significant diel differences in use of water depth, although our sample size was relatively small.

Limitations to Modeling Bull Trout Habitat Use

Despite the need for validation of species–habitat relationships, most habitat studies have not been rigorously tested with external data sets. Validation exercises allow for added inference regarding the consistency of relationships across systems (Garshelis 2000). However, the primary limitation of this type of modeling approach is the effect of fish density on habitat use and availability. In particular, high density can lead to the use of suboptimal habitats, and at lower densities much of the optimal habitat may go unused (Power 1984; Rosenfeld 2003). Both of these scenarios can increase the difficulty to understand and quantify species–habitat relationships. Ideally, habitat selection would be measured in a system where optimal habitat was saturated (Greene and Stamps 2001; Rosenfeld 2003), allowing us to evaluate changes in habitat use across a range of bull trout densities. However, such an approach would be difficult to implement for an imperiled species (i.e., one with low abundance) or a species such as bull trout, for which the density is typically low even in relatively pristine watersheds (Rieman and McIntyre 1993).

We used logistic regression analyses to develop an empirical model based on habitat characteristics and validated the effectiveness of this model in predicting bull trout presence or absence. Based on this approach, juvenile bull trout presence was significantly affected by cover and bottom water velocity, and adult bull trout presence was significantly affected by depth, cover, velocity, and substrate. However, low densities of bull trout resulted in an unequal number of response cases (1,722 absences versus 73 presences), which can have profound impacts on individual parameter estimates and limit validation exercises (Hosmer and Lemeshow 2000). Despite the significance of multiple explanatory variables and moderate AUR values, our logistic models could not effectively predict bull trout presence, a limitation which may be partially a function of low densities of bull trout (Manel et al. 2001). Despite high specificity values from our cross validation and external validation efforts, the low prevalence of bull trout may artificially inflate these measures (Manel et al. 2001). And, although there are alternative approaches to monitoring presence or absence (see Fielding and Bell 1997), these approaches are limited when data are unbalanced (i.e., more absence than presence data) and when species occur at low densities.

Finally, despite our efforts to minimize disturbances to fish, we acknowledge that our field techniques may have affected our observations of bull trout microhabitat use. The presence of snorkelers within a stream can scare fish out of specific habitat types, potentially resulting in observations of fish use that are not representative of natural habitat use (Peterson et al. 2005). Although we found consistent patterns of microhabitat use across systems, this sampling effect may have been consistently biased, increased the variance around our estimates of habitat use, or both.

Management Implications

Bull trout is a species of fish that exhibits multiple life history forms and occupies a wide range of habitat types across large geographical areas in the Pacific Northwest. Despite these attributes, bull trout are listed under the ESA at the species level and are not delineated into distinct population segments as are other salmonids in the Pacific Northwest (e.g., Chinook salmon *Oncorhynchus tshawytscha*). Thus, understanding the consistency of bull trout habitat relationships across regions, life stages, and life history forms is critical for the recovery and designation of critical habitat for this species.

We demonstrated consistent patterns of bull trout microhabitat use in three relatively unaltered systems; as such, the results from our research can provide benchmarks for restoration activities in degraded systems. The consistency of our findings across systems, with other studies at similar and larger spatial scales, and across life history forms suggests our results may be widely applicable to bull trout across the Northwest. However, our results also indicate that applying predictive models of bull trout habitat use may be problematic owing to the naturally low abundances of this species. We urge caution when using predictive, habitat use models and suggest the use of formal validation procedures when possible.

Lastly, while we have illustrated consistent patterns of habitat use and preference at the microhabitat scale, additional research is necessary to better understand other abiotic factors that affect the distribution of this species (e.g., formal hierarchical analyses; Rieman et al. 2006). In other systems, it may also be important to investigate the role of biotic factors (Orth 1987; Maki-Petays et al. 1999; Rieman et al. 2006), such as forage potential and interactions with others species (e.g., brook trout), and how these factors affect the distribution of and habitat use by bull trout (Gunckel et al. 2002).

Acknowledgments

We would like to thank Tim Whitesel and Darren Gallion (U.S. Fish and Wildlife Service [USFWS]) for technical advice, Gary P. Thiede and Kris Homel for logistical contributions and field technician supervision, and Nolan Banish for providing additional data. Darren Gallion, Wayne Wurtsbaugh, Edward Evans, Mary Conner, Howard Schaller, and three anonymous reviewers provided constructive insight on earlier drafts of this manuscript. Funding for this project was provided by the USFWS and the U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit. Eric Larson, Melinda Malek, Travis Sanderson, Travis Scott, Jeremy Mull, Brittany Stewart, Mike Davis, Ryan Kumpf, Jim Hearsey, David Lillard, Andy Dean, Kieth Hofer, Nate Charbonneau, Holly Campbell, Doug Martin, and Dan Cullen helped with data collection in the field. Reference to trade names does not imply endorsement by the U.S. Government.

References

Al-Chokhachy, R. 2006. An assessment of the population dynamics and limiting factors of a fluvial bull trout population. Doctoral dissertation. Utah State University, Logan.

Al-Chokhachy, R., P. Budy, and H. Schaller. 2005. Understanding the significance of redd counts: a comparison between two methods for estimating the abundance of and monitoring bull trout populations. North American Journal of Fisheries Management 25:1505–1512.

Baltz, D. M. 1990. Autecology. Pages 585–600 *in* C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Banish, N. P. 2003. Diel summer habitat use by bull trout, *Salvelinus confluentus*, in eastern Cascade streams. Master's thesis. University of Georgia, Athens.

Baxter, C. V. 2002. Fish movement and assemblage dynamics in a Pacific Northwest riverscape. Doctoral dissertation. Oregon State University, Corvallis.

Baxter, J. S. 1997. Summer daytime microhabitat use and preference of bull trout fry and juveniles in the Chowade River, British Columbia. Fisheries Management Report 107, University of British Columbia, Vancouver.

Baxter, J. S., and J. D. McPhail. 1997. Diel microhabitat preferences of juvenile bull trout in an artificial stream channel. North American Journal of Fisheries Management 17:975–980.

Bonneau, J. L., R. F. Thurow, and D. L. Scarnecchia. 1995. Capture, marking, and enumeration of juvenile bull trout and cutthroat trout in small, low-conductivity streams. North American Journal of Fisheries Management 15:563–568.

Bovee, K. D. 1982. A guide to stream habitat analysis using the instream flow incremental methodology. U.S. Fish and Wildlife Service, Instream Flow Information Paper 12, Fort Collins, Colorado.

Bovee, K. D. 1996. A comprehensive overview of the instream flow incremental methodology. National Biological Service, Fort Collins, Colorado.

Budy, P., R. Al-Chokhachy, and G. P. Thiede. 2004. Bull trout population assessment and life history characteristics in association with habitat quality and land use: a template for recovery planning. Utah Cooperative Fish and Wildlife Research Unit, Logan.

Clarke, L. R., D. T. Vidergar, and D. H. Bennett. 2005. Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. Ecology of Freshwater Fish 14:267–277.

Cunjak, R. A. 1996. Winter habitat of selected stream fishes and potential impacts from land use activity. Canadian Journal of Fisheries and Aquatic Sciences 53:267–282.

Dunham, J., B. Rieman, and G. Chandler. 2003. Influences of temperature and environmental variables on the distribution of bull trout within streams at the southern margin of its range. North American Journal of Fisheries Management 23:894–904.

Fausch, K. D., and T. G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 49:682–693.

Fausch, K. D., C. E. Torgerson, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. Bioscience 52:483–498.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology, and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Science 63:133–143.

Freeman, M. C., Z. H. Bowen, and K. D. Bovee. 1999. Transferability of habitat suitability criteria: response to comment. North American Journal of Fisheries Management 19:626–628.

Freeman, M. C., Z. H. Bowen, and J. H. Crance. 1997. Transferability of habitat suitability criteria for fishes in warmwater streams. North American Journal of Fisheries Management 17:20–31.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring habitat use, selection, and importance. Pages 111–164 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York.

Geist, D. R., J. Jones, C. J. Murray, and D. D. Dauble. 2000. Suitability criteria analyzed at the spatial scale of redd clusters improved estimates of fall Chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat use in the Hanford Reach, Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 57:1636–1646.

Greene, C. M., and J. A. Stamps. 2001. Habitat selection at low population densities. Ecology 82(8):2091–2100.

Guay, J. C., D. Boisclair, D. Rioux, M. Leclerc, M. Lapointe, and P. Legendre. 2000. Development and validation of numerical habitat models for juveniles of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 57:2065–2075.

Gunckel, S. L., A. R. Hemmingsen, and J. L. Li. 2002. Effect of bull trout and brook trout interactions on foraging, habitat, feeding behavior, and growth. Transactions of the American Fisheries Society 131:1119–1130.

Hayes, D. B., C. P. Ferreri, and W. W. Taylor. 1996. Linking fish habitat to their population dynamics. Canadian Journal of Fisheries and Aquatic Sciences 53:383–390.

Heggenes, J. 2002. Flexible summer habitat selection by wild, allopatric brown trout in lotic environments. Transactions of the American Fisheries Society 131:287–298.

Horan, D. L., J. L. Kershner, C. P. Hawkins, and T. A. Crowl. 2000. Effects of habitat area and complexity on Colorado River cutthroat trout density in Uinta Mountain streams. Transactions of the American Fisheries Society 129:1250–1263.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression, 2nd edition. Wiley, New York.

Imhof, J. G., J. Fitzgibbon, and W. K. Annable. 1996. A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. Canadian Journal of Fisheries and Aquatic Sciences 53:312–326.

Jakober, M. K. 1995. Autumn and winter movement and habitat use of resident bull trout and westslope cutthroat trout in Montana. Master's thesis. Montana State University, Bozeman.

Kershner, J. L., E. K. Archer, M. Coles-Ritchie, E. Cowley, R. C. Henderson, K. Kratz, C. Quimby, D. L. Turner, L. C. Ulmer, and M. R. Vinson. 2004. Guide to effective monitoring of aquatic and riparian resources. U.S. Forest Service General Technical Report RMRS-GTR-121.

Leary, R. F., F. W. Allendorf, and S. H. Forbes. 1993. Conservation genetics of bull trout in the Columbia and Klamath River drainages. Conservation Biology 7:856–865.

Maki-Petays, A., A. Huusko, H. Erkinaro, and T. Muotka. 2002. Transferability of habitat suitability criteria of juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 59:218–228.

Maki-Petays, A., T. Muotka, and A. Huusko. 1999. Densities of juvenile brown trout (*Salmo trutta*) in two subarctic rivers: assessing the predictive capability of habitat preference curves. Canadian Journal of Fisheries and Aquatic Sciences 56:1420–1427.

Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence/absence models in ecology: the need to account for prevalence. Journal of Applied Ecology 38:921–931.

Markle, D. F. 1992. Evidence of bull trout × brook trout hybrids in Oregon. Pages 58–67 *in* P. J. Howell and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain Bull Trout Workshop. American Fisheries Society, Oregon Chapter, Corvallis.

Mesa, M. G., L. K. Weiland, and G. B. Zydlewski. 2004. Critical swimming speeds of wild bull trout. Northwest Science 78:59–65.

Muhlfeld, C. C., S. Glutting, R. Hunt, D. Daniels, and B. Marotz. 2003. Winter diel habitat use and movement by subadult bull trout in the upper Flathead River, Montana. North American Journal of Fisheries Management 23:163–171.

Muhlfeld, C. C., and B. Marotz. 2005. Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. North American Journal of Fisheries Management 25:797–810.

Olden, J. D., D. A. Jackson, and P. R. Peres-Neto. 2002. Predictive models of fish species distributions: a note on proper validation and chance predictions. Transactions of the American Fisheries Society 131:329–336.

Orth, D. J. 1987. Ecological consideration in the development and application of instream flow–habitat models. Regulated Rivers: Research and Management 1:171–181.

Peng, C. J., and R. N. Nichols. 2003. Using multinomial logistic models to predict adolescent behavioral risk. Journal of Modern Applied Statistical Methods 2:177–188.

Peterson, J. T., N. P. Banish, and R. F. Thurow. 2005. Are block nets necessary? Movement of stream-dwelling salmonids in response to three common survey methods. North American Journal of Fisheries Management 25:732–743.

Polacek, M. C., and P. W. James. 2003. Diel microhabitat use of age-0 bull trout in Indian Creek, Washington. Ecology of Freshwater Fish 12:81–86.

Power, M. E. 1984. Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. Journal of Animal Ecology 53:357–374.

Railsback, S. F., and B. C. Harvey. 2002. Analysis of habitat-selection rules using an individual-based model. Ecology 83:1817–1830.

Ratliff, D. E., and P. J. Howell. 1992. The status of bull trout populations in Oregon. Pages 10–17 *in* P. J. Howell and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain Bull Trout Workshop. American Fisheries Society, Oregon Chapter, Corvallis.

Rich, C. F., T. E. McMahon, and B. E. Rieman. and B. E .Thompson. 2003. Local-habitat, watershed, and biotic features associated with bull trout occurrence in Montana streams. Transactions of the American Fisheries Society 132:1053–1064.

Rieman, B. E., D. C. Lee, and R. F. Thurow. 1997. Distribution, status, and likely future trends of bull trout within the Columbia River and Klamath River basins. North American Journal of Fisheries Management 17:1111–1125.

Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service General Technical Report INT-302.

Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124:285–296.

Rieman, B. E., J. T. Peterson, and D. L. Myers. 2006. Have brook trout (*Salvelinus fontinalis*) displaced bull trout (*Salvelinus confluentus*) along longitudinal gradients in central Idaho streams? Canadian Journal of Fisheries and Aquatic Sciences 63:63–78.

Ripley, T., G. Scrimgeour, and M. S. Boyce. 2005. Bull trout (*Salvelinus confluentus*) occurrence and abundance influenced by cumulative industrial developments in a Canadian boreal forest watershed. Canadian Journal of Fisheries and Aquatic Sciences 62:2431–2442.

Rosenfeld, J. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. Transactions of the American Fisheries Society 132:953–968.

SAS Institute. 2000. SAS version 8.01. SAS Institute, Cary, North Carolina.

Selong, J. H., T. E. McMahon, A. V. Zale, and F. T. Barrows. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. Transactions of the American Fisheries Society 130:1026–1037.

Sexauer, H. M., and P. W. James. 1997. Microhabitat use by juvenile bull trout in four streams located in the eastern Cascades, Washington. Pages 361–370 *in* W. C. Mackay, M. K. Brewin, and M. Monita, editors. Friends of the Bull Trout Conference Proceedings, Trout Unlimited Canada, Calgary.

Stevens, D. L., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99:262–278.

Suttle, K. B., M. E. Power, J. M. Levine, and C. McNeely. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. Ecological Applications 14:969–974.

Thomas, J. A., and K. D. Bovee. 1993. Application and testing of a procedure to evaluate transferability of habitat suitability criteria. Regulated Rivers: Research and Management 8:285–294.

Thurow, R. F. 1994. Underwater methods for study of salmonids in the Intermountain West. U.S. Forest Service General Technical Report INT-GTR-307.

Thurow, R. F. 1997. Habitat utilization and diel behavior of juvenile bull trout (*Salvelinus confluentus*) at the onset of winter. Ecology of Freshwater Fish 6:1–7.

Thurow, R. F., J. T. Peterson, and J. W. Guzevich. 2006. Utility and validation of day and night snorkel counts for estimating bull trout abundance in first-to-third-order streams. North American Journal of Fisheries Management 26:217–232.

Vadas, R. L., and D. J. Orth. 2001. Formulations of habitat suitability models for stream fish guilds: do the standard methods work? Transactions of the American Fisheries Society 130:217–235.

Watson, G., and T. W. Hillman. 1997. Factors affecting the distribution and abundance of bull trout: an investigation at hierarchical scales. North American Journal of Fisheries Management 17:237–252.

Williams, J. G., T. P. Speed, and W. F. Forrest. 1999. Comment: transferability of habitat suitability criteria. North American Journal of Fisheries Management 19:623–625.

Zurstadt, C. 2000. Relationships between relative abundance of resident bull trout (*Salvelinus confluentus*) and habitat characteristics in central Idaho mountain streams. Master's thesis. Oregon State University, Corvallis.

Appendix V - Demographic Characteristics, Population Structure, and Vital Rates of a Fluvial Population of Bull Trout in Oregon

authored by

Robert Al-Chokhachy
Phaedra Budy

Utah State University

Transactions of the American Fisheries Society 137:1709–1722, 2008

DOI: 10.1577/T07-247.1

[Article]

Demographic Characteristics, Population Structure, and Vital Rates of a Fluvial Population of Bull Trout in Oregon

ROBERT AL-CHOKHACHY* AND PHAEDRA BUDY

U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit, Department of Watershed Sciences, Utah State University, Logan, Utah 84322-5210, USA

Abstract.—Identification of the factors limiting inland salmonid populations, such as those of the threatened bull trout *Salvelinus confluentus* in the Pacific Northwest, can be particularly challenging due to substantial gaps in our understanding of population demographics, population structure in the presence of multiple life history forms, and vital rates. We implemented a large-scale mark–recapture program over a 5-year period using an innovative combination of active and passive techniques to estimate (1) bull trout age and growth by size-class, (2) the proportion of the population exhibiting resident and migratory behavior, and (3) survival rates (S) for different life stages and life history forms (resident and migratory). Our results suggest that bull trout reached sexual maturity at a relatively small size (200 mm) and young age (3–4 years) and that large individuals (>600 mm) can reach ages greater than 12 years in this fluvial population. Using active and passive mark–recapture methods, we found that large bull trout (>420 mm) were predominantly migratory in behavior (72% were migratory) and that there was considerable variability among other size-classes in the proportion exhibiting migratory behavior. Survival rate varied significantly across size-classes and study years. Juvenile bull trout (120–170 mm) exhibited the lowest annual S on average (0.09) and the highest interannual variability (coefficient of variation = 0.60) in S among size-classes. Fish exhibiting migratory life history patterns generally had higher S than did resident fish; small, juvenile residents had a significantly mean S (0.15; SE = 0.02) than did similarly sized migratory fish (mean S = 0.35; SE = 0.04). Collectively, our results highlight important differences across life history forms within and across populations; these factors must be considered when designing future recovery and management strategies for any single bull trout recovery unit or across larger geographic areas.

The design of sound recovery and management strategies for fish populations requires an understanding of life stages that limit overall population growth and persistence (Wilson 2003; Legault 2005). Identification of limiting life stages often involves the use of population models (Stearns 1992), which require explicit demographic and vital rate information. However, obtaining this information can be temporarily and monetarily challenging and extremely difficult when populations exhibit multiple life history forms, low abundance, and high variability in demographic processes (Al-Chokhachy 2006; Homel and Budy 2008). Nevertheless, this information is necessary for providing a framework to assess the relative effects of various management options, such as harvest practices (e.g., Crowder et al. 1994), restoration efforts (e.g., Hilderbrand 2003), and management scenarios (e.g., Marschall and Crowder 1996).

A sound understanding of population dynamics, demographics, and vital rates is critical to planning effective conservation strategies for bull trout *Salvelinus confluentus*, a species of char that is native to the Pacific Northwest and Canada and that has been listed as threatened under the Endangered Species Act in the United States since 1998 and as a species of special concern in Canada since 1995. Across their native range, bull trout have exhibited substantial declines in population abundance and distribution as a result of habitat degradation and fragmentation (Fraley and Shepard 1989; Rieman and McIntyre 1995; Ripley et al. 2005) and the introduction of nonnative species (Leary et al. 1993). Bull trout are known to exhibit multiple life history forms including anadromous, fluvial, and adfluvial; multiple forms can coexist within a single population (Rieman and McIntyre 1993; Nelson et al. 2002; Homel and Budy 2008). As in many other salmonid populations (e.g., Bonneville cutthroat trout *Oncorhynchus clarkii utah*; Colyer et al. 2005), the migratory component of many bull trout populations has declined significantly (Nelson et al. 2002). As a result, bull trout exist only as subpopulations across the range of their former distribution (Rieman et al. 1997). Bull trout are also known to be generally associated with complex habitats (Muhlfeld and Marotz 2005; Al-Chokhachy and Budy 2007) and to occur in naturally low densities (Rieman and McIntyre 1993). These attributes, in conjunction with the diverse life history strategies, can result in

* Corresponding author: robert.a@aggiemail.usu.edu

Received November 20, 2007; accepted May 26, 2008
Published online December 4, 2008

problematic sampling and monitoring of bull trout populations (Al-Chokhachy 2006).

Despite the listing and current status of bull trout, there are significant gaps in our understanding of bull trout population dynamics and critical vital rates. In particular, there are few empirical estimates of survival rate (*S*), and estimates of *S* that are specific to life stages or life history forms are generally lacking. Additionally, the majority of bull trout research has focused on the migratory individuals from adfluvial populations where migratory and resident fish are easily delineated (e.g., Fraley and Shepard 1989). As such, our understanding of the structure of populations where multiple life history forms coexist is extremely limited but is fundamental for future management actions. Overall, there is little information describing demographic characteristics, *S*, growth, fecundity, and population structure of fluvial bull trout populations. These data gaps limit (1) our understanding of bull trout ecology, (2) our ability to complete formal population viability analyses, and (3) assessments of the effects of different management scenarios on bull trout populations.

In this study, we used 5 years of comprehensive mark–recapture data to evaluate demographic and vital rate information for a fluvial population of bull trout. Our approach is unique, as we combined active capture–recapture data from annual summer sampling and year-round, continuous recapture data from passive instream antennae (Zydlewski et al. 2006) to maximize our understanding of bull trout vital rates and structure in a population containing resident and migratory life history expressions. Within this framework, our specific objectives were to (1) estimate bull trout *S* and factors affecting *S* across multiple size-classes; (2) evaluate potential differences in vital rates across life history forms; (3) quantify bull trout age structure and fecundity; and (4) evaluate the proportion of the population exhibiting migratory behavior. Our estimates of key vital rates and their variability provide critical insight into the ecology and population dynamics of this imperiled species and can aid in identifying factors that limit bull trout populations across the species' native range.

Methods

Study area.—We completed a detailed mark–recapture study on the South Fork Walla Walla River (SFWWR; 2002–2006) in northeastern Oregon (Figure 1). The SFWWR originates in the Blue Mountains at the eastern boundary of the arid steppe of the Columbia River basin and is characterized by hot, dry summers and cold, wet winters. Despite the relatively low elevation (610–1,000 m) of the SFWWR study site, cold groundwater influences maintain regular base flow conditions (base flow discharge = 2.6 m^3/s) and regulate water temperature such that it does not exceed 16°C (Budy et al. 2005); thus, water temperature was probably not a limiting factor during this study (Selong et al. 2001). Habitat conditions within the SFWWR can generally be described as high quality and subject to few forest management activities; however, recreational activities (e.g., hiking) do occur throughout the drainage. Downstream of the SFWWR, habitat conditions degrade longitudinally as water temperature, habitat simplification, channelization, and migration barriers increase.

The SFWWR is located primarily in the Umatilla National Forest and is approximately 21 km in length. We divided the SFWWR into 200-m sample reaches (102 reaches total, average width = 10 m) and used a systematic sampling design (based on an annual 20% minimum sampling rate) to achieve spatial balance in sampling (Stevens and Olsen 2004). Under this approach, our sample reaches were distributed throughout our study site (~1-km intervals between reaches), which enabled us to effectively sample across the headwater reaches, where the majority of spawning occurs, and to sample resident and migratory adults in the reaches farther downstream (Budy et al. 2003).

The fish assemblage within the SFWWR consisted primarily of rainbow trout *O. mykiss,* steelhead (anadromous rainbow trout), Chinook salmon *O. tshawytscha*, mountain whitefish *Prosopium williamsoni*, and sculpins *Cottus* spp. The SFWWR is known to contain a relatively large population of both small (potentially resident) and large (potentially migratory) bull trout (Al-Chokhachy et al. 2005); the abundance of bull trout larger than 120 mm was recently estimated at 10,600 fish (95% confidence interval [CI] = 8,800–16,598 fish; Budy et al. 2007a). The SFWWR did not contain brook trout *S. fontinalis*, which are nonnative competitors of bull trout that have been introduced throughout much of the Pacific Northwest.

Mark–recapture data.—We initiated our mark–recapture efforts in 2002 in the SFWWR; annual sampling began in mid-June and continued until the first week of August. This sampling period generally occurred before the downstream migration of juvenile bull trout from the SFWWR (Homel and Budy 2008) and after the upstream movements of migratory bull trout (Contor et al. 2003; Homel and Budy 2008). Each year, we sampled all selected reaches once using multiple techniques to actively capture and recapture bull trout. To avoid potential sampling bias across size-classes and habitat types, we used a combination of techniques, including snorkeling to corral fish into trap nets, electroshocking downstream to a seine, and

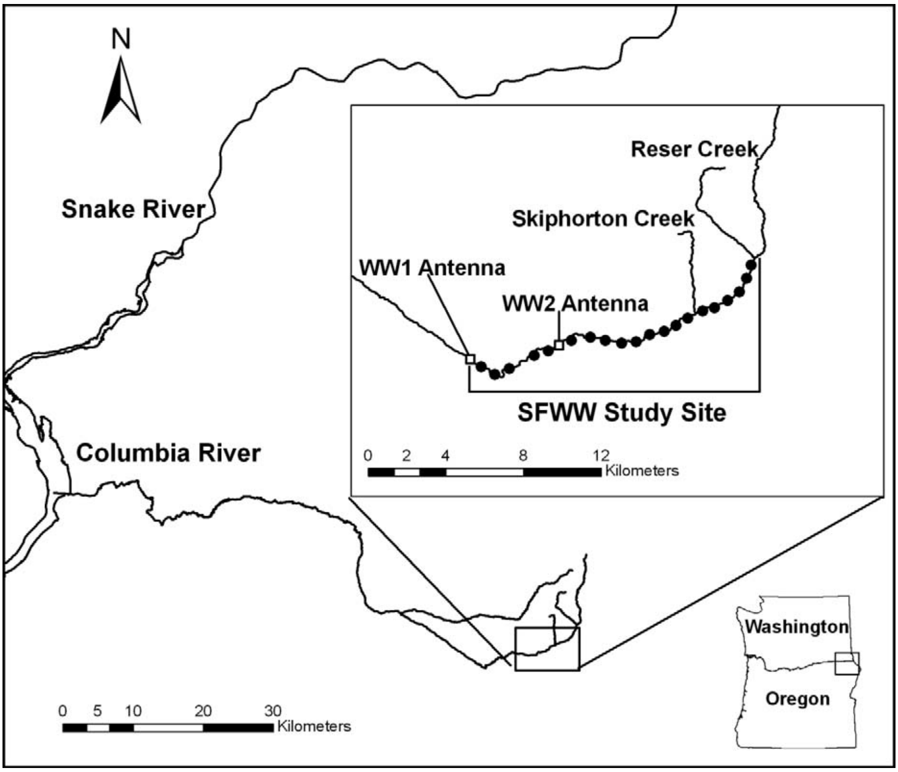

FIGURE 1.—Map of the South Fork Walla Walla River study site in northeastern Oregon, illustrating the locations of two passive integrated transponder (PIT) tag antennae (WW1 and WW2; open squares) and the approximate distribution of sampling reaches (black circles) used to evaluate bull trout age, growth, life history expression, and survival.

angling (Williams et al. 2002; Budy et al. 2003). Upon capture, every bull trout larger than 120 mm was anesthetized, tagged with a year-specific external anchor tag, and given a 23-mm passive integrated transponder (PIT) tag that was surgically implanted (~5-mm incision) in the ventral cavity anterior to the pectoral fins. Double tagging of individuals allowed us to quantify tag retention rates and to estimate the probability of misidentifying a previously tagged individual. After receiving tags, the fish were weighed, measured, and released at the point of capture. Recaptured individuals were anesthetized, checked for tag loss (both anchor and PIT tags), weighed, measured, and released.

Passive PIT tag antennae (hereafter, antennae) were installed in the SFWWR to provide additional recaptures and quantify movement. Two antennae were installed in fall 2002: one (WW1) was located at the downstream end of the study site, and the other (WW2) was situated approximately 6 km upstream from WW1 (Figure 1). Each antenna consisted of rectangular polyvinyl chloride detectors that spanned the entire stream width.

Although our antennae were in place since their deployment in 2002, overall detection efficiency of the antennae was a function of two separate factors. First was the efficiency of detecting a tagged fish that passed through the antennae; this type of efficiency can vary as a result of occasional environmental disturbances (e.g., high-water events) and has been estimated at 80–100% (2004–2005; Homel and Budy 2008). Second, there were short time intervals over which an individual antenna was shut down due to technical difficulties; detection efficiency for these periods was estimated from tagging location information (Global Positioning System data) and antenna recaptures. For example, if a fish tagged upstream from WW2 was detected at WW1 but not at WW2, we recorded a missed detection at WW2, and so on. From this analysis, we estimated overall detection efficiency at the SFWWR antennae to be 50% over the course of this study (Homel and Budy 2008). Nevertheless, while reduced detection efficiency at our antennae may have affected our assessment of population structure, this factor should have minimal effects on our analyses of *S*, as these types of open mark–recapture models estimate capture probability and account for it in the estimation of S.

Age and fecundity.—Each year (2002–2006), we sacrificed up to 10 bull trout from the SFWWR for quantification of age structure and variability in length at age, evaluation of age and length at sexual maturity, and estimation of the length–fecundity relationship. We collected fish across all size-classes (except young of the year) during the first week of August to observe maximum egg development in females. We enumerated all eggs from mature females and collected the sagittal otoliths from each fish. We used two independent observers and a dissecting microscope for aging. Since field observations from snorkel surveys indicated that large bull trout exist in the SFWWR (>620 mm; Budy et al. 2005), we also used a von Bertalanffy length-at-age model to estimate the potential age of these large individuals (multiplicative error model; Quinn and Deriso 1999).

Survival analyses.—We used the Barker model in Program MARK (White and Burnham 1999) to estimate S for the SFWWR population; this open mark–recapture model incorporates capture–recapture data from individual sampling occasions and recapture data between sampling occasions, thus improving the precision of S estimates over models that only incorporate recapture data from sampling occasions (e.g., the Cormack–Jolly–Seber model; Barker 1999). In addition to S, the Barker model also allows estimation of recapture probability (p); the probability of resighting a dead animal (r); the probability of recapturing an animal between sampling intervals (R); the probability of recapturing an animal before the animal dies between sampling intervals (R'); the probability that an animal at risk of capture in time t is also at risk of capture in time $t + 1$ (F); and the probability that an animal not at risk of capture in time t is at risk of capture in time $t + 1$ (F').

We used 5 years of mark–recapture data for these analyses, and we separated each year into two intervals. Interval 1 corresponded to summer field sampling (~June 15–August 15) and included active captures and recaptures (i.e., electroshocking) as well as all antenna recaptures. Interval 2 corresponded to the interval between the sampling periods (August 16–June 14) and included only the antenna recaptures. Average growth rates calculated from individual recapture data were used to create a stage-based model for six size-classes (121–170, 171–220, 221–270, 271–320, 321–370, and >370 mm) determined from previous bull trout length-at-age analyses (Budy et al. 2003).

We performed two separate mark–recapture analyses for bull trout in the SFWWR. First, we evaluated S across the previously mentioned size-classes. Here, we established a set of a priori models that included group (size-class) and time effects, and we considered relative condition (C) at the time of tagging as an individual covariate. We calculated C for the SFWWR population as

$$C_i = w_i / l_i^{(3.06 \times 0.000006)},$$

where C_i is the relative condition of individual i, w_i is fish weight at tagging, and l_i is fish total length at tagging. For the second set of analyses, we evaluated the difference in vital rates between fish exhibiting resident and migratory life history patterns. In these analyses, we considered any fish that moved below WW1, the lowermost antenna, to be migratory (see next section) and all other fish to be resident. For analyses of life history forms, the a priori models included group, life history expression (resident or migratory), and time.

We used Program MARK to generate the likelihood function value for each model and to estimate Akaike's information criterion corrected for small-sample bias (AIC_c; Burnham and Anderson 1998). For all analyses, models were ranked according to the lowest AIC_c score, and the difference in AIC_c values (ΔAIC_c) between models was used to calculate an Akaike weight (W_i) for each model (Burnham and Anderson 1998). Although the models were ranked according to the lowest AIC_c score, we used model averaging for parameter estimates (i.e., S) to maximize the information gained within a multimodel approach (Burnham and Anderson 1998). We fixed r equal to zero, as there was an extremely low probability of recapturing a dead fish. We initially modeled F and F' separately and then considered models where F was equal to F'; this allowed us to evaluate (using AIC_c scores) whether immigration or emigration was random (i.e., $F = F'$) or directional (i.e., $F \neq F'$) in the SFWWR. Similar to Franklin et al. (2000), we first modeled those parameters that were less pertinent to our analysis (F, F', R, R', and p); we then maintained the model structure of those parameters from the highest-ranking model (i.e., lowest AIC_c) while modeling S. All a priori S models were compared based on AIC_c scores; the model with the lowest AIC_c score that was at least 2 points less than the next-lowest AIC_c score (i.e., $\Delta AIC_c \geq 2$) was considered the most plausible (Burnham and Anderson 1998).

We used the likelihood function in Program MARK to estimate the slope (β) for all parameters, and the logit link function was used to transform β estimates into real estimates of S. We used the 95% CI as an index of statistical significance for each parameter. To avoid type II error from overly conservative CIs (Tyron 2001), we recalculated the 95% CIs for any two

TABLE 1.—Total number of bull trout tagged in each size-class (total length) percentage of the total number of tagged fish contributed by each size-class, average (SE in parentheses) annual growth (mm) of fish that were actively recaptured during mark–recapture sampling, and percentage of fish exhibiting migratory behavior within each size-class in the South Fork Walla Walla River, Oregon, 2002–2006. Migratory percentages were expanded by estimates of antenna detection efficiency (see Methods).

Size-class	Number tagged	Percent of total	Annual growth	Migratory (%)
121–170	928	52.1	53.6 (8.2)	12.1
171–220	326	18.3	71.1 (7.6)	23.3
221–270	171	9.6	52.8 (7.2)	19.9
271–320	84	4.7	37.1 (7.4)	11.9
321–370	71	4.0	25.6 (7.0)	14.1
371–420	78	4.4	19.9 (2.2)	35.9
>420	122	6.9	15.1 (2.7)	72.1

comparisons as:

$$\beta_x \pm t(\bar{\mathrm{E}}) \times \mathrm{SE}_x,$$

where $E = (\sqrt{\mathrm{SE}_x^2 + \mathrm{SE}_y^2}/(\mathrm{SE}_x + \mathrm{SE}_y)$ and where β_x is the estimate for group x, $\bar{E}$ is the average of E-values across all pairwise combinations, SE_x is the standard error for group x, SE_y is the standard error for group y, and t is the t-value (set at 1.96 for all groups). We considered differences among parameter estimates to be significant when the 95% CIs did not overlap with those of comparable groups.

Since formal goodness-of-fit tests are not valid when individual covariates are modeled in mark–recapture analyses (Cooch and White 2005), we evaluated potential sources of model error using supplemental information independent of Program MARK. Specifically, we used active capture–recapture data to evaluate the percentage of fish that lost their PIT tags and the percentage that lost anchor tags; we multiplied these two estimates to produce an overall estimate of the probability of misidentifying a tagged fish as unmarked. In addition, we assessed potential size bias in capture methods by comparing the average length frequency distribution from capture data with that from snorkel data collected in similar sample reaches in the SFWWR (see Al-Chokhachy et al. 2005 and Al-Chokhachy 2006 for more detail on snorkel methods).

Migratory proportion estimate.—We used active marking and recapture data and passive recaptures at antennae to estimate the percentage of the SFWWR population that exhibited migratory behavior. Any bull trout that moved below WW1, which corresponded to a distance of over 12 km from the downstream limit of the core spawning area, was considered to be a migratory individual (Homel 2007). We estimated the proportion of each size-class that exhibited migratory behavior as:

$$\text{Proportion migratory}_s = (m_s/t_s)/a_e,$$

where s represents size-class, m_s is the number of individuals in a particular size-class that moved below WW1, t_s is the total number of marked individuals in a particular size-class, and a_e is antenna efficiency (50%).

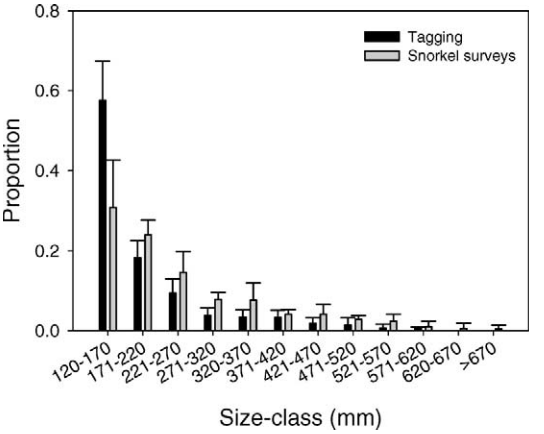

FIGURE 2.—Mean (+2SE) annual length frequency distribution (total length) of passive integrated transponder tagged bull trout and bull trout observed during snorkel surveys in the South Fork Walla Walla River, Oregon, from 2002 to 2006.

Results

From 2002 to 2006, we marked 1,780 individual bull trout, observed unique recaptures for 412 individuals, and recorded 713 total recaptures in the SFWWR (Table A.1). The size distribution of bull trout was dominated by smaller, potentially immature bull trout; 70% of the fish sampled were smaller than 220 mm (Table 1; Figure 2). Our recapture data suggest that bull trout growth rates were relatively consistent up to 270 mm, at which growth declined consistently with increasing size.

Age and Fecundity

Based on otolith aging techniques, bull trout appeared to be relatively long lived in the SFWWR; the maximum age observed in the subset of sacrificed fish was 9 years (Figure 3a). Age was estimated for a total of 33 individual bull trout across a wide range of fish lengths (98–564 mm), and there was considerable variability in length at age for fish larger than 250 mm (Figure 3a). The highest variability occurred in age-5 fish, which ranged from 292 to 452 mm. Juveniles and small adults (<220 mm), however, exhibited little

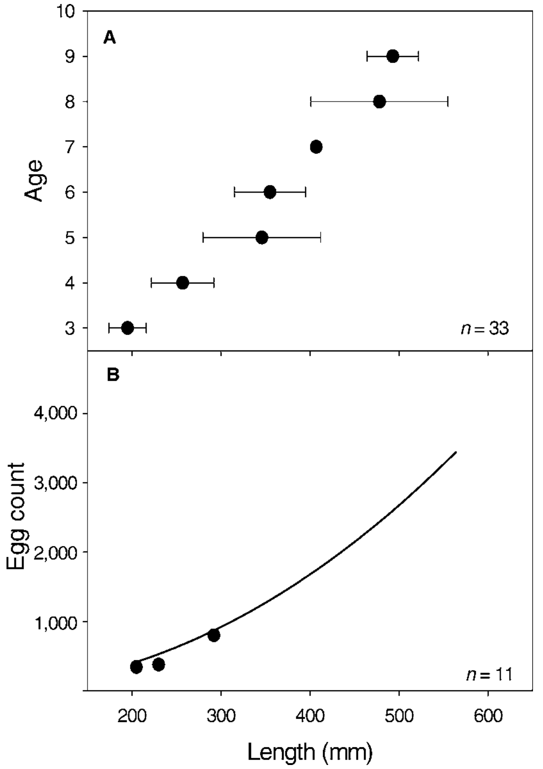

FIGURE 3.—Relationship between bull trout total length (mm) in the South Fork Walla Walla River, Oregon (2002–2006), and **(a)** age (males and females) or **(b)** fecundity (number of eggs/female; $y = 0.0013x^{2.34}$, where y = fecundity and x = length; $R^2 = 0.95$).

variability in length at age. The von Bertalanffy results ($F_{33} = 166.93$, $P \leq 0.0001$) suggested that large bull trout (observed in snorkel surveys) in the SFWWR can reach 12 years of age:

$$L = 2.308[1 - e^{-0.00254(t+0.462)}],$$

where L is the length of the fish, t is age, and e is the base of natural logarithms.

During the study, we were only able to obtain fecundity data from 11 sacrificed mature individuals. Based on examination of these individuals, bull trout in the SFWWR appeared to achieve sexual maturity at approximately 200 mm or at age 3–4 (Figure 3b). The number of eggs increased significantly with size, yielding the following relationship between length and fecundity (df = 9, $R^2 = 0.95$):

$$y = 0.0013x^{2.34},$$

where y is the number of eggs per female and x is fish length.

Mark–Recapture Analyses

Survival.—Based on our analyses of bull trout S, the top model included size-class (group) and time, and C was an individual covariate modeled as an interaction across size-classes and time periods (W_i = 66.3%; Table 2). We observed significant differences in model-averaged estimates of bull trout S across size-classes (Figure 4A–F). In particular, 120–171-mm fish exhibited significantly lower S than all other size-classes (Figure 4A); in contrast, S did not differ significantly across all other size-classes. Our top-three models (total W_i = 96.7%) included time as an additive parameter, where the differences in S across groups were consistent over the course of the study (Table 2), and we found little evidence of interaction effects (i.e., group × time; W_i = 3.3%; Table 2). We observed significantly lower S in 2004 (across all size-classes) than in all other study years (Figure 4). Our top model included C modeled as an interactive effect with size-class (Table 2). However, our results suggested that C only significantly affected the model fit for juvenile bull trout S (120–170 mm size-class, $\beta = 5.60$, SE = 2.09), whereas it did not affect the model fit of S for fish larger than 170 mm.

The top model identified from life history form analyses suggested that bull trout S differed between migratory and resident fish (W_i = 98.2%; Table 3). For these analyses, we used results from size-class analyses (i.e., differences in S across groups) and size-class-specific information about movement (percentage of fish exhibiting the migratory life history pattern in a given size class; see next section) to combine fish into three size-classes (120–170, 171–320, and >320 mm). Similar to the previous analyses, S varied across time, and the lowest annual estimates of S were observed in 2004. Bull trout exhibiting migratory movement patterns had higher S across size-classes (Figure 5A–C), but only the small (120–170-mm) migratory fish (average S = 0.35, SE = 0.04) exhibited significantly higher S than similarly sized resident fish (average S = 0.15, SE = 0.02).

Capture.—In size-class analyses, capture rate differed by size-class and time (Table 4), and we observed relatively high variability in capture rate for each size-class (Table 4). Capture rates for 171–220-mm bull trout were significantly lower than those for bull trout exceeding 370 mm, but no significant difference was observed for any other size-class comparison (Table 4). The probability R varied by group and time; the highest value was observed for bull trout larger than 370 mm (average R = 0.50, SE = 0.05), and the lowest value was observed for 271–320-mm fish (average R = 0.13, SE = 0.02); this pattern was consistent with our antenna

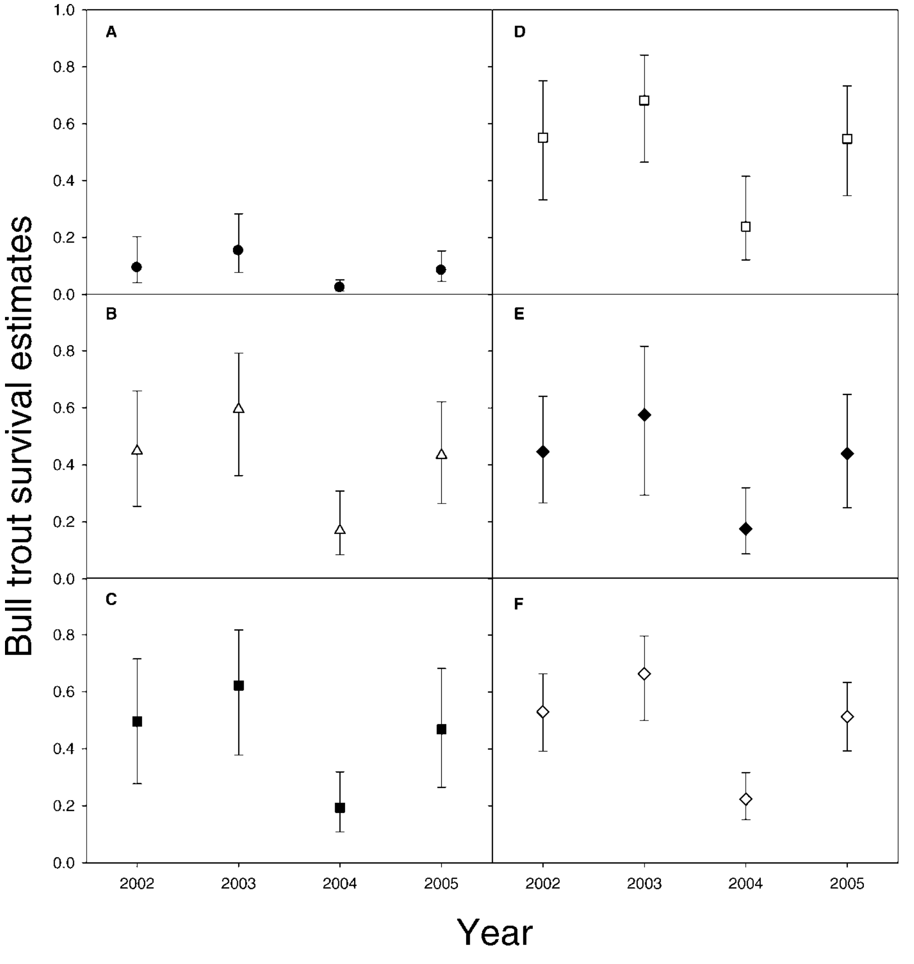

FIGURE 4.—Estimates of survival rate (±95% confidence interval) calculated from mark–recapture analyses of six bull trout size-classes (total length) in the South Fork Walla Walla River, Oregon, 2002–2005: **(A)** 120–170 mm, **(B)** 171–220 mm, **(C)** 221–270 mm, **(D)** 271–320 mm, **(E)** 321–370 mm, and **(F)** larger than 370 mm .

TABLE 2.—Summary of model selection among Barker mark–recapture models used to estimate bull trout survival rate (S) across size-classes in the South Fork Walla Walla River, Oregon, 2002–2006 (g = group or size-class; t = time; C = relative condition; period symbol = no difference across time or among size-classes; + = additive parameter; × = interaction effect). The Barker model includes six parameters: S; capture probability (p); probability of recapturing a fish between sampling occasions (R); probability of recapturing a fish before it dies between sampling occasions (R'); probability that a fish at risk of capture in time t is also at risk of capture in time $t + 1$ (F); probability that a fish not at risk of capture in time t is at risk of capture in time $t + 1$ (F'); and probability of resighting a dead animal (r), which was fixed to equal 0. Akaike's information criterion corrected for small-sample bias (AIC_c), Akaike weight (W_i), and likelihood of each model are shown.

S varies by	Model	AIC_c	W_i	Model likelihood
g, t as an additive parameter, c as an interactive parameter with g	$S_{[g+t+(c\times g)]}p_{(g+t)}R_{(g+t)}R'_{(g+t)}F_{(.)}F'_{(.)}$	3,284.8	0.633	1.000
g, t as an additive parameter	$S_{(g+t)}p_{(g+t)}R_{(g+t)}R'_{(g+t)}F_{(.)}F'_{(.)}$	3,286.7	0.245	0.388
g, t, and c as an additive parameters	$S_{(g+t+c)}p_{(g+t)}R_{(g+t)}R'_{(g+t)}F_{(.)}F'_{(.)}$	3,288.8	0.089	0.141
g, t as an interactive parameter	$S_{(g\times t)}p_{(g+t)}R_{(g+t)}R'_{(g+t)}F_{(.)}F'_{(.)}$	3,290.8	0.032	0.051
g, t as an interactive parameter (p varies as an interaction with t)	$S_{(g\times t)}p_{(g\times t)}R_{(g+t)}R'_{(g+t)}F_{(.)}F'_{(.)}$	3,302.9	0.000	0.000

TABLE 3.—Summary of model selection among Barker mark–recapture models used to estimate bull trout survival rate (S) for fish exhibiting resident (res) and migratory (mig) behavior in the South Fork Walla Walla River, Oregon, 2002–2006 (g = group, one of three size-classes [120–170, 171–320, and >320 mm total length]; t = time; $+$ = additive parameter; $\times$ = interaction effect). Akaike's information criterion corrected for small-sample bias (AIC_c), Akaike weight (W_i), and likelihood of each model are shown. See Table 2 for a description of Barker model parameters.

S varies by	Model	AIC_c	W_i	Model likelihood
g, t as an additive parameter	$S_{(g+t)}p_{(g+t)}R_{(g\times t)}R'_{(g)}F_{(\text{res,mig})}F'_{(t)}$	2,758.1	0.982	1.000
g (no difference between res and mig), t as an additive parameter	$S_{(g+t;\text{no res,mig})}p_{(g+t)}R_{(g\times t)}R'_{(g)}F_{(\text{res,mig})}F'_{(t)}$	2,766.1	0.018	0.018
g, t as an interactive parameter	$S_{(g\times t)}p_{(g+t)}R_{(g\times t)}R'_{(g)}F_{(\text{res,mig})}F'_{(t)}$	2,777.6	0.000	0.000
g (no difference between res and mig), t as an interactive parameter	$S_{(g\times t;\text{no res,mig})}p_{(g+t)}R_{(g\times t)}R'_{(g)}F_{(\text{res,mig})}F'_{(t)}$	2,783.2	0.000	0.000
g, t as an interactive parameter; p varies by g	$S_{(g\times t)}p_{(g)}R_{(g\times t)}R'_{(g)}F_{(\text{res,mig})}F'_{(t)}$	2,796.1	0.000	0.000

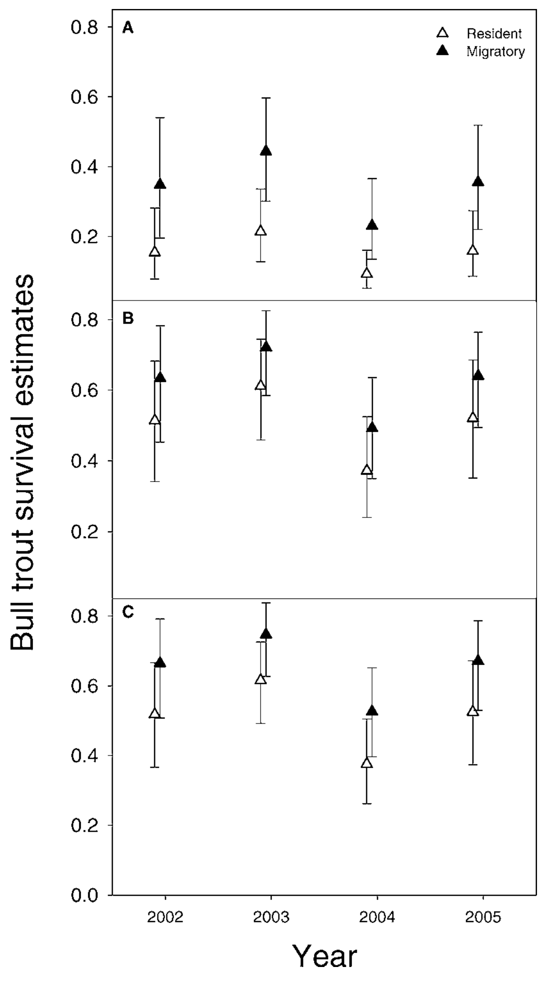

FIGURE 5.—Estimates of survival rate (±95% confidence interval) calculated from mark–recapture analyses of resident and migratory bull trout from three size-classes (total length) in the South Fork Walla Walla River, Oregon, 2002–2005: **(A)** 120–170 mm, **(B)** 171–320 mm, and **(C)** larger than 320 mm.

recaptures during these intervals and with estimates of the proportion of fish exhibiting migratory behavior within a size-class. The R' value also varied by group and time. Similar to results for R, the highest R' was observed for fish larger than 370 mm (average $R' = 0.15$, SE = 0.04), and significantly lower values were estimated for size-classes between 171 and 320 mm (Table 4).

We observed substantial differences in capture rate between fish exhibiting resident and migratory life history patterns. Capture probability differed across size-classes, life history types, and time periods (Table 5). The estimated p for 120–170-mm migratory fish (average $p = 0.77$, SE = 0.08) was significantly higher than that for similarly sized resident fish (average $p = 0.36$, SE = 0.09), but we found no significant difference in comparisons of other size-classes (Table 5). The value of R varied as an interaction between groups (size-classes and life history forms); however, R' varied only across life history forms but not across time. As expected, R and R' values were significantly higher for fish exhibiting migratory movement patterns than for resident fish. This result was consistent across all size-classes except the 120–170-mm size-class, for which R did not differ (Table 5).

Immigration and emigration.—Model selection results from size-class analyses suggested that emigration and immigration were nonrandom during this study (i.e., $F \neq F'$; Table 4). The probability F did not differ by size-class or time, and average F was 0.78 (SE = 0.05), suggesting a relatively high level of emigration. On the contrary, we found very low estimates of F' (average = 0.00; SE was inestimable), indicating very little immigration from other potential local populations.

Life history form analyses suggested a similar pattern of nonrandom immigration (Table 5). Estimates of F did not vary by size-class but did vary by life history form, and F was significantly higher for bull

TABLE 4.—Model-averaged estimates (SE in parentheses) of six parameters (defined in Table 2) from Barker mark–recapture models used to estimate survival rates of six bull trout size-classes (total length) in the South Fork Walla Walla River, Oregon, 2002–2006.

Size-class (mm)	*p*	*R*	*R′*	*F*	*F′*
120–170	0.41 (0.11)	0.25 (0.03)	0.07 (0.03)	0.80 (0.05)	0.00 (na)
171–220	0.20 (0.07)	0.23 (0.03)	0.05 (0.01)	0.80 (0.05)	0.00 (na)
221–270	0.39 (0.11)	0.17 (0.02)	0.02 (0.01)	0.80 (0.05)	0.00 (na)
271–320	0.57 (0.11)	0.13 (0.02)	0.05 (0.02)	0.80 (0.05)	0.00 (na)
321–370	0.61 (0.11)	0.36 (0.04)	0.08 (0.02)	0.80 (0.05)	0.00 (na)
>370	0.75 (0.09)	0.50 (0.05)	0.15 (0.04)	0.80 (0.05)	0.00 (na)

trout exhibiting migratory movement ($F = 0.85$, SE = 0.07) than for resident fish ($F = 0.36$, SE = 0.09). Although variable, we observed no differences in F' between life history forms ($F' = 0.31$, SE = 0.16).

Goodness of fit.—We found potential evidence for violations of mark–recapture assumptions in our data (but see Discussion). In particular, we observed substantial differences in length frequency distribution between bull trout observed during snorkel surveys and those captured for mark–recapture analyses. Our results indicated that we captured small (120–170-mm) juvenile bull trout in a higher proportion than was observed during snorkel surveys (i.e., positive sample bias), but no substantial difference between methods was observed for the other size-classes (Figure 5). However, we did not find any indication of tag loss. Specifically, PIT and anchor tag retention rates were 93% and 85%, respectively; the probability of a fish losing both tags and thus being misidentified was 1%.

Migratory Proportion of the Population

In the SFWWR, individuals from all bull trout size-classes (>120 mm) exhibited migratory movements (i.e., moved below WW1; Table 1). The highest percentage (72.1%) of migratory behavior was observed in bull trout larger than 420 mm, and relatively high (35.9%) migratory behavior was exhibited by 371–420-mm fish. The percentage of all juveniles or small adults expressing migratory behavior was relatively low (range = 11.9–23.3%), but the high numbers of fish in these smaller size-classes (particularly 120–220 mm) indicate that a substantial number of fish in the SFWWR are migratory.

Discussion

Field estimates of key demographic and vital rates can provide valuable insight into the dynamics of the population of interest and can increase our understanding of other conspecific populations for which limited information is available (Crowder et al. 1994; Williams et al. 2002). In this investigation, we used 5 years of mark–recapture sampling and field techniques to quantify critical components for evaluating bull trout population viability and persistence, including demographic and vital rates. Additionally, we quantified the population structure of a fluvial bull trout population that contained both resident and migratory fish (Al-Chokhachy et al. 2005). With our results, we address substantial gaps in the current understanding of bull trout biology and provide a template for future bull trout research and recovery efforts.

Demographic and Vital Rates

Across their native range, bull trout can exhibit multiple life history forms, suggesting that discrete differences in demographic and vital rates exist between forms. Furthermore, while much of our current knowledge of bull trout population demographics has come from adfluvial populations (e.g., Fraley and Shepard 1989), many of the populations through-

TABLE 5.—Model-averaged estimates (SE in parentheses) of six parameters (defined in Table 2) from Barker mark–recapture models used to estimate survival rates of bull trout exhibiting resident and migratory behavior (three size-classes [total length] within each life history type) in the South Fork Walla Walla River, Oregon, 2002–2006.

Size-class (mm)	*p*	*R*	*R′*	*F*	*F′*
Resident					
120–170	0.36 (0.09)	0.14 (0.12)	0.04 (0.01)	0.36 (0.09)	0.31 (0.16)
171–320	0.49 (0.10)	0.06 (0.04)	0.03 (0.02)	0.36 (0.09)	0.31 (0.16)
>320	0.73 (0.08)	0.26 (0.12)	0.00 (0.04)	0.36 (0.09)	0.31 (0.16)
Migratory					
120–170	0.77 (0.08)	0.28 (0.11)	0.88 (0.05)	0.85 (0.07)	0.31 (0.16)
171–320	0.47 (0.10)	0.32 (0.10)	0.94 (0.05)	0.85 (0.07)	0.31 (0.16)
>320	0.94 (0.03)	0.71 (0.08)	0.77 (0.07)	0.85 (0.07)	0.31 (0.16)

out the Pacific Northwest exhibit a fluvial (both resident and migratory) life history. Thus, it is important to quantify potential differences in key population-level characteristics (e.g., *S*) between life history forms, which may reveal the need for diverse management actions within a single recovery unit.

Using otolith age estimation, we found bull trout to be relatively long lived in the SFWWR (>9 years), and this age structure is similar to that of adfluvial populations (Fraley and Shepard 1989; Mogen and Kaeding 2005). In contrast, bull trout in the SFWWR achieved sexual maturity at much-smaller sizes (200 mm) and much-earlier ages (3–5 years) than have been reported for adfluvial populations (>480 mm: Baxter and Westover 2000; 6–9 years: Johnston et al. 2007). Differences in size and age at sexual maturity between adfluvial and riverine bull trout may be even more pronounced for strictly resident fish, which can achieve sexual maturity at approximately 150 mm (Hemmingsen et al. 2001). In the SFWWR, we were unable to differentiate between strictly resident and migratory bull trout based on fecundity data (e.g., Downs et al. 2006; but see Homel 2007), and large differences in size at sexual maturity and growth rate may occur between life history types. In addition, there may be considerable variability in the proportion of fish that has achieved sexual maturity within any given size-class or age-group (Hutchings 1996; Hutchings and Jones 1998; Swenson et al. 2007). Ultimately, further work evaluating the differences and variability in age and size at maturity may be important for understanding bull trout population dynamics, the relative contributions of different life history forms to overall population growth, and appropriate management strategies (Johnston et al. 2007).

Age- and stage-specific estimates of *S* are critical for identifying the life stages that potentially limit a population and its future viability (Williams et al. 2002). Our research is unique in that we used a combination of active and passive sampling techniques to quantify the first published estimates of *S* for multiple size-classes, age-classes, and life history forms of a fluvial bull trout population. We found considerable variability in annual *S* among size-classes, but no evidence of size-class $\times$ time interaction effects; these data suggest that the relative differences in bull trout *S* among size-classes were consistent through time. Our results indicate that large, stream-level disturbances affect bull trout *S* independent of size-class. For example, while there was little variability in maximum and minimum temperatures in the SFWWR during our study, the amount of precipitation was variable across years and 2004 was characterized as having higher-than-average precipitation (study period average = 114.9 cm, SE = 9; 2004 average = 136.5 cm; U.S. Department of Agriculture, High Ridge Snow Telemetry Station, unpublished data). The higher river flows and velocities associated with the wet year of 2004 may have resulted in lower *S* for bull trout, which typically use slow-water habitats (Thurow 1997; Muhlfeld and Marotz 2005; Al-Chokhachy and Budy 2007). Ultimately, the mechanism linking these large-scale environmental patterns and bull trout *S* is unclear; however, our results do indicate the influence of large-scale processes on population-level vital rates independent of size-class.

We were unable to directly compare our estimates of bull trout *S* with estimates from conspecific populations due to the overall lack of field estimates of *S*, particularly for different size-classes, age-classes, and life history forms. However, *S*-values for juvenile bull trout (120–170 mm) in the present study were similar, albeit slightly lower, than those observed for fluvial brook trout juveniles in the northeastern United States (apparent $S = 0.218$, SE = 0.15; Petty et al. 2005), whereas *S* for bull trout larger than 170 mm appeared to be similar to those of other inland, stream-dwelling salmonids (range of apparent $S = 0.42$–0.54; Budy et al. 2007b). We observed little variability in the annual *S* of adult bull trout (>170 mm), which indicates that once a bull trout reaches this particular size threshold there is little variation in the sources and rates of mortality. Despite our inability to compare our field estimates with those describing other bull trout populations, the inherent differences in age and size at maturity, migration pattern (e.g., Muhlfeld and Marotz 2005), and subadult rearing (e.g., lacustrine versus riverine), among other factors, suggest the presence of substantial differences in vital rates between life history forms.

Bull trout that exhibited large movements (i.e., moved below WW1) demonstrated substantially higher *S* than did fish that remained upstream of WW1. These results are contradictory to previously reported patterns of migratory bull trout distribution (Rieman et al. 1997) and abundance (Nelson et al. 2002). In the SFWWR, this higher *S* may be the result of multiple factors, including greater growth and metabolic rates in warmer downstream reaches (e.g., Thurow 1987) or a reduction in intraspecific competition with the longitudinal decrease in bull trout density (e.g., Paul et al. 2000; but see Johnston et al. 2007). Despite the higher *S* for fish exhibiting migratory behavior, the link between *S* and movement below WW1 is unclear due to the high variability in full trout movement patterns (Muhlfeld and Marotz 2005). In the Walla Walla River, habitat conditions are highly degraded due to a diversion structure (~20 km below WW1) that removes a substantial amount of water from the river; water temperatures below this structure exceed 25°C, habitat is greatly simplified, and flows are reduced to minimal levels (~0.71 m^3/s) during summer. Nevertheless, longer movements (>20 km) to these degraded sections by bull trout tagged in the SFWWR study site have been observed in radiotelemetry studies (Mahoney 2002) and through detections during 2005 at a recently installed additional antenna (21 km below WW1). The condition of downstream degraded reaches suggests that bull trout exhibiting these longer migrations could experience relatively high mortality rates.

Despite the high level of habitat quality in the SFWWR above WW1, environmental disturbances within the low-elevation Blue Mountain systems may result in generally lower *S* for fish remaining in the headwaters. In particular, the relatively high gradient and the potential for flashy, high-flow events (e.g., rain on snow) could result in lower *S* for fish exhibiting a more-resident life history; low abundance of resident bull trout in Mill Creek, a tributary of the Walla Walla River (Sankovich et al. 2003), is consistent with this idea. Furthermore, some bull trout populations in Oregon are considered to be devoid of resident fish (J. Dunham, U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, personal communication); this suggests that the *S* of resident fish results from different landscape-level attributes (e.g., Dunham and Rieman 1999).

We used *C* as a surrogate for fish health (Murphy et al. 1991) and found that this factor accounted for a substantial amount of variability in bull trout *S* in the SFWWR. The *C* of an individual can be affected by a number of different biotic (e.g., food availability) and abiotic (e.g., water temperature) factors. In our study, *C* only accounted for a significant amount of variability in the *S* of juveniles (120–170 mm), indicating a link between factors that affect the *C* (e.g., competition for resources; Paul et al. 2000) and ultimately the *S* of juveniles. On the contrary, the lack of improvement in model fit with *C* for fish larger than 170 mm suggests that once a fish has obtained a particular length, *S* is unaffected by *C*. In the SFWWR, this ontogenetic change may result from different physiological abilities (e.g., swimming ability), changes in foraging opportunities as fish shift to increased piscivory on juvenile resident and anadromous salmonids (Rieman and McIntyre 1993; Clarke et al. 2005), or simply the escape from cannibalism risk upon achieving a larger size (e.g., Beauchamp and Van Tassell 2001). However, in systems that are depauperate in juvenile forage fishes, particularly where native populations of anadromous and resident salmonids have been extirpated or have largely declined or where water temperatures are above 16°C, individual *C* may have a greater effect on the *S* of larger bull trout.

Limitations of mark–recapture analyses.—We acknowledge there may be limitations with our mark–recapture analyses of bull trout *S*. Particularly, we were not able to perform formal goodness-of-fit evaluations, which can affect the overall rank of models (i.e., AIC_c values) and provide insight into violations of model assumptions or structure (Cooch and White 2005). In our analyses, the consistent structure among our top models (total $W_i = 96.7\%$), where *S* varied by group and time (as an additive term), suggests that changing the AIC_c scores through adjustment in the overdispersion parameter (Cooch and White 2005) would not have altered the general model structure of our results. However, we acknowledge that overdispersion would result in higher variance in bull trout *S* estimates (i.e., precision) but would not affect our point estimates (Cooch and White 2005).

We found tag loss to be minimal in this study, but there is some indication of size bias in our capture methods. This difference between the number of bull trout captured and the number observed during snorkel surveys may be the result of low juvenile detection efficiency during snorkeling (Thurow et al. 2006). In addition, we were unable to evaluate for violations of the assumption of homogeneous capture probabilities, but such violations generally lead to only a small negative bias in estimates of *S* (Williams et al. 2002). Next, we used a multiage mark–recapture model in which fish transitioned from one size-class to the next based on average growth. With this approach, variability in annual growth could have caused some reduction in the precision of *S* estimates for bull trout larger than 170 mm (Williams et al. 2002) and limited our power to detect significant differences in *S* of these groups. Despite the potential limitations, our ability to incorporate field estimates of age and growth into our analyses of *S*, our use of multiple sampling methods and year-round capture–recapture data, and the high sampling effort and sample size should have minimized the bias in our results (Barker 1992; Manly et al. 1999; Williams et al. 2002).

Finally, we acknowledge that the length of our study may not have been conducive to obtaining robust estimates of *F* and *F*′, and we urge caution in direct interpretation of these results. In particular, long-lived species like the bull trout may exhibit relatively long temporary migrations (i.e., rearing in downstream habitats), and robust estimates of these large-scale movements may require studies of considerably longer duration. However, the uncertainty in these parameters generally has little effect on estimates of *S* produced by the Barker model (M. Conner, Utah State University, personal communication).

Population Structure

Bull trout are known to exhibit multiple life history forms within a population, but the contribution of different size-classes within each life history form to overall population abundance is largely unknown. We found that individuals from all size-classes greater than 120 mm exhibited migratory behavior, and the majority of movement was exhibited by fish larger than 420 mm. Our movement results differ from early research, which suggested that bull trout larger than 300 mm were migratory in fluvial populations (e.g., Rieman and McIntyre 1993). We found that only 46% of bull trout greater than 320 mm exhibited migratory behavior (i.e., movements > 12 km from the lower limit of the core spawning area); however, a large percentage (72%) of bull trout larger than 420 mm did exhibit increased migratory behavior. These results could change over time, however, as fish that appear to be resident in behavior may express migratory patterns in subsequent years. Similar to other fluvial (Nelson et al. 2002) and adfluvial (Fraley and Shepard 1989; Downs et al. 2006) populations, SFWWR bull trout exhibited considerable variability in age and size at migration. Overall, managers considering plans for habitat restoration and flow regulation within migratory corridors should incorporate habitat requirements for both juvenile and adult bull trout (Homel and Budy 2008).

We acknowledge that there may be some uncertainty associated with our assessment of bull trout population structure in the SFWWR. This uncertainty is largely due to detection efficiency at the WW1 antenna (Zydlewski et al. 2006). Although our efficiency estimate (50%) was similar to that reported for small streams (e.g., 40–60%; S. Anglea, Biomark, Inc., Boise, Idaho, personal communication), seasonal differences in efficiency could have resulted in underestimation of the migratory fish contribution to the overall SFWWR population (i.e., low detection efficiency during peak migration periods; Homel 2007). However, previous analyses by Homel (2007) did not indicate any seasonal pattern of potential bias due to low detection efficiency or power outages across years.

Conclusions

Our research focused on assessing general patterns of population demographics, structure, and vital rates in a relatively large population of fluvial bull trout. With this, we have provided the first comprehensive field estimates of population structure in a fluvial population containing multiple life history forms and the first estimates of S for different life stages and life history forms. The information available for adfluvial and fluvial bull trout populations suggests that distinct differences (e.g., size at sexual maturity, growth) exist between life history forms (but see Homel 2007) and that different management, restoration, and recovery plans are necessary for bull trout populations composed of these different forms. Our results provide managers with critical information for evaluating the viability of bull trout populations and a template for analyzing the effects of various management and restoration strategies for this imperiled species.

Acknowledgments

Reviews of previous manuscript drafts and helpful suggestions were provided by M. Conner, E. Evans, W. Wurtsbaugh, and H. Schaller. Funding for this project was provided by the U.S. Fish and Wildlife Service's Columbia River Fisheries Program Office and the U.S. Geological Survey's Utah Cooperative Fish and Wildlife Research Unit. Field data collection assistance was given by C. Gabriel, S. Vatland, E. Larson, M. Malek, T. Sanderson, T. Scott, J. Mull, B. Stewart, M. Davis, R. Kumpf, J. Hearsey, D. Lillard, A. Dean, K. Hofer, N. Charbonneau, H. Campbell, D. Martin, D. Cullen, T. Grubb, T. Nye, T. Varney, S. Scott, D. McPhie, R. Rasmussen, and B. Nauman. We thank G. P. Thiede for logistical oversight and K. Homel for field supervision. Reference to trade names does not imply endorsement by the U.S. Government.

References

Al-Chokhachy, R., P. Budy, and H. Schaller. 2005. Understanding the significance of redd counts: a comparison between two methods for estimating the abundance of and monitoring bull trout populations. North American Journal of Fisheries Management 25:1505–1512.

Al-Chokhachy, R. 2006. Identifying the limiting factors and trends of bull trout (*Salvelinus confluentus*) populations in eastern Oregon. Doctoral dissertation. Utah State University, Logan.

Al-Chokhachy, R., and P. Budy. 2007. Summer microhabitat use of fluvial bull trout in eastern Oregon streams. North American Journal of Fisheries Management 27:1068–1081.

Barker, R. 1992. Effect of heterogeneous survival on bird-banding model confidence interval coverage rates. Journal of Wildlife Management 56:111–116.

Barker, R. J. 1999. Joint analysis of mark recapture, resighting and ring-recovery data with age-dependence and marking-effect. Bird Study 46:82–90.

Baxter, J. S., and W. T. Westover. 2000. An overview of the Wigwam River bull trout program (1995–1999): habitat conservation trust fund final report. Baxter Environmental, Fisheries Project Report KO 58, Nelson, British Columbia, Canada.

Beauchamp, D. A., and J. J. Van Tassell. 2001. Modeling seasonal trophic interactions of adfluvial bull trout in

Lake Billy Chinook, Oregon. Transactions of the American Fisheries Society 130:204–216.

Budy, P., R. Al-Chokhachy, and G. P. Thiede. 2003. Bull trout population assessment and life-history characteristics in association with habitat quality and land use in the Walla Walla River basin: a template for recovery planning. Annual report to the U.S. Fish and Wildlife Service, RWO-38. Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan.

Budy, P., R. Al-Chokhachy, K. Homel, and G. P. Thiede. 2005. Bull trout population assessment in northeastern Oregon: a template for recovery planning. Annual report to the U.S. Fish and Wildlife Service, RWO-38. Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan.

Budy, P., R. Al-Chokhachy, and G. P. Thiede. 2007a. Bull trout population assessment in northeastern Oregon: a template for recovery planning. Annual Progress Report to the U.S. Fish and Wildlife Service, RWO-38. Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan.

Budy, P., G. P. Thiede, and P. McHugh. 2007b. A quantification of the vital rates, abundance, and status of a critical population of endemic cutthroat trout. North American Journal of Fisheries Management 2:593–604.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Clarke, L. R., D. T. Vidergar, and D. H. Bennett. 2005. Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. Ecology of Freshwater Fish 14:267–277.

Contor, C., A. Sexton, J. Volkman, B. Mahoney, T. Hansen, E. Hoverson, P. Kissner, C. Crump, S. Narum, A. Talbot, and M. Powell. 2003. Walla Walla basin natural production monitoring and evaluation report. Bonneville Power Administration Project 2000-03900, Portland, Oregon.

Cooch, E., and G. White. 2005. Program MARK: a gentle introduction, 4th edition. Available: www.phidot.org/software/mark/docs/book. (November 2007).

Colyer, W. T., J. L. Kershner, and R. H. Hildebrand. 2005. Movements of fluvial Bonneville cutthroat trout in the Thomas Fork of the Bear River, Idaho-Wyoming. North American Journal of Fisheries Management 25:954–963.

Crowder, L. B., D. T. Crouse, S. S. Heppell, and T. H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications 4:437–445.

Downs, C. C., D. Horan, E. Morgan-Harris, and R. Jakubowski. 2006. Spawning demographics and juvenile dispersal of an adfluvial bull trout population in Trestle Creek, Idaho. North American Journal of Fisheries Management 26:190–2000.

Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometric landscape characteristics. Ecological Applications 9:642–655.

Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology, and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Science 63:133–143.

Franklin, A. B., D. R. Anderson, R. J. Gutierrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539–590.

Hemmingsen, A. R., S. L. Gunckel, and P. J. Howell. 2001. Bull trout life history, genetics, habitat needs, and limiting factors in central and northeast Oregon. Bonneville Power Administration, Project 1994–05400, Portland, Oregon.

Hilderbrand, R. H. 2003. The roles of carrying capacity, immigration, and population synchrony on persistence of stream-resident cutthroat trout. Biological Conservation 110:257–266.

Homel, K. 2007. Evaluating genetic population structure and movement patterns of bull trout (*Salvelinus confluentus*) in northeast Oregon. Master's thesis. Utah State University, Logan.

Homel, K., and P. Budy. 2008. Temporal and spatial variability in the migration patterns of juvenile and subadult bull trout in northeastern Oregon. Transactions of the American Fisheries Society 137:869–880.

Hutchings, J. A. 1996. Adaptive phenotypic plasticity in brook trout, *Salvelinus confluentus*, life histories. Ecoscience 3:25–32.

Hutchings, J. A., and E. B. Jones. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences 55:22–47.

Legault, C. M. 2005. Population viability analysis of Atlantic salmon in Maine, USA. Transactions of the American Fisheries Society 134:549–562.

Johnston, F. D., J. R. Post, C. J. Mushens, J. D. Stelfox, A. J. Paul, and B. Lajeunesse. 2007. The demography of recovery of an overexploited bull trout, Salvelinus confluentus, population. Canadian Journal of Fisheries and Aquatic Sciences 64:113–126.

Leary, R. F., F. W. Allendorf, and S. H. Forbes. 1993. Conservation genetics of bull trout in the Columbia and Klamath River drainages. Conservation Biology 7:856–865.

Mahoney, B. 2002. Walla Walla basin summer steelhead and bull trout radio telemetry project. Bonneville Power Administration, Portland, Oregon.

Manly, B. F., L. L. McDonald, and T. L. McDonald. 1999. The robustness of mark–recapture methods: a case study for northern spotted owl. Journal of Agricultural, Biological, and Environmental Statistics 4:78–101.

Marschall, E., and L. B. Crowder. 1996. Assessing population responses to multiple anthropogenic effects: a case study with brook trout. Ecological Applications 6:152–167.

Mogen, J. T., and L. R. Kaeding. 2005. Identification and characterization of migratory and nonmigratory bull trout populations in the St. Mary River drainage, Montana. Transactions of the American Fisheries Society 134:841–852.

Muhlfeld, C. C., and B. Marotz. 2005. Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. North American Journal of Fisheries Management 25:797–810.

Murphy, B. R., D. W. Willis, and T. A. Springer. 1991. The relative weight index in fisheries management: status and needs. Fisheries 16(2):30–38.

Nelson, M. L., T. E. McMahon, and R. F. Thurow. 2002. Decline of the migratory form in bull charr, *Salvelinus confluentus*, and implications for conservation. Environmental Biology of Fishes 64:321–332.

Petty, J. T., P. J. Lamothe, and P. M. Mazik. 2005. Spatial and seasonal dynamics of brook trout populations inhabiting a central Appalachian watershed. Transactions of the American Fisheries Society 134:572–587.

Paul, A. J., J. R. Post, G. L. Sterling, and C. Hunt. 2000. Density-dependent intercohort interactions and recruitment dynamics: models and a bull trout (*Salvelinus confluentus*) time series. Canadian Journal of Fisheries and Aquatic Sciences 57:1220–1231.

Quinn, T. J., II, and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service General Technical Report INT-302.

Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124:285–296.

Rieman, B. E., D. C. Lee, and R. F. Thurow. 1997. Distribution, status, and the likely future trends of bull trout within the Columbia River and Klamath River basins. North American Journal of Fisheries Management 17:1111–1125.

Ripley, T., G. Scrimgeour, and M. S. Boyce. 2005. Bull trout (*Salvelinus confluentus*) occurrence and abundance influenced by cumulative industrial developments in a Canadian boreal forest watershed. Canadian Journal of Fisheries and Aquatic Sciences 62:2431–2442.

Sankovich, P. M., S. J. Starcevich, A. R. Hemmingsen, S. L. Gunckel, and P. J. Howell. 2003. Migratory patterns, structure, abundance, and status of bull trout populations from subbasins in the Columbia Plateau and Blue Mountain Provinces. Bonneville Power Administration, Project 199405400, Portland, Oregon.

Selong, J. H., T. E. McMahon, A. V. Zale, and F. T. Barrows. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. Transactions of the American Fisheries Society 130:1026–1037.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Stevens, D. L., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99:262–278.

Swenson, E. A., A. E. Rosenberger, and P. J. Howell. 2007. Validation of endoscopy for determination of maturity in small salmonids and sex of mature individuals. Transactions of the American Fisheries Society 136:994–998.

Thurow, R. 1987. Evaluation of the South Fork Salmon River steelhead trout fishery restoration program. Idaho Department of Fish and Game, Lower Snake River Fish and Wildlife Compensation Plan, Contract 14-16-0001-86505, Boise.

Thurow, R. F. 1997. Habitat utilization and diel behavior of juvenile bull trout (*Salvelinus confluentus*) at the onset of winter. Ecology of Freshwater Fish 6:1–7.

Thurow, R. F., J. T. Peterson, and J. W. Guzevich. 2006. Utility and validation of day and night snorkel counts for estimating bull trout abundance in first- to third-order streams. North American Journal of Fisheries Management 26:217–232.

Tyron, W. W. 2001. Evaluating statistical difference, equivalence, and indeterminacy using inferential confidence intervals: an integrated alternative method of conducting null hypothesis statistical tests. Psychological Methods 4:371–386.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, California.

Wilson, P. H. 2003. Using population projection matrices to evaluate recovery strategies for Snake River spring and summer Chinook salmon. Conservation Biology 17:782–794.

Zydlewski, G. B., G. Horton, T. Dubreuil, B. Letcher, S. Casey, and J. Zydlewski. 2006. Remote monitoring of fish in small streams: a unified approach using PIT tags. Fisheries 31:492–502.

Appendix: Bull Trout Recapture Data

TABLE A.1.—Number of tagged bull trout that were recaptured from six size-classes (total length) in the South Fork Walla Walla River, Oregon, 2002–2006. Recaptures are reported for each year (summer field sampling) and interval (the period between annual sampling events). Recapture totals account for average annual growth, which was determined from field estimates and figured into the number of recaptures in the next field season.

	Number of fish recaptured								
Size-class (mm)	Interval 2002–2003	Summer 2003	Interval 2003–2004	Summer 2004	Interval 2004–2005	Summer 2005	Interval 2005–2006	Summer 2006	Interval 2006–2007
120–170	5	[a]	28	[a]	34	[a]	17	[a]	14
171–220	3	3	19	8	13	3	9	5	13
221–270	1	0	5	6	8	4	6	7	8
271–320	0	4	2	4	6	12	6	6	3
321–370	3	5	5	3	2	4	4	15	14
371–420	2	4	13	1	6	5	7	6	7
>420	11	12	30	26	28	15	12	24	19

[a] None of the 120–170-mm fish were available for recapture, as all of them entered the 170–220-mm size class.

Appendix VI - Temporal and Spatial Variability in Migration Patterns of Juvenile and Subadult Bull Trout in Northeastern Oregon

authored by

Kristen Homel
Phaedra Budy

Utah State University

Transactions of the American Fisheries Society 137:869–880, 2008

DOI: 10.1577/T07-019.1

[Article]

Temporal and Spatial Variability in the Migration Patterns of Juvenile and Subadult Bull Trout in Northeastern Oregon

KRISTEN HOMEL
Department of Ecology, Montana State University, 29 AJM Johnson Hall, Bozeman, Montana 59717, USA

PHAEDRA BUDY*
U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit, Department of Watershed Science, Utah State University, 5210 Old Main Hill, Logan, Utah 84322, USA

Abstract.—Conservation planning for threatened bull trout *Salvelinus confluentus* requires the identification of temporal and spatial movement patterns to better understand the patch size and connectivity requirements of different behavioral strategies (e.g., resident and migratory) and life stages (e.g., juvenile and adult). Although these patterns have been identified for adults, less is known about the movement patterns of juvenile and subadult bull trout. Thus, we evaluated the movement patterns and abiotic and biotic cues associated with migration timing of fluvial juvenile and subadult (150–300 mm) bull trout in the South Fork Walla Walla River, northeastern Oregon. From 2002 to 2005, we tagged 1,636 individuals with passive integrated transponder (PIT) tags and monitored subsequent movements (within the study area) and migrations (exiting of the study area) by PIT tag detection at antennae and active detection during the mark–recapture sampling season. Juveniles and subadults exhibited downstream movements and migrations throughout the year; movement and migration activity peaked in August, and migrations occurred predominantly at night (94%). We modeled migration timing in response to abiotic and biotic cues and observed distinct seasonal patterns in migration timing that were associated with changes in minimum temperature. However, the seasonal models based on temperature explained only 23–35% of the variation in migration timing, suggesting the influence of additional variables. Based on the temporal and spatial continuum of movement observed here, we believe that management must address the occupancy of multiple habitat types and migration corridors throughout the year.

In an environment characterized by instability or degradation, fish populations that contain both resident and migratory individuals are better able to persist in the face of change (Northcote 1992; Lichatowich 1999). These life history strategies are of particular importance, as they represent evolutionary diversity that has allowed fish to adapt to and take advantage of various resources in the environment (Dingle 1996). Furthermore, these strategies can be negatively affected by changes to the environment (Schlosser 1991; Quinn and Adams 1996). For imperiled species in particular, it is critical to determine the patch size and connectivity requirements associated with multiple behavioral strategies. For example, highly mobile anadromous sockeye salmon *Oncorhynchus nerka* can move distances greater than 900 km while utilizing disparate habitat patches and migratory corridors, whereas kokanee (lacustrine sockeye salmon) can spend their entire life cycle in a single lake (Groot and Margolis 1991). Ultimately, these diverse life history forms may be important to population persistence because they (1) disperse population-level mortality risk via occupation of multiple habitat patches through time, (2) facilitate gene flow, and (3) can reestablish populations in unoccupied habitat patches (Gross 1991; Jackson et al. 2001).

The migration patterns of salmonids have been widely studied. Historic migration patterns of Pacific salmon are believed to have occurred on a spatial and temporal continuum before populations were severely exploited and before impoundments altered flow regimes and decreased connectivity (Lichatowich 1999). In contrast, current Pacific salmon migrations tend to occur during discrete time periods (e.g., seasons) and are stock specific (e.g., spring Chinook salmon *O. tshawytscha*), and the duration of the migration is related to the specific strategy employed (fluvial, adfluvial, or anadromous; Groot and Margolis 1991). Other salmonids (e.g., chars *Salvelinus* spp.: Nordeng 1983; cutthroat trout *O. clarkii*: Schrank and Rahel 2004) demonstrate migration patterns that are much more variable in timing and distance. In addition, these fish may switch seasonally or annually from a migratory tactic to a resident one (Hilderbrand and Kershner 2000; McDowall 2001).

Salmonids respond to different migration cues across

* Corresponding author: phaedra.budy@usu.edu

Received January 24, 2007; accepted November 5, 2007
Published online May 1, 2008

life stages and geographic regions. Temperature is associated with the downstream dispersal of smolts (Whalen et al. 1999) and with spring and fall migrations (Swanberg 1997; Jonsson and Jonsson 2002), while discharge is associated with migration timing for multiple life stages (Quinn and Adams 1996; Downs et al. 2006). The seasonal and diel timing of smoltification (Thorpe and Morgan 1978; McCormick et al. 1998; Byrne et al. 2003) and migration (McCormick et al. 1998; Riley et al. 2002; Muhlfeld et al. 2003) is associated with photoperiod. Salow (2005) alluded to the possibility that precipitation provides a cue for migration. The evidence for a diverse array of migration cues illustrates how environmental variability or heterogeneity may result in differential migration responses across the range of a species or between species.

Bull trout *Salvelinus confluentus* are native to the Pacific Northwest and exhibit a complex array of migration patterns. Throughout their range, bull trout co-occur in resident and migratory forms (Rieman and McIntyre 1993). Adult resident fish may be 150–300 mm total length (TL), while adult migratory fish may grow to well over 600 mm (Fraley and Shepard 1989). Bull trout require cold, clean water and have been associated with complex habitat (Rieman and McIntyre 1993). Many factors (e.g., habitat degradation, fragmentation, and migration barriers) have contributed to rangewide declines, particularly for the migratory form, and the species is listed as threatened under the U.S. Endangered Species Act (USFWS 1999; Nelson et al. 2002).

Adult bull trout exhibit migrations across broad temporal and spatial scales (up to 250 km; Fraley and Shepard 1989; Swanberg 1997; Baxter 2002) and in association with many cues. Both adfluvial and fluvial adults typically initiate spawning migrations to natal streams in the late spring or summer as temperatures approach 10–12°C and as the hydrograph decreases (Goetz 1989; Elle and Thurow 1994). The fish then migrate out of the system (postspawn period) as temperatures decrease in the fall (Fraley and Shepard 1989; Flatter 2000; Hostettler 2004). Some adults may hold over in the natal stream and emigrate during the subsequent spring (K. Homel, personal observation), but in general little migration is observed during the winter unless anchor ice or harsh river conditions displace the fish (Jakober et al. 1998; Hostettler 2003). Overall, adult bull trout migrations tend to occur over discrete time periods that vary across basins (Fraley and Shepard 1989; Swanberg 1997).

In contrast to adult migration patterns, juvenile and subadult migration patterns are not as well understood and cues for migration have not been formally tested. Most bull trout migrate at age 2, although some age-1 and age-3 fish also migrate (Pratt 1992). The distance and rate of migrations vary considerably both with body size (Hostettler 2004) and seasonal changes in discharge or temperature (Salow 2005; Downs et al. 2006). In addition, these variables can affect migration of young-of-year and juvenile fish differentially (Downs et al. 2006). As the migratory life history form is of particular conservation importance, it is critical to identify (1) the role of migratory cues in determining life history characteristics and (2) the subsequent effects of altering those cues on survival and population demographics.

Our goal was to evaluate the downstream migration patterns of fluvial juvenile and subadult bull trout (120–300 mm TL) to better understand the migration time frame and distance and the potential migration cues. Although the distinction between migration and movement is important and has been discussed extensively (Dingle 1996), it is not the focus of this research. Therefore, for the purpose of this study, we define migratory movements (hereafter, migration) as annual downstream movements between distinct habitat types and we define diel and seasonal movements (hereafter, movement) as upstream or downstream movements within the same habitat type. We combined active mark–recapture techniques with passive integrated transponder (PIT) tag detection at instream antennae to (1) monitor the daily and seasonal movements of juvenile and subadult bull trout, (2) determine the timing of downstream migration, and (3) identify potential cues that may prompt this migration.

Methods

Study area.—The South Fork Walla Walla River (SFWWR) is a snowmelt-dominated second-order stream in northeastern Oregon (Figure 1). Bear, Skiphorton, and Reser creeks are the major tributaries of the SFWWR, and most observed spawning activity occurs in proximity to these tributaries. Within the SFWWR, the habitat is generally of high quality and is subject to limited recreational activity (particularly in the headwaters). Downstream of the confluence with the North Fork Walla Walla River, the habitat conditions become degraded, as evidenced by increased water temperature, simplified channel and habitat, presence of impoundments, and depletion of flow by irrigation withdrawals.

Study design.—This work was part of a larger research effort aimed at creating a general template for recovery planning of bull trout across the species' range (Al-Chokhachy et al. 2005; Al-Chokhachy 2006; Homel 2007). Within the larger effort, we conducted a mark–recapture–resight study to evaluate population

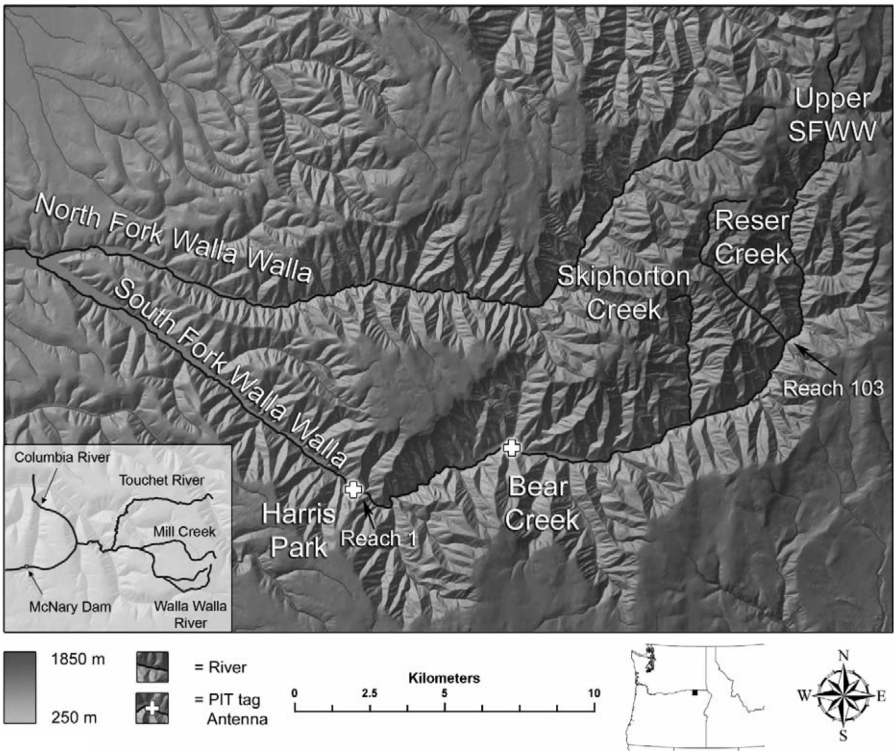

FIGURE 1.—Map of the South Fork Walla Walla River (SFWWR) study area, Oregon, showing locations of antennae used to monitor movements and migrations of passive integrated transponder (PIT) tagged juvenile and subadult bull trout.

size and structure. For the current study, we continued a mark–recapture sampling design described by Al-Chokhachy et al. (in press) and summarized briefly here. We set the lower bound of our study site at Harris County Park and the upper bound 21 km upstream at Reser Creek (Figure 1); the study site was then divided into 103 adjacent reaches of approximately 200 m each. During each study year (2002–2005), we systematically sampled 20 equidistant index reaches and an additional 20 variable reaches (Al-Chokhachy et al., in press). By systematically sampling the entire study area, we were able to account for spatial heterogeneity in the distribution of bull trout and monitor the migrations originating throughout the study area.

Fish capture and marking.—To avoid size bias in our sampling, we used multiple techniques to capture fish, including backpack electrofishing downstream to a seine, trapnetting, use of baited minnow traps, angling, and snorkeling to a seine. All active sampling occurred during summer base flow conditions (June–August). Captured bull trout were weighed, measured, and scanned for PIT tags. Fish exceeding 120 mm TL were anesthetized in a solution of tricaine methanesulfonate (MS-222). Once a fish became unresponsive to stimuli, we made a 3-mm ventral incision, implanted a 23-mm PIT tag into the body cavity, and marked the fish externally with a Floy tag for mark–resight analysis (Al-Chokhachy et al. 2005). After implantation, fish were held in a flow-through recovery tank until full equilibrium was restored. We released fish in slow water close to the point of capture.

Quantification of movement and migration.—From 2003 to 2005, we used both active mark–recapture sampling and PIT tag detection at fixed antennae to monitor upstream and downstream fish movements that occurred within the study area and downstream migrations of juveniles and subadults exiting the study area. In 2002, we installed two antennae in the SFWWR (Harris Park and Bear Creek sites; Figure 1) to record the date, time, and individual tag number of marked fish that passed through the antenna loop. The antenna at Harris Park was located at the major transition in habitat quality described above. According to a definition of migration based on a functional shift in habitat quality, fish moving downstream of this antenna would be considered migratory. The antenna at Bear Creek was located 7 km upstream of Harris Park and was used to quantify diel and seasonal movement occurring within our study area. We inferred upstream and downstream movement direction for all individuals that swam through both antennae; movement direction was also inferred for fish that swam through a single antenna after active capture. For example, if a fish was captured and tagged in reach 78 and subsequently detected at the Bear Creek antenna (reach 37), then we inferred a downstream movement. Detections of individual fish were the basis for (1) quantifying movement within the study area, (2) determining which component of the population was migratory (i.e., migrated downstream past the Harris Park antenna to exit the study area), and (3) establishing the time frame and distance over which migration occurred. In addition, although not explicitly part of this study, three other PIT tag antennae were located further downstream from our study area (Nursery Bridge Dam on the Walla Walla River, 24 km below Harris Park; Touchet River; and Mill Creek) and allowed for detection of fish that migrated even further downstream.

Abiotic and biotic variables.—Abiotic and biotic variables that could serve as potential cues for migration were measured primarily at the Harris Park antenna on the SFWWR. We collected hourly stream temperature from 2004 to 2005 based on data from a gauging station at the Harris Park site. We obtained daily precipitation and photoperiod data from local gauging stations (U.S. Department of Agriculture, High Ridge Snow Telemetry site) and conducted instream validation of photoperiod with a Licor light meter. Here, we define daytime as the hours of visible light (approximately 1 h before sunrise to 1 h after sunset). Next, we measured stream discharge at the Harris Park site in 2004 and 2005 using a Marsh-McBirney FloMate flowmeter; this information corroborated gauge height measurements that were recorded electronically and continuously at the same site. Finally, we examined the presence of spawning adults as a potential cue for migration. By active sampling and passive detection at antennae, we monitored the upstream and downstream migrations of previously tagged large fish in our system to determine the time frame in which they could potentially influence juvenile and subadult migration timing.

Data analysis.—We evaluated several aspects of movement and migration in the SFWWR. First, we assessed diel, seasonal, and annual movement timing of bull trout within the study area. We summarized both upstream and downstream movements based on all passive detections of fish (2003–2005) at the Bear Creek and Harris Park antennae. We used mark–recapture detections to further define movement direction for fish that only passed through a single antenna.

Detection efficiency at passive antennae is a complex function of (1) antenna efficiency, or the ability of the antennae to detect a tagged fish and (2) the occurrence of temporary time periods when antennae are inoperable due to uncontrollable events (Zydlewski et al. 2006). Previously, the U.S. Fish and Wildlife Service (Columbia River Fisheries Program Office, unpublished data) estimated antenna efficiency at the Harris Park site to be 80–100% (i.e., this is the percentage of tags passing through the antenna loop that were detected; the range in detection is influenced by environmental conditions). Given this high level of antenna efficiency, we were more concerned with the frequency of antenna operation. We assessed the operating frequency based on (1) the known number of missed detections and (2) periods of inoperability. Because we had multiple antennae and multiple active sampling recapture events, we knew which fish had traveled out of the study area and returned. If a fish was detected at the uppermost antenna (Bear Creek) and then detected months later at Nursery Bridge Dam but not at Harris Park (located between the other two sites), a missed detection at the Harris Park antenna was therefore indicated. Periods of known missed detections at Harris Park corresponded with periods of power outages that caused antennae to be inoperable. As such, we summed the total number of hours of Harris Park antenna inoperability and divided it by the total number of hours encompassed by our multiyear study to estimate daily antenna efficiency. From 2003 to 2005, this calculation of antenna efficiency was highly variable (50–100%). Therefore, to capture all potential cues for migration timing across a yearly cycle, we used a subset of our detection data from a period of nearly continuous antenna operation for formal statistical evaluation of downstream migration cues and timing for bull trout exiting the study area at Harris Park. Data collected from September 1, 2004, to December 31, 2005, were used for statistical models, as consistently high detection efficiency (80–100%) was observed for this period.

We considered a set of 12 a priori candidate models based on biological hypotheses of factors influencing annual migration timing in other populations of bull trout or other species. Using linear regression techniques in the Statistical Analysis System (version 9.1; SAS Institute 2002), we quantified the number of migrants per unit time (10 d) in response to the following combinations of abiotic and biotic variables and their interactions: (1) minimum temperature, (2) maximum temperature, (3) discharge, (4) precipitation, (5) photoperiod, (6) number of upstream-migrating

TABLE 1.—Summary of five highest-ranked annual models and highest-ranked seasonal models describing the influence of abiotic and biotic variables on the number of passive integrated transponder tagged juvenile and subadult bull trout detected as migrating past fixed antennae on the South Fork Walla Walla River, northeastern Oregon, during each 10-d period in 2003–2005 (N = sample size; T_{min} = minimum temperature, °C; Q = gauge height, m; precip = precipitation, cm; adults = number of upstream-migrating adult bull trout; adj. R^2 = adjusted coefficient of determination). For each model, the slope (β) from the regression equation is reported for the included explanatory variables; dashes indicate variables that were excluded from a model. Ranks were based on Akaike's information criterion (AIC); the AIC difference (ΔAIC) between each model and the best model (i.e., that with the lowest AIC) is also shown. For the seasonal models, sample sizes varied among seasons, so AIC scores were comparable only within a season.

			β				Model statistics				
Model	N	Intercept	T_{min}	Q	Precip	Adults	P	F	Adj. R^2	AIC	ΔAIC
Annual											
1	54	0.42	0.07	-	-	-	0.11	2.6	0.03	−41.98	0.00
2	54	0.3	0.09	-	-	−0.11	0.13	2.11	0.04	−41.65	0.33
3	54	−670.79	0.08	0.34	-	-	0.22	1.58	0.02	−40.59	1.39
4	54	0.9	-	-	−0.51	-	0.34	0.94	0.00	−40.32	1.66
5	54	0.5	0.06	-	−0.26	-	0.26	1.39	0.02	−40.22	1.76
Seasonal											
Fall	23	3,748.23	0.22	1.9	-	-	0.02	4.88	0.31	−18.00	
Winter	4	1.62	−0.32	-	-	-	0.06	5.02	0.31	−17.13	
Spring	10	2.87	−0.29	-	-	-	0.05	5.31	0.35	−12.40	
Summer	17	−4.01	0.64	-	-	−0.22	0.13	2.61	0.23	−7.59	

adult bull trout, (7) a global model that included all variables except maximum temperature, (8) discharge and the minimum temperature × photoperiod interaction, (9) discharge × precipitation interaction, (10) minimum temperature and precipitation, (11) minimum temperature and discharge, and (12) minimum temperature and number of adult upstream migrants. We ranked these 12 annual models according to Akaike's information criterion (AIC; Burnham and Anderson 2002) and selected the five highest-ranked models (i.e., those that had the lowest AIC scores; Table 1). We then evaluated seasonal models of migration timing and cues (using variables from the five highest-ranked annual models) and selected the highest-ranked model for each season based on AIC scores. Due to unequal sample sizes across seasons, seasonal models were only compared with other models describing the same season (e.g., each winter model was compared with only winter models; Table 1).

Results

Movement Patterns within the Study Area

Over the course of our study, we detected a large degree of movement within the bull trout population and recaptured fish up to 14 km from the initial tagging location. During 2002–2005, we PIT-tagged 1,636 bull trout (120–720 mm TL); from 2003 to 2005, the Bear Creek and Harris Park antennae recorded 938 fish detections. At Harris Park, most (94%) of the downstream migration detections for all size-classes occurred at night (nighttime detections = 143; daytime detections = 9). Juveniles and subadults (120–300 mm TL on the tagging date) accounted for 1,312 of the tagged fish and 539 of the detections of fish moving upstream or downstream past the Bear Creek and Harris Park antennae; these detections occurred throughout the entire year (Figure 2). Of the 286 juvenile and subadult detections at Bear Creek, 37%

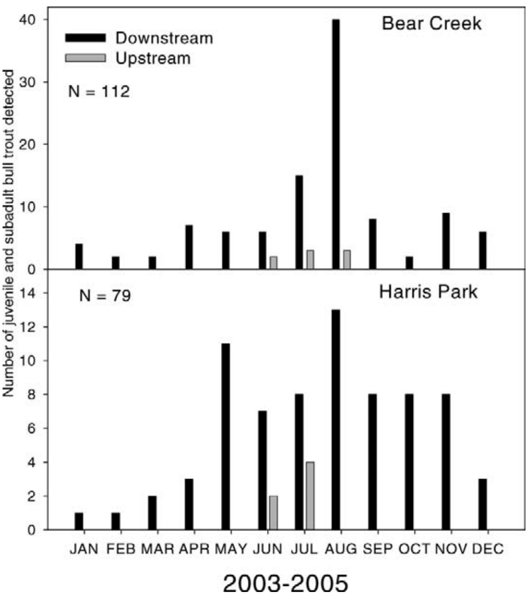

FIGURE 2.—Monthly detections of upstream (gray bars) and downstream (black bars) movements made by passive integrated transponder–tagged juvenile and subadult bull trout (120–300 mm total length) at two stationary antennae (Bear Creek and Harris Park; the y-axis scale differs between sites) on the South Fork Walla Walla River, northeastern Oregon, 2003–2005.

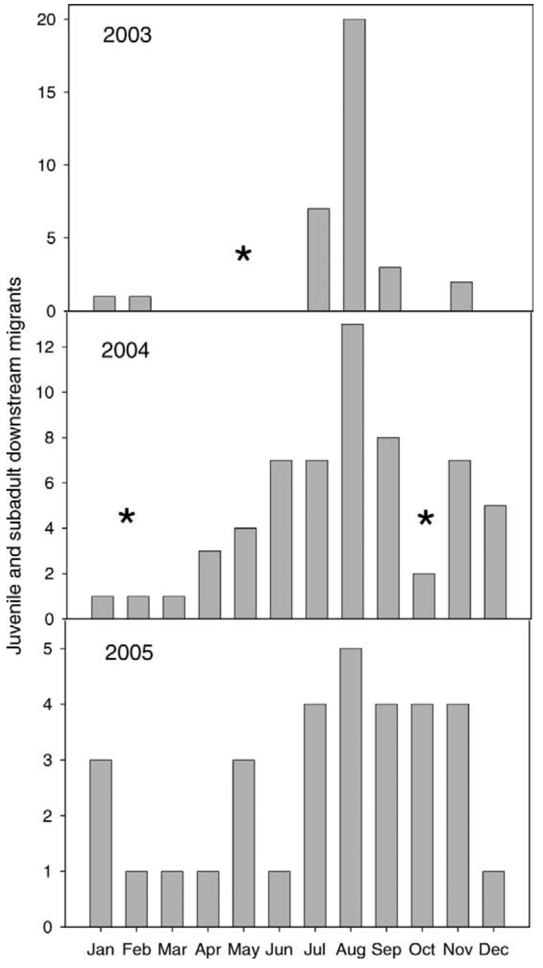

FIGURE 3.—Downstream migration timing of passive integrated transponder–tagged juvenile and subadult bull trout (120–300 mm total length) detected at stationary antennae (Bear Creek and Harris Park) on the South Fork Walla Walla River, northeastern Oregon, 2003–2005 (the *y*-axis scale differs among years). Asterisks indicate periods in which an antenna was inoperable or was operating at low (<50%) efficiency. Because of variable detection in 2004 at Harris Park (the downstream antenna, used to detect fish exiting the study area), movement direction could not be identified for many of the fish that were detected at only one antenna in 2005.

were of downstream movement, 2% were of upstream movement, 53% were repeat detections of stationary fish, and 8% could not be assigned a movement direction (Figure 2). Of the 253 juvenile and subadult detections at Harris Park, 29% were of downstream movement, 2% were of upstream movement, 65% were repeat detections of stationary fish, and 4% could not be assigned a movement direction (Figure 2). Of the 180 juvenile and subadult fish detected as moving downstream, 74 exited the study area at Harris Park and were therefore considered migratory.

Downstream Migration Timing and Distance

Bull trout exhibited temporal and spatial variation in downstream migration patterns. Juveniles and subadults migrated downstream past the Harris Park antenna throughout the entire year; an initial downstream pulse of migrants was detected in the spring, and a larger pulse was detected in August (Figure 3). In addition, 10 juveniles and subadults were detected at Nursery Bridge Dam (Figure 1) in January and February. None of the bull trout marked in the SFWWR was detected at any antenna on the Columbia River or on other tributaries to the Walla Walla River (e.g., Mill Creek and Touchet River). A fish from the SFWWR would have to migrate 127 km to be detected at a Columbia River antenna.

Abiotic and Biotic Variables

During 2002–2005, abiotic and biotic variables differed across years; however, for illustration, we report variables measured from September 2004 to December 2005, which corresponds to period used for modeling of migration timing. Maximum water temperature in the study area was 15.25°C, and minimum temperature approached 1.00°C (Figure 4). Flows peaked in the late spring (gauge height = 602.07 m [1,975.3 ft], corresponding to a flow of ~4.25 m^3/s [150 ft^3/s]) concurrent with snowmelt runoff and peaked again in December (602.13 m [1,975.5 ft]) in response to precipitation (Figure 4). The SFWWR received 86.86 cm of precipitation (primarily in March–April) in 2005 (Figure 4). From 2003 to 2005, we observed consistent patterns of adult migration; adults moved upstream into the study area in May and June and exhibited postspawn downstream movements in September (Figure 5). During the modeled period of migration timing, we detected 20 tagged adults migrating upstream primarily in June and July but more untagged adults were known to have migrated upstream based on spawner counts and active sampling (Al-Chokhachy et al. 2005; Al-Chokhachy 2006; Homel 2007).

Influence of Cues on Migration

We modeled the migration timing of 54 juveniles and subadults from September 1, 2004, to December 31, 2005; although migration varied seasonally, it could not be predicted solely from environmental and biological cues. Of the 12 models tested, the five highest-ranked models were not significantly different from each other according to AIC. Our most

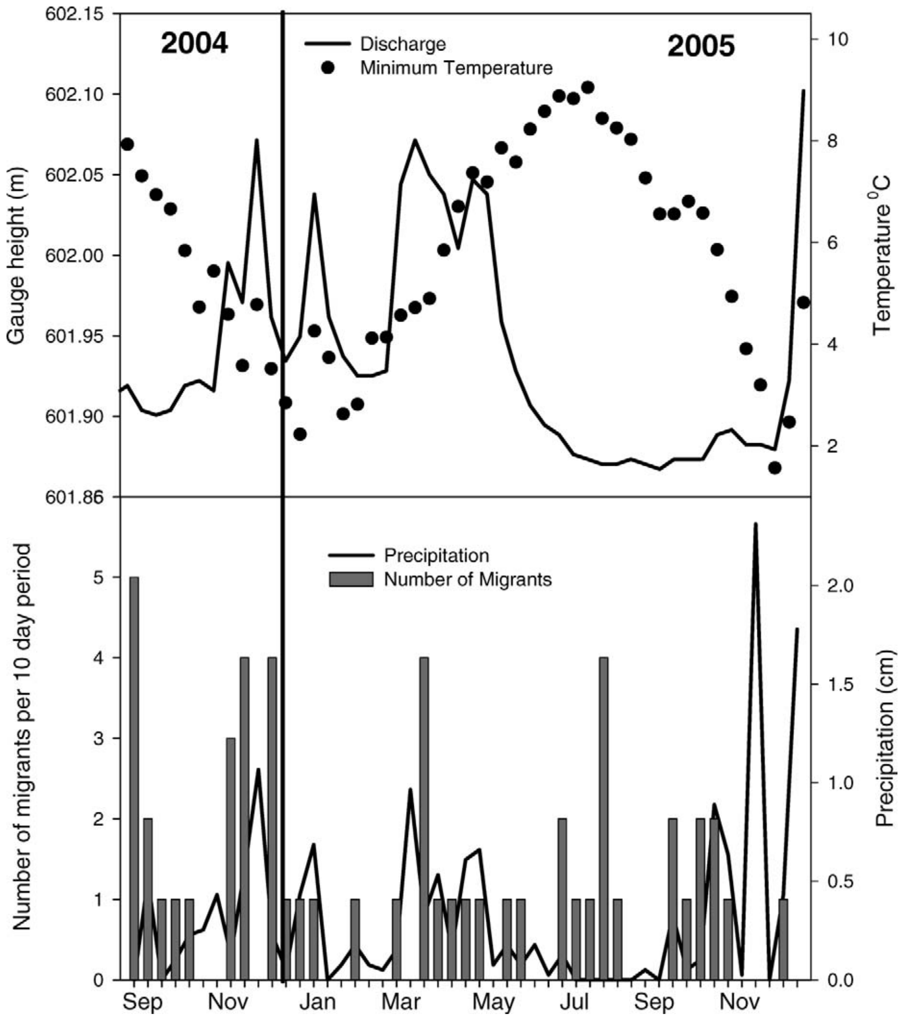

FIGURE 4.—Migration timing of juvenile and subadult bull trout (120–300 mm total length) per 10-d period (bottom panel) in relation to precipitation (cm; bottom panel), minimum temperature (°C; top panel), and discharge (as represented by gauge height, m; top panel) in the South Fork Walla Walla River, northeastern Oregon, 2004–2005.

parsimonious model of migration cues included only minimum temperature (number of migrants/10-d period $= 0.42 + [0.07 \times \text{minimum temperature}] + \varepsilon$, where $\varepsilon =$ error term; $R^2 = 0.03$; $P = 0.11$; Table 1). Given the high degree of variability in migration observed across seasons, we subsequently modeled seasonal migration in response to the environmental and biological variables that appeared in the highest-ranked annual models. Within each season, there was a clear best model (i.e., one that differed from the other models by more than two AIC points; Burnham and Anderson 2002). The highest-ranked models for winter and spring indicated that migration timing was negatively related to changes in minimum temperature (winter: $R^2 = 0.31$, $P = 0.06$; spring: $R^2 = 0.35$, $P = 0.05$; Table 1). Summer migration timing was positively related to changes in minimum temperature and negatively related to the number of adults moving upstream ($R^2 = 0.23$, $P = 0.13$; Table 1). Finally, the highest-ranked model of fall migration indicated that migration timing was positively related to changes in minimum temperature and stream discharge ($R^2 = 0.31$, $P = 0.02$; Table 1).

Discussion

Our evaluation of juvenile and subadult bull trout movement patterns and the variables providing cues for migration revealed that movement and migration occur

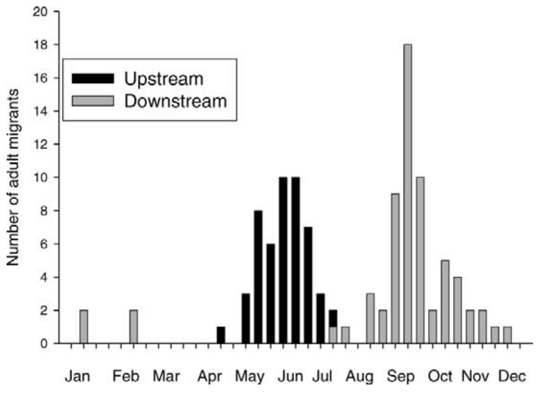

FIGURE 5.—Timing of upstream (black bars) and downstream (gray bars) migration by passive integrated transponder tagged adult bull trout (>300 mm total length) detected in the South Fork Walla Walla River, northeastern Oregon, 2003–2005.

continuously. Within our study area, we detected upstream and downstream movements throughout the year, and the longest movement from initial capture location to subsequent recapture location was 14 km. Similarly, downstream migration occurred throughout the year and almost exclusively at night. Several migratory fish were eventually detected at Nursery Bridge Dam, while others inhabited the SFWWR and Walla Walla River between the Harris Park and Nursery Bridge Dam antennae. The seasonal timing of migration was significantly and differentially associated with minimum temperature (every season), discharge (fall only), and the presence of upstream-migrating adults (summer only), but those associations explained only a portion of the variation in migration timing.

Historically, bull trout migration patterns have been described as occurring over discrete time frames (e.g., Fraley and Shepard 1989; Swanberg 1997). However, we observed a much broader temporal continuum of migration that was consistent with reports for other systems. Hemmingsen et al. (2001b) observed a similar movement pattern of fluvial juvenile bull trout in nearby Mill Creek (movement peaks occurred in spring and fall), and Downs et al. (2006) noted continuous migration of adfluvial juvenile bull trout in Idaho (spring and fall peaks). As such, it appears that the timing of juvenile and subadult migrations is more flexible and continuous than the discrete migrations of adults.

In contrast to the categorical movement distances typically used to describe bull trout life history forms (e.g., 0–2-km movements by residents; Jakober 1995), movement and migration distances within the study population occurred on a spatial continuum. Juvenile and subadult bull trout exhibited movements of up to 14 km in the study area, and several bull trout migrated 45 km from the initial tagging location (based on detection at Nursery Bridge Dam). Bull trout movement distances within our study area were longer than those typically associated with resident fish (Jakober 1995; Chandler et al. 2001). According to our definition of migration (entailing a distinct habitat shift), movements that occurred within our study area would not constitute migration and therefore could be attributed to resident fish. If so, the greater distance moved by these resident fish relative to observations in other systems (e.g., Jakober 1995; Chandler et al. 2001) illustrates a potential movement variability that could be related to local productivity, habitat availability, or behavioral plasticity. The migration distances we observed for fish that exited the study area (up to 45 km from Reser Creek to Nursery Bridge Dam) were similar to those observed in Oregon by Hemmingsen et al. (2001a); however, we found that fish did not migrate to a common destination and that they inhabited areas of the stream that were previously considered to be migratory corridors. Regardless of our definitions for the observed behavioral patterns, the outcome is the same: throughout the year, fish are using (and moving through) the entire SFWWR, including areas once considered migratory corridors.

Migration patterns varied temporally and spatially and also differed between daytime and nighttime. As in other studies (Jakober 1995; Ratliff et al. 1996), we found that most migrations occurred at night, particularly in the hours after sunset and just before sunrise. Nighttime movements are important in allowing smaller bull trout to escape the predation risk from larger bull trout and other predators. Along with commencing migrations at night, bull trout also display a distinct diel habitat shift into shallower water, a strategy that may allow them to prey on smaller conspecifics (Muhlfeld et al. 2003). The combination of diel movements and habitat shifts reflects an evolutionary adaptation that allows bull trout to maximize foraging opportunity while minimizing mortality risk and probably contributes to increased overall fitness (Werner and Hall 1988).

Based on seasonal models, bull trout migrated differentially across seasons and in association with changes in minimum temperature, discharge, and the presence of adult upstream migrants (during select seasons). However, environmental and biological variables alone did not explain the overall variability in migration patterns. Whereas maximum stream temperature is commonly identified as a limiting factor for bull trout (Selong and McMahon 2001), we found that minimum temperature was more closely associated with seasonal migration timing and that the association differed across season. The mechanism by which temperature influences migration probably differs across seasons. For example, anchor ice in winter may prompt downstream movement (Jakober et al. 1998), whereas declining temperatures in the fall may act as a migration cue by decreasing fish metabolism or the availability of forage (Leggett 1977) and by marking the transition between summer hyperphagia and slower rates of consumption in winter (Lagler et al. 1962).

We observed less-consistent effects of discharge and the presence of adult upstream migrants on migration timing. Rather than observing an effect of discharge on migration timing in the spring (during peak flows), we observed a positive association in the fall. However, it is possible that a relation between spring discharge and migration timing was obscured because discharge both peaks and reaches base flow during this season. The association between summer migration timing and upstream-migrating adults was anticipated, as this was the only season in which adult migrants could influence migration timing (via predation: Beauchamp and Van Tassell 2001). Ultimately, while biological and physical explanations of the effects of temperature, discharge, and the presence of adult upstream migrants as stimuli for migration are feasible, the low overall explanatory power of our models suggests that other contributing factors probably influence migration patterns.

Despite the large number of fish that were tagged across multiple years of sampling, there were two notable limitations to our study: (1) variable detection efficiency at antennae and (2) the inability to tag and monitor movements of fish smaller than 120 mm TL. The variability in detection efficiency was primarily due to a few unavoidable episodes of antenna inoperability (electrical outages at both antennae in 2003 and 2004 and a fire near the Bear Creek antenna in 2005) rather than to high variation in antenna efficiency (Zydlewski et al. 2006). Nevertheless, our data set of known migrants might have been larger if the antennae had operated 100% of the time. The Bear Creek antenna was among the first remote, solar-powered antennae to be installed via helicopter deposit of equipment into roadless wilderness. While this approach allowed us to monitor movements and obtain recaptures in an upper headwater area of a bull trout stream that has rarely been studied at this scale, we were limited by the logistics and technology available. We were forced to infer movement direction based on the known capture location and eventual detection at an antenna location; recent advances have addressed this issue with the installation of multiple antennae at a single location.

Second, because we only tagged and monitored the movements of fish larger than 120 mm TL, our inferences about juvenile and subadult movement patterns do not apply to smaller fish. Fish that are smaller than 120 mm TL (i.e., age 0 or 1) may show alternate movement patterns in response to cues that are important for larger fish, or they may respond to cues that have no influence on movements of larger fish. For example, Hemmingsen et al. (2001a) observed a large number of bull trout (89–250 mm fork length; very few were below 120 mm) migrating downstream in late April and early May. For these fish, discharge may be a more important migration cue than temperature change. Furthermore, Mogen and Kaeding (2005) observed that juvenile bull trout commenced migrations at age 2 or 3. These studies suggest that our tagging and monitoring of larger juvenile bull trout allowed us to describe the majority of downstream movements. Nevertheless, it will still be important to also quantify small-fish movements and associated cues.

Despite these potential limitations, our work represents the first multiple-year study to use both active (mark–recapture) and passive (antenna) detection techniques and a very large number of tagged individuals to examine movement patterns of a fluvial bull trout population. This intense sampling effort allowed us to identify individuals that exhibited migratory movements, assess the timing of migration, statistically evaluate multiple environmental and biological variables that might act as cues for migration, and describe the distribution of migration distances. Rather than select large fish for a priori monitoring (e.g., telemetry study), our mark–recapture technique allowed us to acquire movement information for the whole population of fish exceeding 120 mm with little sample bias (Al-Chokhachy 2006; Al-Chokhachy et al., in press). Finally, this study employed multiple sampling and monitoring techniques that together provided a thorough and detailed description of the continuum of migratory behavior displayed within the SFWWR population.

The observed year-round temporal and spatial migration continuum of juvenile and subadult bull trout has some important management implications. While previous discussions of migration patterns have suggested that fish use migratory corridors during discrete time intervals and that they move in association with various cues in the environment, our study demonstrates that fish (1) move and migrate throughout the year, (2) can respond unpredictably to specific cues or combinations of cues when commencing migration, and (3) utilize supposed migratory corridors as year-round habitat in some cases. In the same way that our understanding of trout migration evolved from the restricted movement paradigm (Gowan et al. 1994) to a broader understanding of variable movement patterns (Gowan and Fausch 1996; Bahr and Shrimpton 2004), our results indicate that a reevaluation of bull trout movement pattern descriptions is warranted.

Acknowledgments

We would like to acknowledge Howard Schaller, Darren Gallion, Don Anglin, Paul Sankovich, Courtney Newlon, Marshall Barrows, Tim Bailey, Brian Mahoney, and Bob Bower for provision of data, assistance, and guidance. Dale and Judy Johnson, John Ehart, George Ehmer, and Dwayne Wright provided considerable help with field logistics, and our numerous technicians all contributed to the success of this project. We thank Susan Durham for her statistical insight in the analysis of this study and Patty Kuhns for technical editing. We would especially like to thank Gary Thiede and Robert Al-Chokhachy for substantial planning, coordination, logistical, and design contributions to this study. This research was funded by the Columbia River Fisheries Program Office of the U.S. Fish and Wildlife Service, the Utah Cooperative Fish and Wildlife Research Unit of the U.S. Geological Survey, and the Vice President for Research at Utah State University (fellowship for K.H.). Tim Whitesel and Mike Pfrender reviewed previous drafts of this manuscript.

References

Al-Chokhachy, R. 2006. An assessment of the dynamics and limiting factors of a fluvial bull trout population. Doctoral dissertation. Utah State University, Logan.

Al-Chokhachy, R., P. Budy, and M. Conner. In press. Detecting changes in population abundance of a threatened species: understanding the accuracy, precision, and costs of our efforts. Conservation Biology.

Al-Chokhachy, R., P. Budy, and H. Schaller. 2005. Understanding the significance of redd counts: a comparison between two methods for estimating the abundance of and monitoring bull trout populations. North American Journal of Fisheries Management 25:1505–1512.

Bahr, M. A., and J. M. Shrimpton. 2004. Spatial and quantitative patterns of movement in large bull trout (*Salvelinus confluentus*) from a watershed in northwestern British Columbia, Canada, are due to habitat selection and not differences in life history. Ecology of Freshwater Fish 23:294–304.

Baxter, C. V. 2002. Fish movement and assemblage dynamics in a Pacific Northwest riverscape. Doctoral dissertation. Oregon State University, Corvallis.

Beauchamp, D. A., and J. J. Van Tassell. 2001. Modeling seasonal trophic interactions of adfluvial bull trout in Lake Billy Chinook, Oregon. Transactions of the American Fisheries Society 130:204–216.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inferences: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.

Byrne, C. J., R. Poole, G. Rogan, M. Dillane, and K. F. Whelan. 2003. Temporal and environmental influences on the variation in Atlantic salmon smolt migration in the Burrishoole system 1970–2000. Journal of Fish Biology 63:1552–1564.

Chandler, J. A., M. A. Fedora, and T. R. Walters. 2001. Pre- and post-spawn movements and spawning observations of resident bull trout in the Pine Creek watershed, eastern Oregon. Pages 167–172 *in* M. K. Brewin, A. J. Paul, and M. Monita, editors. Bull trout II conference proceedings. Trout Unlimited Canada, Calgary, Alberta.

Dingle, H. 1996. Migration: the biology of life on the move. Oxford University Press, Oxford, UK.

Downs, C. C., D. Horan, E. Morgan-Harris, and R. Jakubowski. 2006. Spawning demographics and juvenile dispersal of an adfluvial bull trout population in Trestle Creek, Idaho. North American Journal of Fisheries Management 26:190–200.

Elle, S., and R. Thurow. 1994. Rapid River bull trout movement and mortality studies. Job 1 *in* S. Elle, R. Thurow, and T. Lamansky. Job performance report: rivers and streams investigations. Idaho Department of Fish and Game, Boise.

Flatter, B. J. 2000. Life history and population status of migratory bull trout in Arrowrock Reservoir, Idaho. Master's thesis. Boise State University, Boise, Idaho.

Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Science 63:133–143.

Goetz, F. 1989. Biology of the bull trout, *Salvelinus confluentus*, a literature review. U.S. Forest Service, Willamette National Forest, Eugene, Oregon.

Gowan, C., and K. D. Fausch. 1996. Mobile brook trout in two high elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences 53:1370–1381.

Gowan, C., M. K. Young, K. D. Fausch, and S. C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences 74:2626–2637.

Groot, C., and L. Margolis. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Gross, M. R. 1991. Salmon breeding behavior and life history evolution in changing environments. Ecology 72:1180–1186.

Hemmingsen, A. R., B. L. Bellerud, D. V. Buchanan, S. L. Gunckel, and J. K. Shappart. 2001a. Bull trout life history, genetics, habitat needs, and limiting factors in central and northeast Oregon. Annual Report (1997) to Bonneville Power Administration, Project 95-54, Portland, Oregon.

Hemmingsen, A. R., S. M. Gunckel, P. M. Sankovich, and P. J. Howell. 2001b. Bull trout life history, genetics, habitat needs, and limiting factors in central and northeast Oregon. Annual Report, Bonneville Power Administration, Project Number 199405400, Portland, Oregon.

Hilderbrand, R. H., and J. L. Kershner. 2000. Movement patterns of stream-resident cutthroat trout in Beaver Creek, Idaho–Utah. Transactions of the American Fisheries Society 129:1160–1170.

Homel, K. 2007. Evaluating the genetic population structure and movement patterns of bull trout in northeast Oregon. Master's thesis. Utah State University, Logan.

Hostettler, L. 2003. Migration of juvenile bull trout (*Salvelinus confluentus*) from the North Fork Boise River. 2001 juvenile bull trout radio tagging interim report. U.S. Bureau of Reclamation, Snake River Area Office, Boise, Idaho.

Hostettler, L. 2004. Influence of fish size and environmental factors on the extent and rate of autumn downstream migration by bull trout in the Boise River basin, Idaho. Juvenile bull trout movement study. Final Report. U.S. Bureau of Reclamation, U.S. Bureau of Reclamation–Boise State University Cooperative Grant Agreement 1425–01fc107320, Boise, Idaho.

Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater communities–the role of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58:157–170.

Jakober, M. J. 1995. Autumn and winter movement and habitat use of resident bull trout and westslope cutthroat trout in Montana. Master's thesis. Montana State University, Bozeman.

Jakober, M. J., T. E. McMahon, R. F. Thurow, and C. C. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society 127:223–235.

Jonsson, N., and B. Jonsson. 2002. Migration of anadromous brown trout *Salmo trutta* in a Norwegian river. Freshwater Biology 47:1391–1401.

Lagler, K. F., J. E. Bardach, and R. R. Miller. 1962. Ichthyology. Wiley, New York.

Leggett, W. C. 1977. The ecology of fish migrations. Annual Review of Ecology and Systematics 8:285–308.

Lichatowich, J. 1999. Salmon without rivers: a history of the Pacific salmon crisis. Island Press, Washington, D.C.

McCormick, S. D., L. P. Hansen, T. P. Quinn, and R. L. Saunders. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55(Supplement 1):77–92.

McDowall, R. M. 2001. Anadromy and homing: two life history traits with adaptive synergy in salmonid fishes? Fish and Fisheries 2:78–85.

Mogen, J., and L. R. Kaeding. 2005. Identification and characterization of migratory and nonmigratory bull trout populations in the St. Mary River drainage, Montana. Transactions of the American Fisheries Society 134:841–852.

Muhlfeld, C. C., S. Glutting, R. Hunt, D. Daniels, and B. Marotz. 2003. Winter diel habitat use and movement by subadult bull trout in the upper Flathead River, Montana. North American Journal of Fisheries Management 23:163–171.

Nelson, M. L., T. E. McMahon, and R. F. Thurow. 2002. Decline of the migratory form in bull charr, *Salvelinus confluentus*, and implications for conservation. Environmental Biology of Fishes 64:321–332.

Nordeng, H. 1983. Solution to the "char problem" based on Arctic char (*Salvelinus alpinus*) in Norway. Canadian Journal of Fisheries and Aquatic Sciences 40:1372–1387.

Northcote, R. G. 1992. Migration and residency in stream salmonids—some ecological considerations and evolutionary consequences. Nordic Journal of Freshwater Research 67:5–17.

Pratt, K. L. 1992. A review of bull trout life history. Pages 5–9 *in* P. J. Howell and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain bull trout workshop. American Fisheries Society, Oregon Chapter, Corvallis.

Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology 77:1151–1162.

Ratliff, D. E., S. L. Thiesfeld, W. G. Weber, A. M. Stuart, M. D. Riehle, and D. V. Buchanan. 1996. Distribution, life history, abundance, harvest, habitat and limiting factors of bull trout in the Metolius River and Lake Billy Chinook, Oregon, 1983–1994. Information Report. Oregon Department of Fish Wildlife, Portland.

Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service General Technical Report INT-302.

Riley, W. D., M. O. Eagle, and S. J. Ives. 2002. The onset of downstream movement of juvenile Atlantic salmon, *Salmo salar* L., in a chalk stream. Fisheries Management and Ecology 9:87–94.

Salow, T. 2005. Inferences from weir counts of population size and environmental influence on migration timing for adfluvial bull trout (*Salvelinus confluentus*) in the north and middle forks of the Boise River, Idaho. summary report for the Boise River Cooperative Bull Trout Monitoring project to U.S. Bureau of Reclamation, Snake River Area Office, Boise, Idaho.

SAS Institute. 2002. Statistical Analysis System, version 9.1. SAS Institute, Cary, North Carolina.

Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. BioScience 41:704–712.

Schrank, A. J., and F. J. Rahel. 2004. Movement patterns in inland cutthroat trout (*Oncorhynchus clarki utah*): management and conservation implications. Canadian Journal of Fisheries and Aquatic Sciences 61:1528–1537.

Selong, J. H., and T. E. McMahon. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerances in fishes. Transactions of the American Fisheries Society 130:1026–1037.

Swanberg, T. R. 1997. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. Transactions of the American Fisheries Society 126:735–746.

Thorpe, J. E., and R. I. G. Morgan. 1978. Periodicity in Atlantic salmon, *Salmo salar* L. smolt migration. Journal of Fish Biology 12:541–548.

USFWS (U.S. Fish and Wildlife Service). 1999. Determination of threatened status for bull trout in the coterminous United States. Final Rule. Federal Register 64:210(1 November 1999):58909–58933.

Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate–predation risk trade-off. Ecology 69:1352–1366.

Whalen, K. G., D. L. Parrish, and S. D. McCormick. 1999. Migration timing of Atlantic salmon smolts relative to environmental and physiological factors. Transactions of the American Fisheries Society 128:289–301.

Zydlewski, B. G., G. Horton, T. Dubreuil, B. Letcher, C. Sean, and J. Zydlewski. 2006. Remote monitoring of fish in small streams: a unified approach using PIT tags. Fisheries 31:492–502.

Appendix VII - Incorporating Movement Patterns to Improve Survial Estimates for Juvenile Bull Trout

authored by

Tracy Bowerman
Phaedra Budy

Utah State University

North American Journal of Fisheries Management 32:1123–1136, 2012

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1080/02755947.2012.720644

ARTICLE

Incorporating Movement Patterns to Improve Survival Estimates for Juvenile Bull Trout

Tracy Bowerman*
Department of Watershed Sciences, Utah State University, 5210 Old Main Hill, Logan, Utah 84322-5210, USA

Phaedra Budy
U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit, Department of Watershed Sciences, Utah State University, 5210 Old Main Hill, Logan, Utah 84322-5210, USA

Abstract
Populations of many fish species are sensitive to changes in vital rates during early life stages, but our understanding of the factors affecting growth, survival, and movement patterns is often extremely limited for juvenile fish. These critical information gaps are particularly evident for bull trout *Salvelinus confluentus*, a threatened Pacific Northwest char. We combined several active and passive mark–recapture and resight techniques to assess migration rates and estimate survival for juvenile bull trout (70–170 mm total length). We evaluated the relative performance of multiple survival estimation techniques by comparing results from a common Cormack–Jolly–Seber (CJS) model, the less widely used Barker model, and a simple return rate (an index of survival). Juvenile bull trout of all sizes emigrated from their natal habitat throughout the year, and thereafter migrated up to 50 km downstream. With the CJS model, high emigration rates led to an extreme underestimate of apparent survival, a combined estimate of site fidelity and survival. In contrast, the Barker model, which allows survival and emigration to be modeled as separate parameters, produced estimates of survival that were much less biased than the return rate. Estimates of age-class-specific annual survival from the Barker model based on all available data were 0.218 ± 0.028 (estimate ± SE) for age-1 bull trout and 0.231 ± 0.065 for age-2 bull trout. This research demonstrates the importance of incorporating movement patterns into survival analyses, and we provide one of the first field-based estimates of juvenile bull trout annual survival in relatively pristine rearing conditions. These estimates can provide a baseline for comparison with future studies in more impacted systems and will help managers develop reliable stage-structured population models to evaluate future recovery strategies.

Knowledge of a species' life history and associated vital rates is crucial for development of effective conservation and recovery strategies (Williams et al. 2002). For many fish species, population dynamics are extremely sensitive to changes in survival at early life stages (Houde 1994; Hilborn et al. 2003). However, demographic rates are often difficult to assess between egg deposition and subadult stages, in part because survival rates during early stages are typically relatively low and can be highly variable (Bradford 1995). Although they are sometimes costly to obtain, life-stage-specific estimates of survival can be used to evaluate the relative contribution of various subadult stages to overall population change and identify targets for management (Caswell 2001; Morris and Doak 2003; Gross et al. 2006). Further, precise estimates of survival can help managers comprehend the magnitude of variability that may occur naturally as a result of environmental factors, such as density-dependent interactions, relative to anthropogenic influences (e.g., Johnston et al. 2007).

Mark–recapture studies provide a way to estimate survival and other key demographic information specific to individual

*Corresponding author: tracybowerman@gmail.com
Received February 1, 2012; accepted July 31, 2012

cohorts or life stages (e.g., Lebreton et al. 1992; White and Burnham 1999). However, estimation of demographic rates may be complicated for highly migratory species, both because of the effort needed to recapture mobile individuals and because animal movement patterns can affect interpretation of survival estimates (Cilimburg et al. 2002; Horton and Letcher 2008). For example, estimates of apparent survival (φ) generated using the common Cormack–Jolly–Seber (CJS) model are a combined estimate of true survival and site fidelity, the probability that an animal remains available for recapture within the study area (White and Burnham 1999; Sandercock 2006). With CJS estimates, it is not possible to distinguish permanent emigration from mortality or temporary emigration from capture probability (Barker et al. 2004; Horton and Letcher 2008). As a result, frequent emigration of marked organisms from the study area can confound estimates of apparent survival, and this issue has previously limited studies that sought to estimate the survival of migratory stream-dwelling fishes (e.g., Paul et al. 2000; Letcher et al. 2002). However, recent advances in technology have allowed researchers to improve recapture and resighting probabilities, while new analytical techniques have improved the ability to incorporate movement patterns into mark–recapture survival analyses.

The use of passive integrated transponder (PIT) tags has become increasingly common in fisheries research. Novel technology, including mobile PIT tag readers and passive (stationary) in-stream antennas, now often accompany the use of PIT tags. These technical advances offer a promising means of increasing the spatial and temporal extent of resight information (Zydlewski et al. 2006). Fish marked with PIT tags can be located by a researcher actively moving a mobile PIT tag reader through a study site (e.g., Roussel et al. 2000). In comparison, a passive in-stream antenna (PIA) can be operated continually to detect PIT-tagged fish as they swim past a stationary location in the stream. Both of these methods allow detection (i.e., resight) of marked individuals without handling or harassment.

Although PIT tag data acquired at PIAs can help describe fish movement patterns within a stream system, resight data collected on a continual basis cannot be incorporated into many standard mark–recapture survival models. In the common CJS model, for example, captures and recaptures must take place over a short time period relative to the time between sampling events to ensure that survival probability is constant among individuals (Lebreton et al. 1992). A more recent model developed by Barker (1997) similarly requires captures during discrete events, but can also incorporate resights of marked animals during the intervals between discrete sampling periods. Whereas captures usually occur within a specific study area, resights of marked animals are assumed to take place throughout the range of the population of interest. Inclusion of this information allows for direct estimation of true survival and site fidelity as distinct parameters (Barker and White 2001; Barker et al. 2004). This model is uncommon in the fisheries literature (but see Buzby and Deegan 2004; Al-Chokhachy and Budy 2008), although it appears promising for studies that include numerous data types (Barker et al. 2004) or for fishes that exhibit coexisting life history strategies and diverse migration patterns (Buzby and Deegan 2004; Horton and Letcher 2008).

One such fish species that demonstrates a range of movement patterns is the bull trout *Salvelinus confluentus*. The bull trout is a threatened species of stream-dwelling char that exhibits variability in life history types, migration patterns, and maturation schedules (Bahr and Shrimpton 2004; Johnston and Post 2009). Bull trout populations often include both migratory and nonmigratory (resident) life history types (McPhail and Baxter 1996; Homel et al. 2008). Adults typically spawn in cold headwater streams which also serve as rearing habitat for juveniles. Bull trout usually disperse between ages 1 and 4, migrating downstream into larger river systems and lakes where they may reside for several years before returning to natal waters to spawn, although resident adult bull trout may inhabit the upper portions of a watershed throughout their lives (Fraley and Shepard 1989; Ratliff 1992; Rieman and McIntyre 1993). For bull trout, high within-population variability and behavioral plasticity encumber the quantification of movement patterns and survival estimates. Bull trout migration distances can range from just a few kilometers to more than 200 km (McPhail and Baxter 1996; Hogen and Scarnecchia 2006), further complicating the estimation of demographic parameters.

Considerable research has been conducted to describe migratory behavior and habitat use for individual bull trout populations (Swanberg 1997; Bahr and Shrimpton 2004; Watry and Scarnecchia 2008), but the majority of these studies have focused on adults. Information about bull trout life history requirements and vital rates is still relatively sparse, particularly for early life stages. Very few studies have assessed juvenile bull trout migration patterns, rates of survival, or the environmental factors affecting survival. Life-stage-based population projection models developed for bull trout suggest that population growth may be most sensitive to changes in the survival of large adults and early life stages (Rieman and McIntyre 1993; Al-Chokhachy 2006). However, the predictive ability of such models is currently limited by a lack of empirical survival estimates specific to subadult stages.

To our knowledge, reliable estimates of survival for juvenile age-classes (<120 mm total length [TL]) are unavailable for bull trout. Previous studies assessed relative survival for early age-classes of bull trout by comparing abundances between years but did not produce precise juvenile survival estimates (Paul et al. 2000; Johnston et al. 2007). Al-Chokhachy and Budy (2008) used mark–recapture methods to develop stage-specific survival estimates for bull trout larger than 120 mm TL, but their study did not include smaller individuals. Obtaining survival estimates specific to juvenile stage classes will help fill an important gap in our understanding of factors that determine bull trout survival at different life stages. Estimates of stage-specific survival rates will also aid in identifying the life stages to target for recovery and improve the ability of population models to predict population-level responses to environmental changes.

To evaluate migration patterns and estimate survival rates for juvenile bull trout, we conducted an intensive mark–recapture study within one of several important spawning areas used by a relatively large population of bull trout in the South Fork Walla Walla River (SFWW), Oregon. The population of bull trout in the SFWW exhibits both migratory and resident life history forms (Homel et al. 2008), and migration distance and timing can be highly variable (Homel and Budy 2008). Prior to this study, little was known about juvenile bull trout dispersal and survival rates in this system.

The overall goal of this research was to provide insight into a stage of bull trout life history which has previously not been well quantified and which has important implications for understanding how juvenile life stages affect population growth and persistence. To meet this goal, the specific objectives of this study were to (1) quantify and better understand the movement patterns exhibited by juvenile bull trout (70–170 mm TL) and (2) incorporate knowledge of juvenile migration rates into mark–recapture analyses to obtain the most precise estimates of survival for bull trout during these influential early life stages.

METHODS

Study Area

We conducted this study over approximately 600 m of Skiphorton Creek directly upstream of the confluence with the SFWW (Figure 1). Skiphorton Creek originates in the foothills of the Blue Mountains in northeastern Oregon and enters the SFWW approximately 113 km upstream from the Columbia River. The Skiphorton Creek study area has an average slope of 3–5%, a mean width of 5 m, and a mean water depth of 0.24 m. The study area is characterized by complex habitat, including numerous small side channels, pools, undercut banks, and large woody debris. Bull trout primarily use Skiphorton Creek for spawning and juvenile rearing, and the fish assemblage is composed of juvenile or small resident bull trout (primarily <170 mm TL) and rainbow trout *Oncorhynchus mykiss* and/or juvenile steelhead (anadromous rainbow trout). Skiphorton Creek is located on roadless forest lands, and owing to the remote location, sampling was limited to the snow-free months of June through October.

We also gathered additional data throughout the SFWW and main-stem Walla Walla River (WW), both considerably larger

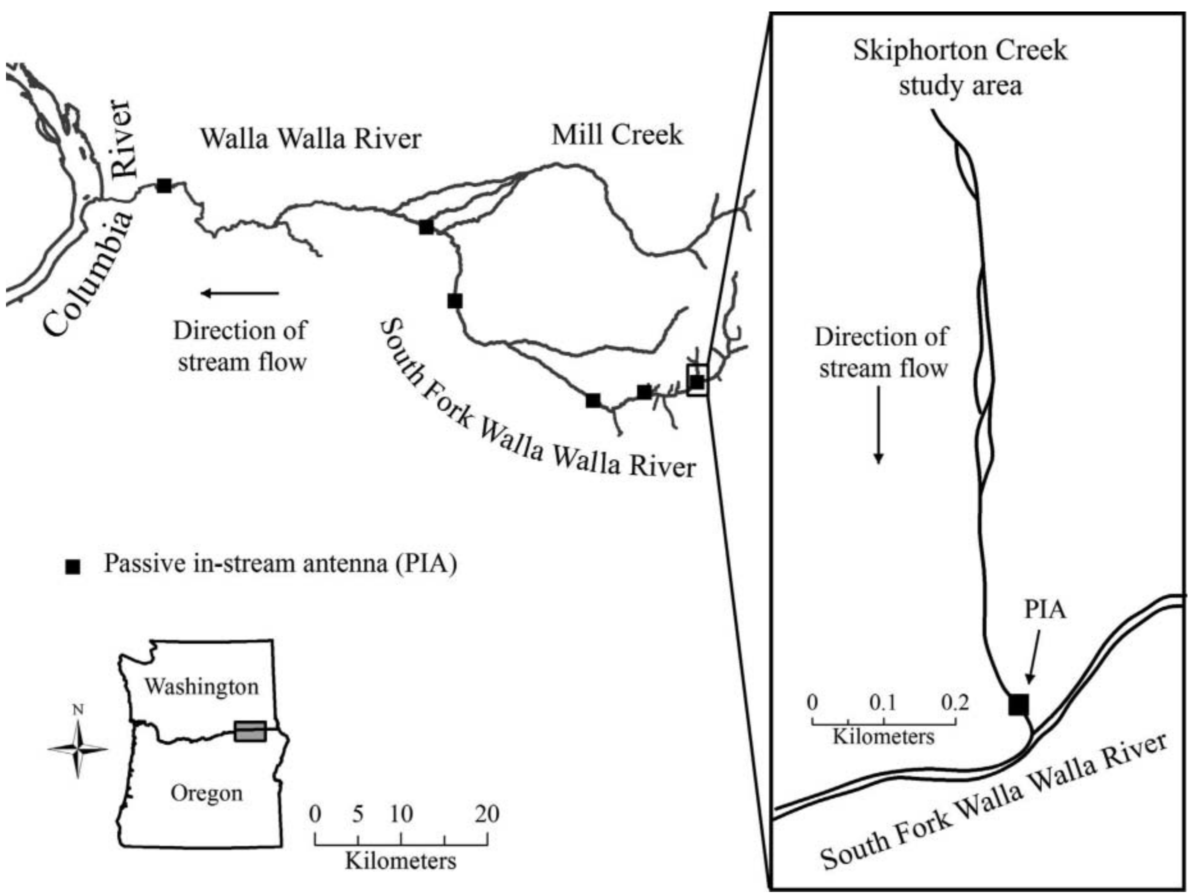

FIGURE 1. Map of the Skiphorton Creek study area, where juvenile bull trout were initially captured and marked. Marked fish could be resighted throughout the South Fork Walla Walla and Walla Walla rivers, including at any of the six passive in-stream antennas (PIAs) located downstream of the study area.

streams than Skiphorton Creek. Bull trout spawn throughout approximately 20 km of the upper SFWW and its tributaries, and adult and subadult bull trout use the entire SFWW and WW (43 and 81 km in length, respectively) for migration and overwintering habitat (Anglin et al. 2009).

Mark, Recapture, and Resight Techniques

Mark and recapture.— We conducted two discrete mark–recapture sampling events during the summers of 2007 and 2009 and three in 2008 (Table 1). We captured bull trout in Skiphorton Creek by chasing fish with a low-voltage electrical current downstream into a seine (hereafter referred to as "electroseining"). We constrained the number of electroseining events to minimize the stress to juvenile fish, and we gathered initial data on all captured fish between 70 and 170 mm TL. We anaesthetized, weighed, measured, and marked bull trout with both an external fin clip and an internal PIT tag (12.5 mm Full Duplex 134.2 kHz) surgically inserted into the peritoneal cavity. We double-marked all individuals to identify recaptures and quantify tag retention rates. We checked all recaptured fish for tag loss and recorded the unique PIT tag code. We released all fish near the point of capture after full equilibrium had been restored.

Mobile resights.—In 2008 and 2009, we also used a mobile PIT tag reader to detect marked fish throughout the Skiphorton Creek study area. We refer to this type of sampling as "mobile resight" surveys to remain consistent with the literature on Barker models, in which the term "resight" has been used to refer to any method for obtaining observations of marked animals other than physical live recaptures. The mobile reader consisted of a backpack-mounted tuner and receiver connected to a 0.35-m × 0.35-m triangular antenna at the end of an extendable pole (Biomark BP portable antenna; see Roussel et al. 2000; Cucherousset et al. 2005; Keeler et al. 2007). The reader's maximum vertical PIT tag detection distance ranged between 0.15 and 0.35 m, depending on the orientation of the tag and the reader's tuning. Lateral read range was extremely limited, such that a PIT tag had to be directly below the triangular antenna to be identified.

During each mobile resight survey, the operator waded upstream through the entire study area, passing the reader over all areas of the streambed at a height that would allow for PIT tag detection. The operator recorded the date, time, and exact location of each PIT tag. Each mobile resight sampling period took approximately 8 h, and all surveys were conducted by the same person to minimize sampling variability. We performed mobile resight surveys both during the day and at night and compared the recapture probabilities between these two time periods. We generally conducted mobile resight sampling approximately 1 week after electroseining mark–recapture events (Table 1) to assess mortalities following tagging.

Tag recoveries.—During the mobile resight surveys, we did not actually see marked fish, so we could not be certain whether (1) the PIT tag had been shed from a fish that was still alive, (2) the PIT tag was in a live fish, or (3) the marked fish had died but the tag remained in the river. We addressed the first possibility by double-marking all fish with both a PIT tag and external fin clip. Because the observed rate of PIT tag retention was high (see Results), we assumed that immobile tags represented dead fish. We distinguished between a live resight and a "tag recovery" in the following manner: after detecting a PIT tag with the mobile

TABLE 1. Sampling schedule and methods used to capture, recapture, or resight juvenile bull trout. Fish were captured by electroseining (ES) and resighted with a mobile PIT tag reader (MPR) in Skiphorton Creek. Marked fish were resighted during intervals between discrete sampling events at a passive in-stream antenna at the downstream end of the study area (PIA_{SH}) and at five passive in-stream antennas (PIA_{WW}) as well as via ancillary capture (ANC) throughout the South Fork Walla Walla and Walla Walla rivers.

Sampling date	Resight interval (d)	Number marked	Live recaptures/ resights	Live resights	Dead recoveries	Sampling method
Jul 10–13, 2007		86	0			ES
	34			0	0	PIA_{WW} + ANC
Aug 14–15, 2007		65	14			ES
	261			6	0	PIA_{WW} + ANC
May 2–3, 2008		52	5			ES
	67			2	0	PIA_{WW} + ANC
Jul 7–8, 2008		94	3			ES
	34			4	3	PIA_{WW} + ANC + PIA_{SH}
Aug 13–19, 2008		123	23			ES + MPR
	293			62	5	PIA_{WW} + ANC + PIA_{SH}
Jun 8–15, 2009		107	12			ES + MPR
	36			34	0	PIA_{WW} + ANC + PIA_{SH}
Jul 21–31, 2009		142	79			ES + MPR
	363			101	4	PIA_{WW} + ANC + PIA_{SH}
Total	1,108	669	136	209	12	

reader, the operator tapped on the substrate adjacent to the tag location, and if the tag was in a different place following the disturbance, the observation was considered a live resight. To be considered a tag recovery, a PIT tag had to be found immobile in the same location during two consecutive mobile surveys. Although we did not actually observe dead fish, we used the term "recovery" to describe detections of immobile PIT tags, to remain consistent with previous mark–recapture literature in which the term "dead recovery" has been used (Barker et al. 2004).

Passive in-stream antenna arrays and ancillary resight data.— In addition to sampling within the Skiphorton Creek study area, we collected continuous resight data from marked fish as they swam past stationary PIAs. As part of a large-scale, multiyear research project (see Al-Chokhachy and Budy 2008), five PIAs operated in the SFWW and WW river system located approximately 7, 16, 38, 52, and 103 km downstream from the Skiphorton Creek study area (Figure 1). The devices operated year-round, except for short periods when maintenance was required, and enabled us to gather resight data at multiple locations outside of the immediate study area. In 2008 and 2009, we installed one additional PIA at the downstream end of Skiphorton Creek (Skiphorton PIA) to identify when fish emigrated from the study area. We used a solar panel to generate power for the remote site; the PIA only operated between 24 July and 28 September 2008 and from 8 June to 30 September 2009, when sufficient sunlight was available.

Bull trout marked in Skiphorton Creek were also recaptured throughout the entire SFWW and WW system via several different methods. Each summer, as part of the larger study mentioned previously, approximately 20 km of the SFWW were sampled for bull trout via electroseining, and all recaptures of fish marked in Skiphorton Creek were recorded. Marked bull trout were also recaptured throughout the year at screw traps and via research-related angling at multiple locations on the WW. Fish recaptured in the SFWW or WW were considered "ancillary resights" collected during the intervals between discrete mark–recapture sampling periods. Although ancillary resights made up a small proportion of the total data, this additional sampling allowed us to consider marked fish to be at risk of recapture anywhere in the geographic range of interest (Barker 1997; Barker et al. 2004).

Juvenile Movement Patterns

We evaluated the timing, direction, distance, and frequency of juvenile bull trout movement within the study area and throughout the SFWW and WW based on data combined from all of the sampling methods described above. We assumed that any marked fish that was detected in the SFWW or WW or resighted at the Skiphorton PIA had emigrated from the study area. We considered the assumption of emigration valid for the duration of our study because we observed no marked fish to have reentered Skiphorton Creek after having left. For fish detected at the Skiphorton PIA, we used data from physical recaptures to estimate the length at emigration based on a linear equation for the absolute growth rate applicable to short time scales (Isely and Grabowski 2007), namely,

$$Length_{emigration} = Length_{tagging} + 5.23 + 0.099 \times (time_{emigration} - time_{tagging}). \quad (1)$$

We used movement observations to describe emigration rates and timing and examined the impact of emigration on survival estimates.

Survival Analyses

We estimated annual survival probability for two separate age-classes of juvenile bull trout: age 1 (70–120 mm TL) and age 2 (121–170 mm TL), where length at age at initial capture was estimated based on combined length-frequency analyses and otolith aging (Al-Chokhachy and Budy 2008; Budy et al. 2011). All survival analyses were conducted in Program MARK (White and Burnham 1999). First, we estimated apparent survival from a CJS model (Cormack 1964; Jolly 1965; Seber 1965), a model commonly used to assess survival probabilities for a wide range of taxa (e.g., Lebreton et al. 1992; Muir et al. 2001; Letcher et al. 2002). The CJS model only incorporates data obtained from discrete mark–recapture sampling periods, so we only used data collected during electroseining mark–recapture and mobile resight sampling in Skiphorton Creek. We combined mobile resights with active captures in the same discrete sampling period, as mobile resight surveys were conducted shortly after mark–recapture periods. The two parameters estimated by the CJS model are apparent survival (φ_i; the probability that an animal survives and remains in the sample from time i to $i + 1$) and p_i (the probability of encountering an individual given that it is alive and in the sample). Because emigration can confound these two parameters, we also used an ad hoc method in the CJS model to account for known emigration: when we observed an individual emigrate from the study area, we removed its contribution to survival parameter estimation at that time (see Horton and Letcher 2008). We included only known emigrants in this approach, which did not allow us to account for incomplete detection of emigrants.

We compared estimates of apparent survival from the standard and ad hoc CJS models with estimates of survival from the Barker model (Barker 1997; Barker and White 2001). As in the CJS model, mobile antenna resights from within the study area were incorporated into the data from the previous mark–recapture period. In addition to this data, the Barker model also allowed inclusion of data obtained during the interval from i to $i + 1$ between discrete sampling events, which included tag recoveries, resights at PIAs, and ancillary resights throughout the SFWW and WW. If an individual was either recaptured or resighted on more than one occasion during the interval from i to $i + 1$, only a single detection was recorded in the encounter history (Barker et al. 2004). The model complexity necessary to accommodate this additional data results in a total of seven parameters in the Barker model (Barker 1997). In addition to survival (S_i) and recapture (p_i) probabilities, the model parameters include F_i (the probability that an animal at risk of capture at time i is at risk of capture at time $i + 1$ [i.e., has not emigrated from the study area]), F'_i (the probability that an animal not at risk of capture at time i is at risk of capture at time $i + 1$ [e.g., temporary emigration]), R_i (the probability that an animal alive at time i is resighted alive in the interval from i to $i + 1$), and R'_i (the probability that an animal is resighted before it dies in the interval from i to $i + 1$). A final parameter, r_i (the probability that an animal dies and is found dead in the interval from i to $i + 1$) allowed us to incorporate data from tag recoveries. Because we recovered only a relatively small number of tags, we also compared survival estimates between a data set that included tag recoveries and another which did not, where we set $r = 0$.

We assessed model fit using the median $\hat{c}$ approach in program MARK to estimate a variance inflation factor ($\hat{c}$) for the most saturated model given available data (e.g., Horton et al. 2011). Because the variance inflation factor was reasonable (1.98) and we expected that model fit improved with the inclusion of individual covariates, we based model selection on Akaike's information criterion corrected for effective sample size (AIC_c). We considered models with a difference of 0–2 in AIC_c to have substantial support, models with >4 to have considerably less support, and models with >10 to have virtually no support (Burnham and Anderson 2002). Data limitations and model parsimony led us to model some parameters as constant across time and between size-classes.

Our primary parameter of interest was survival, so we used a two-step approach to the model selection process. Initially, we retained high dimensionality in our survival parameters (φ in the CJS model and S in the Barker model) and iteratively modeled the remaining parameters based on a priori knowledge of sampling efficiency and bull trout ecology. With the CJS model, model selection of the less pertinent parameter (recapture probability [p]) resulted in a set of candidate models for which p varied as a function of an increasing trend across sampling periods and with length as an individual covariate. For all candidate Barker models, we modeled p as a function of individual length and r as constant over time and among size-classes. Owing to the variability in resights among sampling intervals (Table 1), we modeled both R and R' as functions of time. Finally, we found strong support for models in which we explicitly modeled permanent emigration by setting F' to 0 and we allowed F to vary as a function of individual length.

After selecting the model structure for the less pertinent parameters, we then focused on modeling survival, the parameter of greatest interest (e.g., Slattery and Alisauskas 2002; Collins and Doherty 2006). In both the CJS and Barker candidate model sets, we estimated survival for the two different age-classes as separate groups and modeled survival in relation to factors determined a priori, including annual variation, time interval, season, and individual covariates measured at the time of tagging, such as length. In addition, we included models with a marking effect to test the hypothesis that survival rates would be lower during the time interval immediately following initial capture. To facilitate comparison of survival estimates and variance between the CJS and Barker model types, we present estimates from the single best model from the set of candidate models.

We compared survival estimates from the top CJS and Barker models with an estimate of the return rate, an index of survival. Return rates can be considered a minimum estimate of true survival, because they do not account for detection probability or site fidelity (Sandercock 2006). We estimated a simple return rate by calculating the proportion of marked fish in each size-class that were recaptured or resighted nine or more months after initial tagging (fish that survived until the subsequent field season and afterward). We estimated a return rate ($\widehat{RR}$) for marked fish from a simple proportion with binomial variance using

$$\widehat{RR} = \frac{Y}{N} \tag{2}$$

$$var(\widehat{RR}) = \frac{\widehat{RR}(1 - \widehat{RR})}{N}, \tag{3}$$

where Y represents the number of marked fish that were resighted and N is the total number of marked fish.

RESULTS

Recaptures and Resights of Marked Fish

Between 2007 and 2009, we marked 669 bull trout in Skiphorton Creek. Nearly 50% were recaptured or resighted at least once ($n = 327$), and approximately 11% multiple times ($n = 71$). The total number of unmarked fish caught in a single mark–recapture sampling period ranged between 52 in May 2008 and 142 in July 2009 (Table 1). The majority of bull trout captured and PIT-tagged were in the age-1 size-class, whereas only 25% of the marked individuals were >120 mm TL (Figure 2).

Multiple techniques were necessary to obtain sufficient data to track the movement patterns of marked individuals and evaluate survival rates, although the efficiency of resighting techniques varied. Data from the mobile PIT tag reader, all PIAs combined, and ancillary resights accounted for 62, 36, and 2% of total resight observations, respectively. The number of fish resighted during each interval between discrete sampling periods increased over the duration of the study (Table 1), as both the number of marked fish and sampling effort increased. In 2007, we resighted no fish between the two summer capture periods and only six between the 2007 and 2008 field seasons. After we added the PIA at the lower end of the Skiphorton Creek study area during 2008 and 2009, PIA resights increased dramatically.

The mobile PIT tag reader enabled us to resight marked bull trout while minimizing disturbance to the stream and fish and was particularly effective when used at night (Table 2). The recapture probability with the mobile PIT tag reader at night

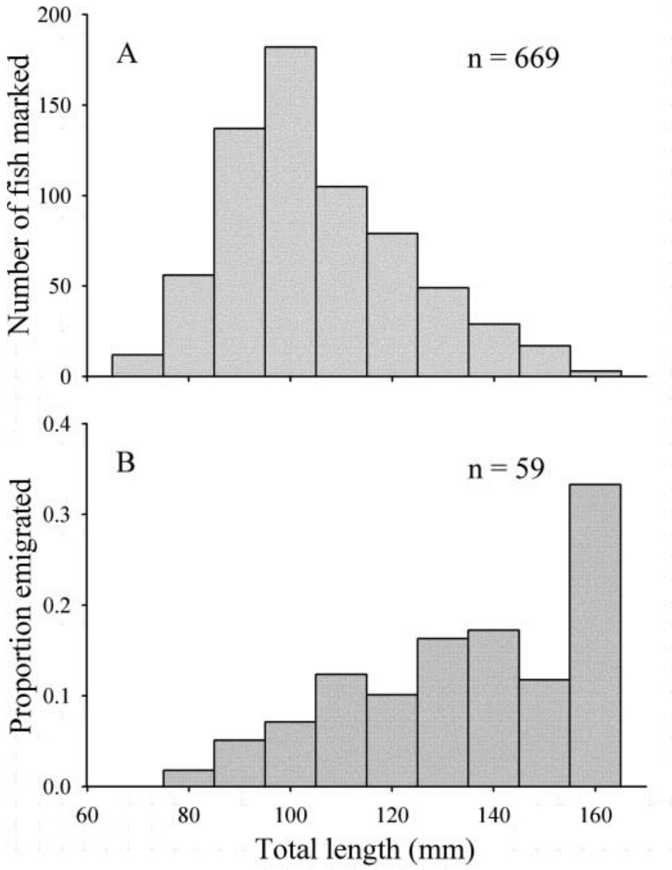

FIGURE 2. **(A)** Length at capture of juvenile bull trout caught in Skiphorton Creek and marked with PIT tags and **(B)** proportion of marked fish in each size-group for which the exact date of emigration from the Skiphorton Creek study area was known. Emigration was determined when PIT-tagged fish were detected at a passive in-stream antenna located at the lower boundary of the study area. Length at emigration was estimated based on a linear growth relationship developed for the study population.

($p = 0.51 \pm 0.04$; estimate $\pm$ SE) was 4.5 times that of the mobile reader during the day ($p = 0.11 \pm 0.02$) and 2.5 times that of electroseine sampling ($p = 0.22 \pm 0.03$). We recaptured only one fish that had shed its PIT tag, resulting in an estimate of 98.8% tag retention. Given this high rate of tag retention, we did not explicitly account for tag loss and considered the 12 tag recoveries found during 2008 and 2009 to represent mortalities in our analyses.

Juvenile Bull Trout Movement Patterns

Recapture data collected via multiple methods allowed us to determine when juvenile bull trout emigrated from the natal spawning/rearing tributary and enabled us to observe bull trout movements throughout the study area and the larger SFWW and WW system. Within the Skiphorton Creek study area, juvenile bull trout moved both upstream and downstream, but the predominant direction of movement was downstream (Figure 3). Movement in the upstream direction occurred at low frequencies within the study area, and the largest recorded upstream movement was only 0.2 km. We observed numerous juvenile bull trout that remained for more than 1 month within 50 m of their original capture location, and in many instances those fish were located in the same habitat unit (e.g., a small pool or eddy) during numerous consecutive sampling periods. The majority of marked fish remained within 0.5 km of their initial capture location until they began a downstream migration, after which many moved rapidly downstream, some traveling up to 6 km in 3 d. We resighted marked fish at various locations throughout the larger SFWW and WW, and the greatest observed travel distance was 53 km downstream from the study area. We did not detect a relationship between stream discharge and movement patterns (Figure 3).

Juvenile bull trout emigrated from the study area at a range of sizes and during all seasons. Based on a linear relationship between juvenile bull trout growth and time, we estimated the length of marked fish for which the exact date of emigration was known (i.e., fish detected passing the Skiphorton PIA). Juvenile bull trout of all sizes exceeding 80 mm TL emigrated from the study area, although the majority of emigrants were longer than 100 mm (Figure 2). The proportion of emigrants increased with fish length, but we did not observe a distinct size threshold at which movement was initiated. Emigration occurred throughout the year, with a slight increase in the emigration rate from late August through October. In the age-1 age-class, 52% of the fish recaptured between 4 and 12 months after initial capture had moved more than 4 km downstream of the study area, and 92%

TABLE 2. Comparison of capture probabilities for the capture and recapture/resight methods used to estimate juvenile bull trout movement and survival. The parameter p is the probability of capturing an individual given that it is alive and in the sample, R is the probability that an animal is resighted alive in the time interval from i to $i+1$, and R' is the probability that an animal is resighted before it dies in that time interval.

Sampling method	Data type	Capture probability (p or R)	SE	Average recapture/ sampling hour
Electroseining	Live recapture	$p = 0.22$	0.03	0.76
Mobile antenna, day	Live resight in study area/dead recovery	$p = 0.11$	0.02	2.29
Mobile antenna, night	Live resight in study area/dead recovery	$p = 0\ 0.51$	0.04	7.55
PIAs + ancillary	Live resight outside study area	$R = 0.19$[a]	0.06	n.a.
PIAs + ancillary	Live resight outside study area	$R' = 0.16$[a]	0.01	n.a.

[a]For the time period when the Skiphorton PIA was operating continuously (maximum observed R).

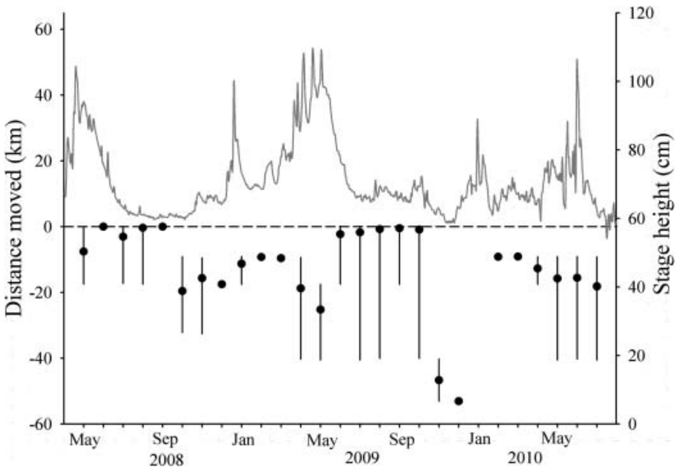

FIGURE 3. Monthly juvenile bull trout migrations (left *y*-axis) and stage height of the South Fork Walla Walla River (right *y*-axis). The circles represent the mean distances moved during the specified month, and the bars represent the maximum and minimum distances moved; positive values represent distances moved upstream, and negative values represent distances moved downstream (a horizontal line at 0 is provided for reference). The continuous gray line depicts stage height.

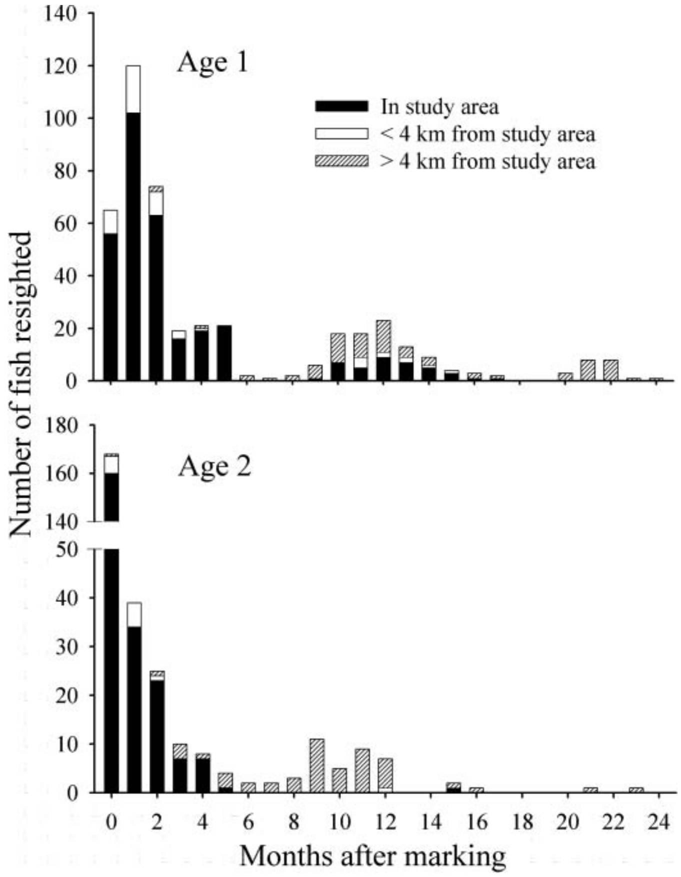

FIGURE 4. Number of age-1 and age-2 bull trout resighted in the Skiphorton Creek study area, within 4 km of the study area, and >4 km away from the study area per month after initial capture and marking.

of the age-2 fish appeared to have emigrated (Figure 4). As a result of high emigration rates and variable emigration timing, a substantial proportion of the marked fish were unavailable for recapture during subsequent sampling periods. Furthermore, no marked fish were detected within the study area more than 18 months after tagging, suggesting that nearly all juveniles emigrated from their natal habitat between age 1 and age 3.

Juvenile Bull Trout Survival Rates

Estimates of survival based on the simple return rate were 0.171 ± 0.017 (estimate $\pm$ SE) for the age-1 class and 0.190 ± 0.030 for the age-2 class (Figure 5). Compared with the return rate, the estimates of apparent survival from the naïve CJS model were extremely biased downward but improved when emigration was included in the models via the ad hoc approach. Point estimates of annual survival using the Barker model were higher than the return rate, and the 95% confidence intervals encompassed the return rate. Across models, the variance associated with survival estimates was greater for age-2 fish, as there were fewer fish marked in this size-class.

The CJS model that minimized AIC$_c$ was constant across time and included separate estimates of apparent survival for the two age-classes and fish length as an individual covariate (Table 3). From this model, the estimate of apparent annual survival for the age-1 class was 0.090 ± 0.018 for a fish with a mean length of 100 mm TL and 0.009 ± 0.009 for the age-2 class based on a mean length of 133 mm. Compared with the return rate, the CJS estimates accounted for only 52% and 5% of the return rate for the two size-classes, respectively (Figure 5). The ad hoc CJS approach resulted in the same best model as the naïve CJS model, and with emigration explicitly incorporated, survival estimates were 0.142 ± 0.023 for the age-1 class (similar to the return rate), but 0.069 ± 0.030 for the age-2 class (only 36% of the return rate). Model selection showed much less support for the model that included a tagging effect, and a likelihood ratio test provided no evidence of a difference in survival during the time period immediately following tagging ($\chi^2 = 1.112$, df $= 2$, $P = 0.57$).

In contrast to the CJS model results, the annual survival estimates from the Barker model were somewhat higher than those from the return rate (Figure 5). Model selection produced identical model ranking for data with and without tag recoveries but led to slightly different estimates of survival with similar precision. For both data sets, the model with the greatest support was one in which survival was constant across time and varied between size-classes (Table 3). Estimated annual survival for the Barker model including dead recoveries was 0.218 ± 0.028 for fish in the age-1 class and 0.232 ± 0.065 for age-2 fish. When tag recoveries were omitted from the data ($r = 0$), the same best-ranking model provided similar estimates of $\hat{S}$ (0.195 ± 0.026 and 0.191 ± 0.062, respectively). Based on the AIC$_c$ values, there was little support for the model that included annual variability in survival, although this was unsurprising

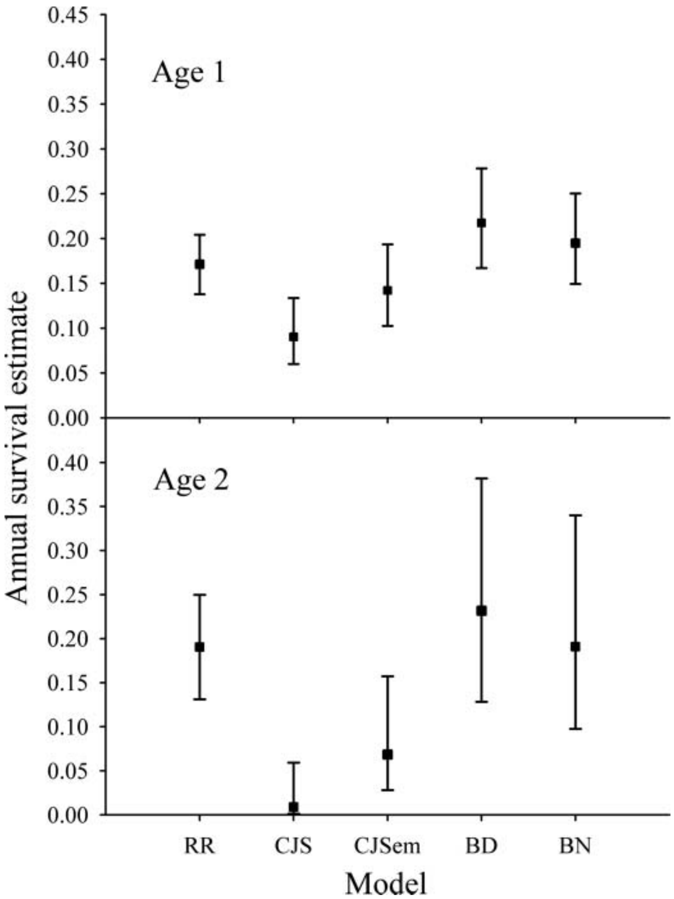

FIGURE 5. Estimates of survival probability for age-1 and age-2 bull trout marked in Skiphorton Creek calculated using different methods (RR = return rate, CJS = naïve Cormack–Jolly–Seber, CJSem = ad hoc CJS with emigration included, BD = Barker model with dead recoveries, BN = Barker model without dead recoveries). Error bars represent 95% confidence intervals.

given that there were only 3 years of data. There was also considerably less support for a model that included a tagging effect, and a likelihood ratio test provided no evidence of lower survival during the time period directly following tagging ($\chi^2 = 1.768$, df = 2, $P = 0.41$).

In addition to providing robust estimates of survival, the Barker model included specific parameters to estimate site fidelity, providing additional insight into juvenile bull trout migration patterns. Model selection demonstrated stronger support for a model in which we explicitly modeled permanent emigration ($F' = 0$) than for a model that included random emigration (Barker and White 2001), which was consistent with our movement observations. In this model, F varied as a function of individual length and parameter estimates indicated that F was negatively related to fish length at marking and decreased sharply for fish larger than 100 mm. Estimates of F were 0.735 ± 0.151 for a fish measuring 90 mm TL, compared with 0.125 ± 0.063 for a 110-mm TL bull trout. This sharp decline in the probability of an individual's remaining at risk of capture was consistent with our observations of emigration rates for bull trout across this range of sizes.

DISCUSSION

Our results provide some of the first estimates of annual survival rates for age-1 and age-2 bull trout based on individual mark–recapture information. Use of multiple recapture and resighting techniques allowed us to assess rates of emigration from natal habitat and to describe the movement patterns of juvenile bull trout. In addition, incorporating emigration into our survival analyses improved the accuracy of annual survival estimates for juvenile bull trout. The results from the Barker model appeared to be the least-biased estimates of survival based on the model types we considered and are the most precise field-based survival rates available for juvenile bull trout of which we are aware. Our study demonstrates the importance of incorporating movement patterns into survival analyses for migratory species and provides an important comparison of contemporary capture–recapture techniques in stream systems.

Mark, Recapture, and Resight Techniques

The use of PIT tags was highly effective in this study, as it enabled us to detect marked fish across a large geographic range with minimal handling. We found 2 of the 12 recovered tags during the sampling period directly after tagging, but we found no evidence that PIT-tagging individuals affected survival estimates. These results correspond with those of previous studies of juvenile salmonids, which have likewise detected no discernible difference in survival between PIT-tagged and non-tagged fish held in a controlled setting (Prentice et al. 1990; Gries and Letcher 2002) or in the wild (Ombredane et al. 1998).

The use of the mobile PIT tag reader allowed us to increase the probability of resighting a marked individual while causing little disturbance to the stream and fish. The mobile reader also enabled us to make an efficient use of our sampling time, as it required only one person to operate (compared with three for the electroseining method) and the entire study area could be scanned in 8 h. The mobile reader was most effective when operated at night, when juvenile bull trout often moved very little from their location as the reader passed over them, even after the operator tapped on the substrate (in contrast with daytime sampling, when fish usually moved immediately). As a result, five resights were initially misidentified as tag recoveries, but the marked fish subsequently changed locations or were detected at downstream PIAs. Thus, we only classified tags as recoveries when they were found in the same place during at least two consecutive sampling periods.

We recovered only 12 tags, and this relatively small number may not have been sufficient to improve the precision of survival estimates from the Barker model. Nonetheless, it is reasonable to expect that larger numbers of tag recoveries would yield greater precision in estimating the parameters of interest (Barker and Kavalieris 2001). Tag recoveries could also have represented

TABLE 3. Survival models for juvenile bull trout captured and marked in Skiphorton Creek, 2007–2009. Two age-classes were modeled as separate groups: age 1 (70–120 mm TL) and age 2 (121–170 mm). Periods indicate no difference across time or among groups, plus signs denote additive parameters, and = 0 indicate parameters set to 0; length at capture was included as an individual covariate. See text for variable descriptions.

Survival varies by	Candidate model	AIC_c	Model likelihood	Number of parameters
CJS models				
Age group + length	$\varphi_{(\text{group + length})}\, p_{(\text{timetrend + length})}$	664.95	1.00	7
Age group	$\varphi_{(\text{group})}\, p_{(\text{timetrend + length})}$	668.87	0.14	5
Year	$\varphi_{(\text{year})}\, p_{(\text{timetrend + length})}$	681.87	0.04	6
Group + tag effect	$\varphi_{(\text{group + tag effect})}\, p_{(\text{timetrend + length})}$	673.25	0.00	9
Barker models				
Age group	$S_{(\text{group})}\, p_{(\text{length})}\, r_{(.)}\, R_{(\text{time})}\, R'_{(\text{time})}\, F_{(\text{length})}\, F'_{(=0)}$	1,839.63	1.00	18
Age group + length	$S_{(\text{group + length})}\, p_{(\text{length})}\, r_{(.)}\, R_{(\text{time})}\, R'_{(\text{time})}\, F_{(\text{length})}\, F'_{(=0)}$	1,841.49	0.39	19
Age group + tag effect	$S_{(\text{group + tag effect})}\, p_{(\text{length})}\, r_{(.)}\, R_{(\text{time})}\, R'_{(\text{time})}\, F_{(\text{length})}\, F'_{(=0)}$	1,844.35	0.09	20
Year	$S_{(\text{year})}\, p_{(\text{length})}\, r_{(.)}\, R_{(\text{time})}\, R'_{(\text{time})}\, F_{(\text{length})}\, F'_{(=0)}$	1,860.91	0.00	19

PIT tags that were shed from fish that were still alive rather than true mortalities. However, based on the high rate of PIT tag retention that we observed, we considered the probability of a shed tag unlikely and therefore did not incorporate tag loss rates in our survival estimates. Other studies of similar-sized juvenile fish have also shown high rates of PIT tag retention (Ombredane et al. 1998; Gries and Letcher 2002). If PIT tag retention were lower than we observed, we would have underestimated true survival (Knudsen et al. 2009) and our annual survival estimates would be conservative.

Passive in-stream antenna arrays stationed at six locations throughout the geographic range of the population allowed us to collect data continually throughout the year, including in winter when our remote field site was inaccessible. Use of multiple PIAs also helped us develop a detailed spatial and temporal understanding of juvenile bull trout movement patterns and emigration rates. Detection efficiency varied among PIAs and at different discharges, but we did not have sufficient data or the analytical ability to incorporate this variability into our analyses. Operation of the PIA at the downstream end of the study area over the entire year would certainly have increased our knowledge of emigration timing and improved the survival estimates from the ad hoc CJS method. However, the Barker model can incorporate data collected opportunistically (Barker 1997) and thus allowed for the inclusion of PIA data even when sites operated at less than 100% detection efficiency.

We observed an increasing trend in the number of recaptures/resights over the course of the study, which likely occurred as a result of increased effort and efficiency over time. This increase in efficiency resulted from the installation of the Skiphorton PIA, the use of the mobile PIT tag reader at night, and the potential improvement in the skill of the person operating the mobile reader. Due to the high emigration rates, variation in emigration timing, and low capture probabilities of juvenile bull trout, multiple resight techniques were necessary to obtain sufficient resight data to estimate survival and characterize movement patterns. Each of these techniques provided data that informed estimates of survival and emigration in a different way. While the use of the mobile PIT tag reader at night resulted in a relatively high capture probability compared with other methods, it only allowed detection of fish that remained in the study area. Data collected at PIAs were integral in monitoring movements throughout the broader range of the population, but the spatial and temporal scope of this research was possible only because there was a preexisting infrastructure of PIAs within the river system. The high cost of obtaining this type of information, both in terms of money and effort, may be prohibitive in many studies. In our research, it would not have been possible to reliably estimate survival without the use of additional resight methods both within and outside of the Skiphorton Creek study area. Thus, the cost of using various sampling techniques relative to the information gained should be weighed carefully within the context of overall study objectives (e.g., Al-Chokhachy et al. 2009).

Juvenile Bull Trout Movement Patterns

Migratory behavior is known to vary among different age-classes of bull trout and among populations (McPhail and Baxter 1996; Monnot et al. 2008). For the population of juvenile bull trout in Skiphorton Creek, emigration from the natal stream occurred across a range of sizes >80 mm TL, and rates of emigration increased with fish length. These results are consistent with those of research in other locations where juvenile bull trout typically migrate from rearing areas into larger rivers between age 1 and 3, with the majority migrating at age 2 (Oliver 1979; McPhail and Baxter 1996). However, our research demonstrated that a surprisingly large proportion of age-1 juveniles emigrated from rearing habitat into the larger SFWW. These data suggest that as juveniles grow larger, selective forces favor migration downstream into larger, warmer, and more productive habitat, despite potentially greater risk of mortality from predators (e.g., adult bull trout) and environmental catastrophes, such as flooding. Our data also showed that after leaving their natal stream juvenile bull trout migrated throughout more than 50 km of downstream habitat in the SFWW and WW, indicating that immature fluvial bull trout used a wide range of rearing habitat throughout the entire river network.

Over the course of this study, juvenile bull trout emigrated from spawning and rearing habitat continuously throughout the year. We observed a pulse of emigration into the SFWW and WW from July through October, when stream discharge is at its lowest and instream barriers may be more difficult to pass. Increased observations during this time period may have been influenced by higher sampling intensity during these months, although other research has similarly demonstrated higher rates of downstream subadult migration during late summer and fall (Oliver 1979; Homel and Budy 2008). Immature bull trout also migrated downstream throughout the remainder of the year, including during winter months, a time period during which adult bull trout are often considered sedentary (Bahr and Shrimpton 2004; Watry and Scarnecchia 2008). These data illustrate the variability of juvenile bull trout migratory behavior, a component of the fluvial life history which is not always considered in management objectives.

Mark–Recapture Models and Annual Survival Estimates

Migration rates and distances are often difficult to quantify for species that exhibit diverse life history characteristics or variation in both migratory behavior and home range size, such as bull trout, coastal cutthroat trout *O. clarkii clarkii*, rainbow trout, and brook trout *Salvelinus fontinalis* (e.g., Trotter 1989; Rodríguez 2002; Meka et al. 2003). Nonetheless, understanding and incorporating movement patterns into capture–recapture studies can dramatically improve estimates of survival and other important vital rates (Cilimburg et al. 2002; Horton and Letcher 2008). In our study, continuous emigration from the study area resulted in a constant loss of marked fish from the study population. The return rate (the minimum estimate of true survival) was higher than the estimates of apparent survival using the CJS model because it included data from individuals resighted anywhere in the geographic range of the population, including fish that had emigrated from Skiphorton Creek. In contrast, the naïve CJS model only used data collected within the study area, from which marked fish emigrated continually, resulting in estimates of apparent survival that were considerably lower than the return rate. This bias was more pronounced for the age-2 class because fish in this size range demonstrated higher emigration rates. When we incorporated emigration directly into encounter histories we observed an improvement over the naïve CJS model, but the ad hoc approach still produced estimates of apparent survival that were biased downward, particularly for the age-2 size-class.

In contrast to the CJS model, the Barker model produced estimates of annual survival which were higher than the observed return rate and similar between the two size-classes (or slightly greater for the age-2 size-class). This latter observation indicates that bull trout survival rates may increase with size and age, which is consistent with many other fish species (Lorenzen 2006). Although we have no way of knowing the true survival rates in the wild, it is reasonable to expect that the true survival rates would be higher than the return rate, which does not account for recapture probability (Martin et al. 1995; Sandercock 2006). In simulation analyses, Horton and Letcher (2008) found that the Barker model yielded robust estimates of survival with very little bias, regardless of whether emigration was temporary or permanent. Given the robust nature of the Barker model and the relative agreement between annual survival estimates derived from this model and observed return rates, we believe that the best estimates for juvenile bull trout annual survival from our study are those obtained from the Barker model.

Our study provides an important baseline of field-based annual survival estimates for age-1 bull trout (70–120 mm TL). Prior to our study, the survival of this age-class represented a significant gap in our understanding of bull trout demography. Our estimates of annual survival rates are within the range of other annual survival estimates for juvenile brook trout, a closely related species (mean $\pm$ SE apparent survival $= 0.218 \pm 0.149$; Petty et al. 2005). For age-2 bull trout, survival estimates for the fish marked in Skiphorton Creek were higher than those for fish from the larger SFWW River (Al-Chokhachy and Budy 2008), where estimates of annual survival for subadult bull trout (120–170 mm TL) varied between 0.025 ± 0.009 and 0.154 ± 0.052, depending on the year. Our results were also comparable to the highest annual return rates for subadult bull trout ($<$270 mm fork length) observed in Mill Creek, another tributary to the Walla Walla River (P. Howell, U.S. Forest Service, unpublished data).

While the higher estimates of annual age-2 bull trout survival in this study may in part reflect the greater sampling intensity in our study design, they may also represent true biological differences in survival between stream types. Our results indicate that survival rates for juvenile bull trout are higher in small tributaries than in larger rivers but also that fish emigrate from these tributaries as they mature. Together, these observations suggest that there may be a trade-off in fitness between the increased risks faced in large rivers (e.g., predation, displacement by flooding) and the faster growth rates associated with warmer, more productive waters (Selong et al. 2001). While emigration from small, hydrologically stable headwater streams may decrease the probability of survival, fish that do survive likely grow faster than their later-emigrating counterparts. The variability in size at which juvenile bull trout emigrate from natal streams may represent an important adaptation that allows populations to hedge their bets in an unpredictable environment (Olofsson et al. 2009).

Conservation and Management Implications

This research describes movement patterns and survival rates for juvenile bull trout ($<$170 mm TL) and provides insight into a life stage that is not well understood. Our data demonstrate that juvenile (ages 1 and 2) fluvial bull trout exhibit a range of migratory behaviors. In the SFWW, juveniles moved from natal rearing habitat to larger rivers throughout the year and across a range of sizes. Based on these data, maintaining diversity in life history adaptations, including the variability in juvenile migratory behavior, may be important for long-term population persistence. Further, juvenile bull trout from 80 to 100 mm TL and larger used habitat throughout the SFWW and main-stem WW in all seasons, suggesting that these size-classes should be considered in management decisions regarding flow regulation and fish passage. In addition to documenting juvenile migratory behavior, our research demonstrates the importance of incorporating emigration rates into survival analyses for species that exhibit variable migration patterns and improves our understanding of the influence of migration on survival rates.

We provide some of the first field-based, empirical estimates of juvenile bull trout annual survival based on marked individuals. These estimates can provide a baseline against which to compare the results of future studies of juvenile bull trout survival in more impacted systems as well as improve our understanding of how various management actions may affect bull trout at specific life stages. Given the sensitivity of bull trout population growth to survival rates at early life stages, stage-specific estimates of vital rates are important for the development and use of reliable stage-structured population models. The survival estimates from this research will help improve the predictive ability of bull trout population viability analyses, which can be used to evaluate population-level responses to different management scenarios and to develop sound recovery plans for this imperiled species.

ACKNOWLEDGMENTS

Funding for this project was provided by the U.S. Fish and Wildlife Service, Columbia River Fisheries Program Office; the U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit (in kind); and the Ecology Center at Utah State University (USU). Additional support was provided by the USU Vice-Presidential Fellowship and the Seeley–Hinckley Scholarship, both awarded to T. Bowerman. This paper was improved by reviews of previous drafts by Carl Saunders, Mary Conner, Charles Hawkins, and Joseph Wheaton. Expert advice was provided by Howard Schaller, David Koons, and Robert Al-Chokhachy. Logistical support was provided by Peter MacKinnon, Gary Thiede, John Ehart, George Ehmer, and Dwayne Wright. Field data were collected with assistance from M. Todd, R. Carpen, M. Mustin, M. Schifiliti, G. Hill, M. Archibald, A. Dean, W. Kern, R. Al-Chokhachy, A. Hill, B. Simcox, S. Petre, L. Tennant, S. Rizza, and C. Cahill. We thank Phil Howell, Paul Sankovich, Courtney Newlon, Don Anglin, Darren Gallion, Ryan Koch, Marshall Barrows, David Hines, William Duke, and the Fish Ecology Lab at USU for providing data and support. This study was performed under the auspices of Utah State University protocol 1082. The use of trade names or products does not constitute endorsement by the U.S. Government.

REFERENCES

Al-Chokhachy, R. 2006. An assessment of the dynamics and limiting factors of a fluvial bull trout population. Doctoral dissertation. Utah State University, Logan.

Al-Chokhachy, R., and P. Budy. 2008. Demographic characteristics, population structure, and vital rates of a fluvial population of bull trout in Oregon. Transactions of the American Fisheries Society 137:1709–1722.

Al-Chokhachy, R., P. Budy, and M. Conner. 2009. Detecting declines in the abundance of a bull trout (*Salvelinus confluentus*) population: understanding the accuracy, precision, and costs of our efforts. Canadian Journal of Fisheries and Aquatic Sciences 66:649–658.

Anglin, D. R., D. Gallion, M. Barrows, R. Koch, and C. Newlon. 2009. Monitoring the use of the mainstem Columbia River by bull trout from the Walla Walla basin. U.S. Fish and Wildlife Service, Columbia River Fisheries Program Office, Final Report to the U.S. Army Corps of Engineers, Vancouver, Washington.

Bahr, M. A., and J. M. Shrimpton. 2004. Spatial and quantitative patterns of movement in large bull trout (*Salvelinus confluentus*) from a watershed in north-western British Columbia, Canada, are due to habitat selection and not differences in life history. Ecology of Freshwater Fish 13:294–304.

Barker, R. J. 1997. Joint modeling of live–recapture, tag–resight, and tag–recovery data. Biometrics 53:666–677.

Barker, R. J., K. P. Burnham, and G. C. White. 2004. Encounter history modeling of joint mark–recapture, tag–resighting and tag–recovery data under temporary emigration. Statistica Sinica 14:1037–1055.

Barker, R. J., and L. Kavalieris. 2001. Efficiency gain from auxiliary data requiring additional nuisance parameters. Biometrics 57:563–566.

Barker, R. J., and G. C. White. 2001. Joint analysis of live and dead encounters of marked animals. Pages 361–367 *in* R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, editors. Wildlife, land, and people: priorities for the 21st century: proceedings of the second international wildlife management congress. The Wildlife Society, Bethesda, Maryland.

Bradford, M. J. 1995. Comparative review of Pacific salmon survival rates. Canadian Journal of Fisheries and Aquatic Sciences 52:1327–1338.

Budy, P., L. B. Tennant, T. Bowerman, and G. P. Thiede. 2011. Bull trout population assessment in northeastern Oregon: a template for recovery planning: 2010 annual progress report to U.S. Fish and Wildlife Service. Utah Cooperative Fish and Wildlife Research Unit, UTCFWRU 2011:1–90, Logan.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer, New York.

Buzby, K. M., and L. A. Deegan. 2004. Long-term survival of adult Arctic grayling (*Thymallus arcticus*) in the Kuparuk River, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 61:1954–1964.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, 2nd edition. Sinauer Associates, Sunderland, Massachusetts.

Cilimburg, A. B., M. S. Lindberg, J. J. Tewksbury, and S. J. Hejl. 2002. Effects of dispersal on survival probability of adult yellow warblers (*Dendroica petechia*). Auk 119:778–789.

Collins, C. T., and P. F. Doherty Jr. 2006. Survival estimates for royal terns in southern California. Journal of Field Ornithology 77:310–314.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429–438.

Cucherousset, J., J. M. Roussel, R. Keeler, R. A. Cunjak, and R. Stump. 2005. The use of two new portable 12-mm PIT tag detectors to track small fish in shallow streams. North American Journal of Fisheries Management 25:270–274.

Fraley, J. J., and B. B. Shepard. 1989. Life-history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Science 63:133–143.

Gries, G., and B. H. Letcher. 2002. Tag retention and survival of age-0 Atlantic salmon following surgical implantation with passive integrated transponder tags. North American Journal of Fisheries Management 22:219–222.

Gross, K., W. F. Morris, M. S. Wolosin, and D. F. Doak. 2006. Modeling vital rates improves estimation of population projection matrices. Population Ecology 48:79–89.

Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences of the USA 100:6564–6568.

Hogen, D. M., and D. L. Scarnecchia. 2006. Distinct fluvial and adfluvial migration patterns of a relict charr, *Salvelinus confluentus,* stock in a mountainous watershed, Idaho, USA. Ecology of Freshwater Fish 15:376–387.

Homel, K., and P. Budy. 2008. Temporal and spatial variability in the migration patterns of juvenile and subadult bull trout in northeastern Oregon. Transactions of the American Fisheries Society 137:869–880.

Homel, K., P. Budy, M. E. Pfrender, T. A. Whitesel, and K. Mock. 2008. Evaluating genetic structure among resident and migratory forms of bull trout (*Salvelinus confluentus*) in northeast Oregon. Ecology of Freshwater Fish 17:465–474.

Horton, G. E., and B. H. Letcher. 2008. Movement patterns and study area boundaries: influences on survival estimation in capture–mark–recapture studies. Oikos 117:1131–1142.

Horton, G. E., B. H. Letcher, and W. L. Kendall. 2011. A multistate capture–recapture modeling strategy to separate true survival from permanent emigration for a passive integrated transponder tagged population of stream fish. Transactions of the American Fisheries Society 140:320–333.

Houde, E. D. 1994. Differences between marine and freshwater fish larvae: implications for recruitment. ICES Journal of Marine Science 51:91–97.

Isely, J. J., and T. B. Grabowski. 2007. Age and growth. Pages 187–228 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Johnston, F. D., and J. R. Post. 2009. Density-dependent life-history compensation of an iteroparous salmonid. Ecological Applications 19:449–467.

Johnston, F. D., J. R. Post, C. J. Mushens, J. D. Stelfox, A. J. Paul, and B. Lajeunesse. 2007. The demography of recovery of an overexploited bull trout, *Salvelinus confluentus*, population. Canadian Journal of Fisheries and Aquatic Sciences 64:113–126.

Jolly, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration–stochastic model. Biometrika 52:225–247.

Keeler, R. A., A. R. Breton, D. P. Peterson, and R. A. Cunjak. 2007. Apparent survival and detection estimates for PIT-tagged slimy sculpin in five small New Brunswick streams. Transactions of the American Fisheries Society 136:281–292.

Knudsen, C. M., M. V. Johnston, S. L. Schroder, W. J. Bosch, D. E. Fast, and C. R. Strom. 2009. Effects of passive integrated transponder tags on smolt-to-adult recruit survival, growth, and behavior of hatchery spring Chinook salmon. North American Journal of Fisheries Management 29:658–669.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Letcher, B. H., G. Gries, and F. Juanes. 2002. Survival of stream-dwelling Atlantic salmon: effects of life history variation, season, and age. Transactions of the American Fisheries Society 131:838–854.

Lorenzen, K. 2006. Population management in fisheries enhancement: gaining key information from release experiments through use of a size-dependent mortality model. Fisheries Research 80:19–27.

Martin, T. E., J. Clobert, and D. R. Anderson. 1995. Return rates in studies of life history evolution: are biases large? Journal of Applied Statistics 22:863–876.

McPhail, J. D., and J. S. Baxter. 1996. A review of bull trout (*Salvelinus confluentus*) life-history and habitat use in relation to compensation and improvement opportunities. British Columbia Ministry of Environment, Lands and Parks, Fisheries Branch, Fisheries Management Report 104, Victoria.

Meka, J. M., E. E. Knudsen, D. C. Douglas, and R. B. Benter. 2003. Variable migratory patterns of different adult rainbow trout life history types in a southwest Alaska watershed. Transactions of the American Fisheries Society 132:717–732.

Monnot, L., J. B. Dunham, T. Hoem, and P. Koetsier. 2008. Influences of body size and environmental factors on autumn downstream migration of bull trout in the Boise River, Idaho. North American Journal of Fisheries Management 28:231–240.

Morris, W. F., and D. F. Doak. 2003. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts.

Muir, W. D., S. G. Smith, J. G. Williams, E. E. Hockersmith, and J. R. Skalski. 2001. Survival estimates for migrant yearling Chinook salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia rivers, 1993–1998. North American Journal of Fisheries Management 21:269–282.

Oliver, G. G. 1979. A final report on the present fisheries use of the Wigwam River with an emphasis on the migration, life-history and spawning behaviour of Dolly Varden char, *Salvelinus malma* (Walbaum). British Columbia Ministry of Environment, Lands and Parks, Fish and Wildlife Branch, Cranbrook.

Olofsson, H., J. Ripa, and N. Jonzén. 2009. Bet-hedging as an evolutionary game: the trade-off between egg size and number. Proceedings of the Royal Society London B 276:2963–2969.

Ombredane, D., J. L. Bagliniere, and F. Marchand. 1998. The effects of passive integrated transponder tags on survival and growth of juvenile brown trout (*Salmo trutta* L.) and their use for studying movement in a small river. Hydrobiologia 371/372:99–106.

Paul, A. J., J. R. Post, G. L. Sterling, and C. Hunt. 2000. Density-dependent intercohort interactions and recruitment dynamics: models and a bull trout (*Salvelinus confluentus*) time series. Canadian Journal of Fisheries and Aquatic Sciences 57:1220–1231.

Petty, J. T., P. J. Lamothe, and P. M. Mazik. 2005. Spatial and seasonal dynamics of brook trout populations inhabiting a central Appalachian watershed. Transactions of the American Fisheries Society 134:572–587.

Prentice, E. F., T. A. Flagg, and C. S. McCutcheon. 1990. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. Pages 317–322 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Ratliff, D. E. 1992. Bull trout investigations in the Metolius River–Lake Billy Chinook system. Pages 37–44 *in* P. J. Howell and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain bull trout workshop. American Fisheries Society, Oregon Chapter, Corvallis.

Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service General Technical Report INT-302.

Rodríguez, M. A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecology 83:1–13.

Roussel, J. M., A. Haro, and R. A. Cunjak. 2000. Field test of a new method for tracking small fishes in shallow rivers using passive integrated transponder (PIT) technology. Canadian Journal of Fisheries and Aquatic Sciences 57:1326–1329.

Sandercock, B. K. 2006. Estimation of demographic parameters from live-encounter data: a summary review. Journal of Wildlife Management 70:1504–1520.

Seber, G. A. F. 1965. A note on the multiple-recapture census. Biometrika 52:249–259.

Selong, J. H., T. E. McMahon, A. V. Zale, and F. T. Barrows. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. Transactions of the American Fisheries Society 130:1026–1037.

Slattery, S. M., and R. T. Alisauskas. 2002. Use of the Barker model in an experiment examining covariate effects on first-year survival in Ross's geese (*Chen rossii*): a case study. Journal of Applied Statistics 29:497–508.

Swanberg, T. R. 1997. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. Transactions of the American Fisheries Society 126:735–746.

Trotter, P. C. 1989. Coastal cutthroat trout: a life history compendium. Transactions of the American Fisheries Society 118:463–473.

Watry, C. B., and D. L. Scarnecchia. 2008. Adfluvial and fluvial life history variations and migratory patterns of a relict charr, *Salvelinus confluentus,* stock in west-central Idaho, USA. Ecology of Freshwater Fish 17:231–243.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California.

Zydlewski, G. B., G. Horton, T. Dubreuil, B. Letcher, S. Casey, and J. Zydlewski. 2006. Remote monitoring of fish in small streams: a unified approach using PIT tags. Fisheries 31:492–502.

Appendix VIII - Evaluating Genetic Structure among Resident and Migratory Forms of Bull Trout (*Salvelinus confluentus*) in Northeast Oregon

authored by

Kristen Homel
Phaedra Budy

Utah State University

Ecology of Freshwater Fish 2008: 17: 465–474
Printed in Malaysia · All rights reserved

ECOLOGY OF
FRESHWATER FISH

Evaluating genetic structure among resident and migratory forms of bull trout (*Salvelinus confluentus*) in Northeast Oregon

Homel K., Budy P, Pfrender ME, Whitesel TA, Mock K. Evaluating genetic structure among resident and migratory forms of bull trout (*Salvelinus confluentus*) in Northeast Oregon.
Ecology of Freshwater Fish 2008: 17: 465–474. © 2008 No claim to original US government works. Journal compilation © 2008 Blackwell Munksgaard

Abstract – Many salmonids express multiple behavioural forms within the same population, representing an evolutionary adaptation to a heterogeneous environment. For bull trout, resident and migratory forms co-occur in streams, but it is unknown whether the two forms assortatively mate. We assessed genetic differentiation between resident and migratory bull trout (using eight microsatellite loci) in the South Fork Walla Walla River. We PIT-tagged and fin-clipped bull trout and assigned individuals to behavioural subpopulations based on movement patterns. The pair-wise F_{ST} value between resident and migratory subpopulations (0.0037) was statistically insignificant, and individual-based analyses of structure using both multivariate and Bayesian approaches showed a lack of genetic structure within the population. These results have important implications for assessing population status and management; while the population may be managed as a single reproductive unit, the phenotypic variation within this population may have fitness consequences and thus merits conservation.

K. Homel[1], P. Budy[2], M. E. Pfrender[3], T. A. Whitesel[4], K. Mock[5]

[1]Department of Ecology, Montana State University, Bozeman, MT, USA, [2]USGS, Utah Cooperative Fish and Wildlife Research Unit, Department of Watershed Science, Utah State University, Logan, UT, USA, [3]Department of Biology, Utah State University, Logan, UT, USA, [4]U.S. Fish and Wildlife Service, Columbia River Fisheries Program Office, Vancouver, WA, USA, [5]Department of Wildland Resources, Utah State University, Logan, UT, USA

Key words: gene flow; bull trout; *Salvelinus;* life-history forms; microsatellites

P. Budy, USGS, Utah Cooperative Fish and Wildlife Research Unit, Department of Aquatic, Watershed, and Earth Resources, Utah State University, Logan, UT 84322, USA;
e-mail: phaedra.budy@usu.edu

Accepted for publication January 17, 2008

Introduction

Many species exhibit behavioural diversification (e.g., multiple behavioural forms in a population or niche specialization) in response to a heterogeneous and changing environment (Northcote 1992; Lichatowich 1999). One common example of this diversification is partial migration, the phenomenon wherein part of the population migrates and part remains resident (Jonsson & Jonsson 1993). Through exploitation of multiple habitat types through time, resident and migratory individuals (from a single population) disperse the risk of that population becoming extinct because of local disturbances and gain access to a greater amount of resources (Gross 1991; Northcote 1992; Lichatowich 1999; Jackson et al. 2001). While natural selection may be favouring both resident and migratory forms under different environmental scenarios (Kaitala et al. 1993), behavioural diversification does not necessarily infer genetic differentiation between behavioural forms. Rather, both forms could be maintained by a stable polymorphism (abiotic and/or biotic conditions may be favourable to the maintenance of both forms over time, Smith 1970; Leimar 2005) or be strictly because of phenotypic plasticity. From a management perspective, a population that contains reproductively isolated forms (representing different behaviours or exploiting different niches) would be managed differently than one containing a single panmictic population that displays a behavioural polymorphism.

For endangered species in particular, the genetic structure within a population (as it relates to behavioural forms) may have implications with respect to (1) definition of species or distinct population segments, (2) monitoring recovery in the target species or populations, (3) assessment of population size, and (4) maintaining connectivity and genetic diversity (US Fish and Wildlife Service, USFWS, 2004). By determining whether different behavioural forms are genetically distinct, how they interact, and how they exploit and adapt to natural environments, we can better understand how anthropogenic impacts may alter the genetic population structure, expression, or prevalence of different behavioural forms (Gross 1991; Neraas & Spruell 2001; Wofford et al. 2005), and select conservation strategies accordingly (Dunham et al. 1999).

Within the salmonids, there is evidence for several patterns of genetic population structure related to sympatric behavioural forms (Osinov 1984; Foote et al. 1989; Wood & Foote 1996; Hendry et al. 2000; Docker & Heath 2003). For example, different morphological or behavioural forms may evolve into reproductive isolation because of exploitation of different niches (arctic char *Salvelinus alpinus,* Skulason et al. 1996; Westgaard et al. 2004; but see Nordeng 1983), or different spawn times or locations (steelhead and rainbow trout *Oncorhynchus mykiss,* Zimmerman & Reeves (2000), sockeye and kokanee *O. nerka*, Foote et al. 1989; Taylor et al. 1996; Wood & Foote 1996). Conversely, a population may exhibit behavioural diversification, yet comprise a single breeding population (e.g., brook char *S. fontinalis*, McLaughlin 2001). At a broad spatial scale, it is possible that behavioural polymorphism (e.g., migration distance, home range size, and consistency in expressing a single behavioural form over time) may differ between populations (Olsson et al. 2006). Furthermore, the degree that different behavioural forms interbreed within a population may vary within a single species (e.g., steelhead and rainbow trout, Docker & Heath 2003; Narum et al. 2004; McPhee et al. 2007; lake whitefish *Coregonus clupeaformis*, Pigeon et al. 2006), with potentially different selection pressures acting on each form (Kaitala et al. 1993; McDowall 2001).

Similar to other salmonids, bull trout (*Salvelinus confluentus*) exhibit a spectrum of behavioural and breeding strategies. Bull trout are a species of char found in the Pacific Northwest, and throughout their range they exhibit resident and migratory forms (i.e., adfluvial, anadromous, and fluvial) within the same population (Rieman & Dunham 2000). Unlike Pacific salmon that demonstrate discrete behavioural forms (e.g., anadromous and adfluvial), the difference between bull trout life-history forms is less distinct, particularly for stream-resident and fluvial fish. Adult bull trout commence spawning migrations into tributaries in the late summer (McPhail & Murray 1979; Shepard et al. 1984). Both stream-resident and migratory bull trout spawn in the fall, and may spawn every year or every other year (Rieman & McIntyre 1993). As such, a single breeding population may be comprised of 4+ generations and potentially multiple behavioural forms (Rieman & McIntyre 1993). Once spawning is complete, fluvial and adfluvial bull trout migrate to over-wintering grounds (Fraley & Shepard 1989) and resident bull trout exhibit limited movement (Jakober et al. 1998). Eggs develop over the winter and fry emerge from early April through May (Shepard et al. 1984). Fry are closely associated with the substrate for an extended period of time (McPhail & Murray 1979). In the spring, peak flows may flush young-of-year bull trout downstream (Downs et al. 2006), but peak first-time outmigration of juveniles occurs in August (Homel and Budy in press). Migratory juvenile and subadult bull trout inhabit larger more productive rivers or lakes for several years before returning to spawn (Shepard et al. 1984; Fraley & Shepard 1989). While fluvial or adfluvial bull trout may exhibit migrations up to 250 km in distance (Fraley & Shepard 1989; Swanberg 1997; Baxter 2002), there is no consistent demarcation based on distance moved that distinguishes the movements of migratory fish from those of resident fish. Furthermore, the only known morphological distinction between resident and migratory bull trout is based on body size after several migrations; migratory fish often attain sizes >600 mm total length (TL) as a result of migrating to larger, more productive streams, while resident fish typically grow to ~300 mm TL (Fraley & Shepard 1989). Writ large, these complicated behavioural, reproductive, and morphological elements confound the definition of specific life-history forms, and the interpretation of the associated genetic structure within bull trout populations.

The genetic structure of bull trout across their range reflects their post-glacial dispersal and subsequent isolation (as a result of habitat fragmentation). Bull trout typically exhibit low genetic variation within populations (e.g., out of 65 bull trout populations examined by Spruell et al. 2003, 56 have $H_S < 0.299$). However, among population structure is typically quite high (Leary et al. 1993; Taylor et al. 1999; Spruell et al. 1999; Kanda & Allendorf 2001; Spruell et al. 2003; Costello et al. 2003; Reiss 2003). For example, Spruell et al. (2003) reported F_{ST} values of 0.635 between two coastal populations of bull trout, and Costello et al. (2003) reported an F_{ST} of 0.40 for two populations in the Kootenay River. Throughout their range, bull trout are typically associated with specific habitat conditions including cold, clean water, and structurally complex habitat (Rieman & McIntyre 1993). Many factors, such as loss of connectivity, habitat degradation, and introduction of non-natives, have contributed to the range-wide decline of bull trout, particularly of the migratory form (Rieman & McIntyre 1993). In response to these threats, bull trout were listed as threatened in the contiguous United States in 1999 (Department of the Interior, U. S. Fish and Wildlife Service 1999). While genetic structure among many bull trout populations has been assessed for conservation planning (e.g., Leary et al. 1993; Spruell et al. 2003; Whiteley et al. 2006), little is known about whether behavioural variability results in patterns of non-random mating between resident and migratory fish within a population. In addition, despite the lack of a clear demarcation between the behavioural categories of 'resident' and 'migratory', differences between these life-history forms are important for assessing the effectiveness of actions directed at recovery (e.g., reconnecting migratory corridors); and, in addition to other criteria, recovery objectives require preserving the diversity of behaviours bull trout express (e.g., resident or migratory forms, emigration age; USFWS, 2002).

In this study, our goal was to evaluate whether variability in behavioural patterns was associated with assortative mating between behavioural forms. Characterization of this genetic structure is important for determining whether this population should be managed as a single panmictic breeding population (that contains behavioural variability), or as distinct populations with genetically distinct behavioural groups. Our previous analyses of the movement patterns within this population demonstrated a continuum of movement across space and time, indicating that movement distance and timing alone were insufficient to define an individuals' life-history strategy as resident or migratory (Homel and Budy in press). However, given the broad array of behaviours that a single life-history form may express, it is insufficient to use movement distance and timing alone as metrics to define life-history forms. Instead, we described behavioural patterns using a functional definition of migration (i.e., migration is annual directed, purposeful movement between distinct habitat types, e.g., Dingle 1996), and determined that our population contains both migratory and resident fish. Those fish exiting the study area were defined as migratory as they are making a directed, distinct shift in habitat types (described in the study area), and many of those fish ultimately completed multiple spawning migrations (further described in the Methods). Therefore, the specific objective of this study was to evaluate whether resident and migratory fish exhibited assortative mating, as demonstrated by genetic differentiation.

Methods

Study area

The South Fork Walla Walla River (SFWW) originates at elevations near 1800 m in the Blue Mountains of Northeast Oregon, confluences with the North Fork Walla Walla near the town of Milton-Freewater, and flows into the Columbia River upstream of McNary Dam (Fig. 1). We selected this river as our study area for two reasons. First, it was known to contain a relatively large population of bull trout (8–12,000 fish, Al-Chokhachy 2006), previously described as containing both resident and migratory forms (Buchanan et al. 1997). Second, the SFWW and main-stem Walla Walla include a range of habitat types from pristine to highly degraded. Within the SFWW, the habitat condition is generally of high quality, with few forest

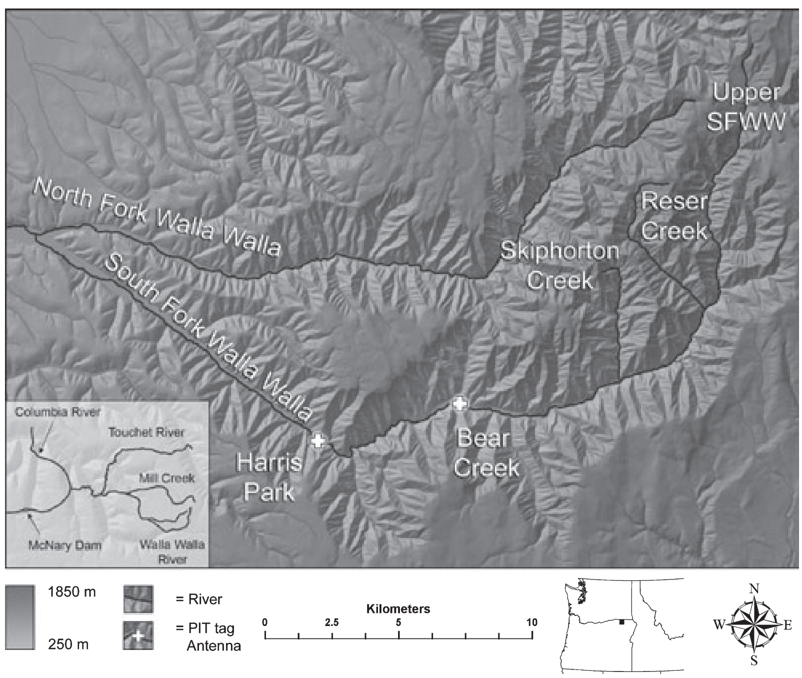

Fig. 1. Map of the South Fork Walla Walla River study area with locations of passive antennae and tributaries marked.

related impacts and limited recreational activity that would impact the stream corridor (particularly in the headwaters, Buchanan et al. 1997). Downstream of the confluence with the North Fork Walla Walla River, the habitat conditions degrade with respect to increased water temperature, simplified channel and habitat, impoundments, and irrigation withdrawals that severely deplete flow (Buchanan et al. 1997), and act as a seasonal migration barrier. Skiphorton Creek and Reser Creek are the major tributaries to the SFWW and most observed spawning activity occurs in proximity to (or within) these pristine tributaries.

Within the Walla Walla Basin watershed, the SFWW, Mill Creek, and the Touchet River all contain populations of bull trout (Buchanan et al. 1997; Fig. 1). According to Oregon and Washington criteria, population status in Mill Creek is 'of special concern' (Buchanan et al. 1997) or alternatively 'healthy' (WDFW, 1997), the Touchet River status is considered 'unknown' (WDFW, 1997), and the SFWW population status is 'low risk' (Buchanan et al. 1997); all subpopulations are listed as 'depressed' by the USFWS (USFWS 2004). Although the SFWW bull trout population is of low extinction risk, irrigation withdrawals and diversion dams along the Walla Walla River prevent interaction (from Spring until Fall) between SFWW bull trout and the bull trout populations from Touchet River and Mill Creek. It is thought that historically bull trout had access to, and used, the Columbia River (Buchanan et al. 1997), but recent telemetry studies (Mahoney 2001, 2002) have not confirmed contemporary use of the Columbia River, and PIT-tagged fish from the SFWW have not been detected at antenna located in Mill Creek or the Columbia (Homel and Budy in press).

Study design phase I: mark-recapture study

This genetics study is a component of a broader effort to gather comprehensive population assessment data on the SFWW, critical for recovery planning (Al-Chokhachy et al. 2005; Al-Chokhachy 2006). For the first phase of this broader effort, we conducted a large mark-recapture study in the main-stem of the SFWW during July and August from 2002–2005 (Al-Chokhachy et al. in press). The study area extended from Harris Park to the confluence with Reser Creek (a distance of 21 stream km, Fig. 1), and was divided into 103 adjacent, 200 meter reaches (Harris Park is reach 1). Each year we systematically sampled every fifth reach (further described in Al-Chokhachy et al. in press), which entailed: (1) capturing bull trout, (2) implanting passive integrated transponder tags (PIT tags) into the ventral cavity of all bull trout >120 mm TL, and (3) removing a 2–5 mm^2 fin clip from the anal fin. We stored fin clips in 100% ethanol until they were processed by a laboratory. From 2002–2005, we captured, tagged, and fin-clipped >1300 bull trout from the main-stem SFWW.

Study design phase II: defining behaviour

In the second phase of this study, we used fish recapture data (from the mark-recapture study), in combination with detection of tagged fish at stationary antennae, to determine the movement patterns and behavioural strategy of individuals in our population (Homel and Budy in press). In 2002, we installed two passive PIT tag antennae in the SFWW (one at Harris Park, and one at Bear Creek, Fig. 1), to record the individual tag number of marked fish that passed through the antenna loop. The antenna at Harris Park was located at a transition point in habitat quality; upstream of Harris Park, the river exhibits complex braiding, in-stream structure, and temperatures within the thermal tolerance of bull trout. Downstream of Harris Park, a paved road follows the course of the river, the river is simplified and/or channelized, and stream temperatures reach or exceed the thermal tolerance of bull trout. Conditions progressively deteriorate downstream of the confluence with the North Fork Walla Walla River. Given this distinct habitat transition, fish moving downstream past the Harris Park antenna would be considered migratory fish.

Based on our annual mark-recapture sampling and antenna detections in the study area, we defined two putative behavioural subpopulations for genetic analysis: (1) 'known migrants,' and (2) 'likely residents.' 'Known migratory' fish were those fish that exhibited a downstream migration, exiting the study area at Harris Park (N = 304). In converse, 'likely resident' fish were fish that were never detected at either antenna, and were recaptured annually in the same or adjacent stream reach (N = 83). As a result of variable antenna detection probability and efficiency during select periods of time in 2003 and 2004 (50–100% resulting from power outages), we could not define a fish as resident, but rather as 'likely resident' given the possibility of a missed migration detection at the Harris Park antenna. However, to mitigate the potential effects of missed detections at the Harris Park antenna on the identification of an individuals' behavioural strategy, we removed all samples from our database that were only detected at the Bear Creek antenna, as these fish could be either resident fish near the antenna, or migratory fish that were not detected at the Harris Park antenna. From 2002–2006, no likely-resident fish were ever detected at either antenna, suggesting that our behavioural definitions were appropriate. These two behavioural classes were used for all subsequent analysis.

Study design phase III: genetic structure

Finally, for this current genetics study, we combined data on the behavioural strategy of individuals with a microsatellite analysis to evaluate behaviourally based neutral genetic structure within one large stream population. From the initial phase of this study, we had >1300 fin clips available to us for genetic analysis. These fin clips were from fish >120 mm TL, representing multiple size classes and both resident and migratory behavioural patterns, and were collected throughout the river from 2002–2005. As we were interested in identifying genetic structure within the population as it relates to behavioural form, we selected samples for which we had described a behavioural strategy. From our pool of 304 migratory bull trout, and 83 likely-resident bull trout, we randomly selected 109 samples for genotyping (migratory $N = 57$, mean TL at capture = 354 mm, range TL = 122–720 mm; likely resident $N = 52$, mean TL at capture = 222 mm, range TL = 139–342 mm).

Genetic processing conditions

We extracted total genomic DNA from 109 fin clips using a 'salting out' protocol (Sunnucks & Hales 1996). We used PCR to amplify 11 microsatellite loci from these templates following the reaction conditions described by the original authors and summarized by the USFWS Abernathy Fish Technology Center (AFTC). These loci were members of a core set of standard bull trout loci, with the forward primers fluorescently labelled (6FAM or HEX): Omm1128 HEX, Sfo18 HEX (Angers et al. 1995), Sco200 6FAM, Sco202 HEX, Sco216 6FAM, Sco220 HEX (DeHaan & Ardren 2005), Sma22 HEX (Crane et al. 2004), Sco102 6FAM, Sco105 6FAM, Sco109 6FAM, Sco110 6FAM (Shaklee, WDFW Olympia, WA, summarized by USFWS AFTC 2003). We conducted PCR using approximately 20 nanograms of sample DNA with a total reaction volume of 15 μl. We assessed the PCR products on a 1.0% agarose gel. Diluted PCR products were run on an ABI3730 DNA analyzer (Applied Biosystems, Inc.) with a LIZ3730 size standard, analyzed using Genescan Software, and scored using GeneMapper software (Applied Biosystems, Inc.). Mention of brand names does not imply endorsement. Although we ran all PCR reactions separately, we combined (multiplexed) PCR products from the following combinations of loci for runs on the ABI3730 DNA analyzer: Sco216 and Sco202, Sco200 and Omm1128, and Sco105 and Sco220. As a quality control measure, we ran replicates of PCR products from a small proportion of the samples on individual lanes to assure that multiplexing did not result in mis-scoring.

Data analysis

We evaluated the null hypothesis of random mating between resident and migratory fish using a combination of complimentary statistical methods. First, we assessed the microsatellite loci for evidence of linkage disequilibrium and Hardy-Weinberg disequilibrium. Next, we compared resident and migratory fish with respect to allelic diversity (A, corrected for unequal sample size with rarefaction), multi-locus expected heterozygosity (He), Fisher's exact test for genic differentiation (comparison of allele frequencies across loci), and F_{ST}, using GENEPOP (Version 3.4, Raymond & Rousset 1995; options 1–6). Next, we conducted a factorial correspondence analysis (FCA) to depict potential clustering of individuals within each behavioural group using the program Genetix (Version 4.05, Belkhir et al. 1996–2004). Finally, we evaluated the genotypes of all samples without *a priori* assumptions about their putative subpopulation of origin to determine the most probable number of subpopulations (K) within the total population using the program Structure (Version 2.1, Pritchard et al. 2000). We selected a burn in length of 100,000 replications, a run length of 100,000, and ran 100 replications using 5 K values (1–5).

Results

Before testing for HWE, we assessed whether our microsatellite loci were polymorphic and in linkage disequilibrium. Two loci, Sfo18 and Sco102, were monomorphic in our samples, and Sco110 was the same locus as Sco216 (based on identical primer sequences), so we removed Sfo18, Sco102, and Sco110 for all subsequent analyses. We found no evidence of linkage disequilibrium between any of the remaining 8 loci ($P > 0.05$). These 8 loci were polymorphic in both putative subpopulations with an observed number of alleles ranging from 3 to 21 (Table 1). Both putative subpopulations, and the entire population as a whole, conformed to expected

Table 1. Total number of observed alleles and allele size range per locus, across all samples and for each subpopulation.

	Total		Resident		Migratory	
Locus	# Alleles	Size range	# Alleles	Size range	# Alleles	Size range
Omm1128	9	275–354	7	275–354	8	275–354
Sco200	7	133–157	6	133–153	7	133–157
Sco202	3	127–135	3	127–135	3	127–135
Sco216	5	239–263	4	239–263	4	239–255
Sco109	11	266–387	10	266–387	8	266–387
Sco105	6	164–208	5	164–208	6	164–208
Sco220	7	299–328	6	299–328	5	299–319
Sma22	21	204–283	17	204–283	18	204–279

Hardy-Weinberg genotypic proportions at all loci ($P = 0.28$).

We evaluated the potential for non-random mating between resident and migratory fish in the SFWW using several statistical tests, all of which failed to demonstrate neutral genetic differentiation between behavioural groups. Allelic diversity (mean number of alleles across loci per subpopulation, with the larger migratory sample size rarefied to the smaller resident sample size) was similar for resident and migratory fish (7.25 and 7.38 respectively). Multi-locus expected heterozygosity (He) and observed heterozygosity (Ho) were also similar for each subpopulation (He = 0.35 and 0.34 respectively, Ho = 0.34 and 0.33 respectively). A pair-wise comparison of allele frequencies across loci was not significantly different for resident and migratory subpopulations according to Fisher's exact test for genic differentiation ($P = 0.85$). This lack of structure between groups was further corroborated by an insignificant pair-wise F_{ST} value of 0.0037 and a similarly low combined F_{IS} value of 0.04.

Based on an individual-based FCA of genetic variation across behaviourally defined groups, we found a complete absence of multidimensional clustering (i.e., genetic structure). The first four principal components in the FCA each explained about 4% of the variation between samples (with the first component explaining 4.85%); thus, a single component was sufficient to describe the variation in our sample. Our initial FCA depicted three outliers for which we could determine no common denominator, although each contained a unique rare allele. We removed these three outliers from the analysis and still found no clustering in our FCA plot based on behavioural form or other potential unidentified structure (Fig. 2). Overall, the similarity in allele frequencies, the low

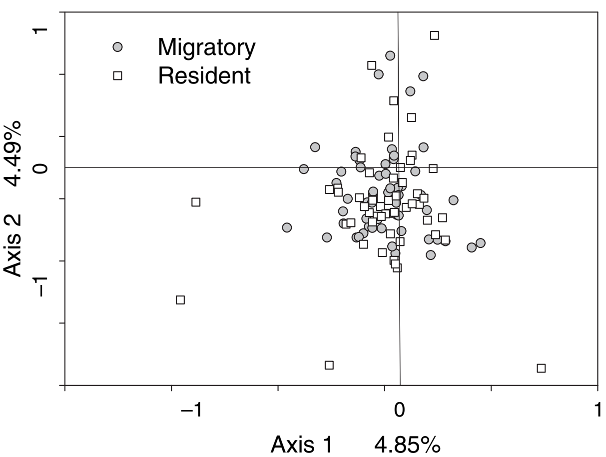

Fig. 2. Factorial correspondence analysis of the multidimensional genotype of 109 resident and migratory samples. Each putative subpopulation is represented by a unique symbol.

F_{ST} values, and the lack of clustering in the FCA plot suggest that resident and migratory fish comprise a single panmictic breeding population, although it is possible that the number of loci or the sample size were inadequate to detect a very low level of assortative mating.

Our Bayesian analysis of potential population structure (ranging from 1 panmictic population to five discrete subpopulations, $K = 1\text{-}5$) using the program Structure demonstrated complete panmixia; all individuals were assigned an equal probability of belonging to each subpopulation, irrespective of the K-value selected, but $K = 1$ had the highest probability. Pair-wise F_{ST} values for all K-groups were low (all < 0.05), indicating that the most likely structure for the population is a single panmictic breeding population.

Discussion

In order to better understand the relationship between behavioural variation and neutral genetic population structure, we evaluated the genotypes of 109 individuals, representing two putative behavioural subpopulations from the SFWW. Based on our genetic results, we failed to reject the null hypotheses that resident and migratory fish comprise a panmictic breeding population.

Our multiple tests for subpopulation structure all indicated that the SFWW bull trout population is panmictic with respect to our defined behavioural groups. While this represents the first such study of interbreeding between behavioural forms in bull trout, similar results have been observed (with varying degrees of interbreeding) for co-occurring arctic char morphs (in a transplant experiment in southern Norway, Nordeng 1983), brook trout behavioural forms ($F_{ST} = 0.0007$ in 2000 and $F_{ST} = 0.012$ in 2001, Theriault et al. 2007), and brown trout (*Salmo trutta*) behavioural forms (Charles et al. 2005). However, in contrast to Nordeng (1983), Westgaard et al. (2004) found significant reproductive isolation between co-occurring arctic char morphs in northern Norway ($F_{ST} = 0.032$). These results suggest that the degree of interbreeding between forms may be mediated by environmental factors or landscape level processes (McLaughlin 2001). Given the variability observed in other salmonids species, it is possible that, across the range of bull trout, the degree of interbreeding between behavioural forms within a population may also vary.

We suggest two possible mechanisms by which interbreeding between forms may occur: (1) both forms may significantly overlap in their selection of spawn sites, resulting in unintentional interbreeding, and (2) small resident males may exhibit the 'sneaking' tactic on large migratory females. In our study of bull trout movement patterns in the SFWW, we observed that resident and migratory fish co-occurred, and that resident fish moved up to 14 km within the study area (during the spawning season, Homel and Budy in press). Previous redd counts in the SFWW by the Oregon Department of Fish and Wildlife identified that the majority of spawning activity occurred from approximately 4 km above Bear Creek, to above Reser Creek, including the Skiphorton and Reser Creek tributaries (Buchanan et al. 1997). However, Al-Chokhachy et al. (2005) demonstrated that most of these redds likely belonged to larger migratory fish. Despite an imprecise knowledge in the spawning location of resident fish, the ubiquitous spawning location of migratory fish would suggest spatial overlap. Furthermore, our data on fish movement suggests that resident and migratory fish are moving upstream to spawning areas at the same time of year (Homel and Budy in press). Potentially, this temporal and spatial overlap in spawning could result in significant interbreeding, independent of mate selection. For example, Docker & Heath (2003) documented gene flow between co-occurring resident rainbow trout and anadromous steelhead, while Narum et al. (2004) detected genetic divergence between those same forms as a result of differing spawn site selection.

A second possible mechanism for interbreeding between forms is that smaller resident males may be selecting larger migratory females as mates through exhibiting a 'sneaking' tactic. While female fish have been shown to assortatively mate with similarly sized male fish (e.g., Japanese char, *Salvelinus leucomaensis*, Maekawa et al. 1994; sockeye salmon, Foote 1989), male fish may exhibit a sneaking tactic, and breed with significantly larger, more fecund female fish (Gross 1991; Groot & Margolis 1991). As a result of that tactic, resident males would be able to increase their fitness relative to breeding with smaller, less fecund resident females. Within the salmonids, there are numerous examples of this tactic. Theriault et al. (2007) noted that gene flow between resident and anadromous brook trout was mediated by resident males mating with both resident and anadromous females. Wood & Foote (1996) documented a similar pattern between male kokanee salmon and female sockeye salmon. Sneaker males have also been documented in coho salmon (*Oncorhynchus kisutch*, Gross 1991) and potentially in rainbow trout (mating with steelhead, Zimmerman & Reeves 2000; Narum et al. 2004). Although not expressly observed in SFWW spawning surveys, it is possible that bull trout may express this sneaking tactic as well.

In our assessment of behaviourally based genetic population structure, there were two potential, albeit minor, limitations to our study: (1) an inability to sample fish smaller than 120 mm TL, and (2) low genetic variability within the population. We only collected fin clips from fish larger than 120 mm TL as this was the smallest size that we could tag, and we needed movement information to analyze genetic structure related to behaviour. However, bull trout are intergenerational breeders, and we do not believe that our failure to sample fish smaller than 120 mm TL resulted in any bias to our results. The second potential limitation to our study was that we detected a low level of genetic variation in our population which could make it difficult to detect subpopulation structure. However, other bull trout populations have expressed similar levels of within-population genetic variation (e.g., bull trout populations in the Yakima River Basin had H_O values ranging from 0.21–0.45 across six microsatellite loci, independent of population size, Reiss 2003). Furthermore, as we used metrics to assess genetic population structure that were relative to the total amount of genetic variation in our population (e.g., F_{ST}), we do not believe that the low genetic variation in our population would have precluded detection of genetic differences between behavioural forms, were they present. While it is possible that the low variation we detected, in combination with our sample size, could have resulted in a type II error, this error would only have precluded the detection of a very low level of assortative mating between resident and migratory fish, and would not otherwise have influenced the interpretation of our results.

Our study represents the first genetic comparison of behavioural forms in bull trout, and was unique in that our *a priori* definition of behavioural groups was based on extensive monitoring of the movement patterns of >1500 fish (Homel and Budy in press). By understanding the continuous movement patterns of our fish, we were able to identify a potential behaviour-related cause for the lack of genetic structure we observed. This pairing of movement studies (via tagging) and genetic analysis improved our fundamental understanding of the evolutionary and ecological interactions between behavioural forms in this population, and how that interaction may shape patterns of random mating between behavioural groups.

In managing the sympatric behavioural forms of an endangered species, it is important to consider limitations in our understanding of behavioural forms, particularly in the case of random mating. The presence of gene flow between sympatric behavioural forms does not necessitate a lack of adaptive variation between these forms, provided that selective pressure for each form outweighs gene flow (Rice & Hostert 1993). However, this common pattern of behavioural diversification and genetic similarity (at neutral markers) reflects our limited understanding of the mechanisms that determine behavioural strategy. In this study, resident and fluvial bull trout in the SFWW comprise a single panmictic breeding population. While we were unable to reject the null hypothesis of panmixia at the level of neutral markers for this population, under different habitat conditions, different connectivity scenarios, greater behavioural differentiation between resident and migratory fish, or over a longer time scale, there is potential that a different genetic pattern could exist. Furthermore, since measures of neutral molecular- and quantitative-genetic variation (Pfrender et al. 2000) and population subdivision (Lynch et al. 1999) are often disconnected, a study of quantitative genetic variation (heritability, h^2) and subdivision (Q_{ST}) based on the behavioural morphs would enhance the context of our conclusions.

Management implications

The potential for behavioural groups within a population to randomly mate presents an interesting opportunity for conservation of bull trout. Rather than create specific recovery goals for each life-history form, our research suggests that management should focus on maintaining phenotypic variation within the population. While we do not yet understand the mechanism driving the adoption of a life-history tactic in bull trout, we do know that multiple life-history forms within a population increase that population's resistance to extirpation (via occupation of multiple habitat patches through time, Gross 1991). Furthermore, both resident and migratory forms fulfill unique ecological functions. Migratory fish make an important demographic contribution to the population as a result of the increased fecundity associated with their larger body size (Al-Chokhachy 2006). Conversely, resident fish fill a predatory niche in the natal stream throughout the year, and potentially could bolster migratory populations via random mating, if behavioural forms can give rise to one another (as suggested in bull trout by Dunham et al. 2003; and demonstrated in sympatric sockeye and kokanee salmon, Taylor et al. 1996). Given the importance of both resident and migratory forms, management must focus on (1) preserving local resident populations (that display local adaptations), and (2) addressing limiting factors for both resident and migratory bull trout.

Acknowledgements

This research was funded by the US Fish and Wildlife Service Columbia River Fisheries Program Office, the US Geological Survey/Utah Cooperative Fish and Wildlife Research Unit, and the Vice President for Research at Utah State University (fellowship for Kris Homel). We would like to acknowledge Howard Schaller, Darren Gallion, Don Anglin, Paul Sankovich, Courtney Newlon, Marshall Barrows, Tim Bailey, Brian Mahoney, and Bob Bower for provision of data, assistance, and guidance. All the genetic data used in this study were processed in the Molecular Ecology laboratory in the Utah State University Department of Wildland Resources. We thank Lee Bjerregaard for his technical assistance with the genetic processing. The US Fish and Wildlife Service Abernathy Fish Technology Center provided genetic results from a pilot study, which contributed to the development of our study design. Dale and Judy Johnson, John Ehart, George Ehmer, and Dwayne Wright provided considerable help with field logistics, and our numerous technicians all contributed to the success of this project. We thank Susan Durham for her statistical insight in the analysis of this study, and Patty Kuhns for technical editing. We would especially like to thank Gary Thiede and Robert Al-Chokhachy for substantial planning, coordinating, logistical, and design contributions to this study.

References

Al-Chokhachy, R.2006. An Assessment of the Dynamics and Limiting Factors of a Fluvial Bull Trout Population. Ph.D. thesis. Logan, UT: Utah State University.

Al-Chokhachy, R., Budy, P. & Schaller, H. 2005. Understanding the significance of redd counts: a comparison between two methods for estimating the abundance of and monitoring bull trout populations. North American Journal of Fisheries Management 25: 1505–1512.

Angers, B., Bernatchez, L., Angers, A. & Desgroseillers, L. 1995. Specific microsatellite loci for brook char reveal strong population subdivision on a microgeographic scale. Journal of Fish Biology 47 (Suppl. A): 177–185.

Baxter, C.V. 2002Fish Movement and Assemblage Dynamics in a Pacific Northwest Riverscape. Ph.D. thesis. Corvallis, Oregon: Oregon State University.

Belkhir, K., Borsa, P., Chikhi, L., Raufaste, N. & Bonhomme, F. 1996–2004. GENETIX 4.05, Logiciel Sous Windows TM Pour la Génétique des Populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, France: Université de Montpellier II, Montpellier.

Buchanan, D.V., Hanson, M.L. & Hooton, R.M. 1997. Status of Oregon's Bull Trout. Portland, Oregon: Oregon Department of Fish and Wildlife.

Costello, A. B., Downs, T. E., Pollard, S. M., Pacas, C. J. & Taylor, E. B. 2003. The influence of history and contemporary stream hydrology on the evolution of genetic diversity within species: an examination of microsatellite DNA variation in bull trout, *Salvelinus confluentus* (pisces: *Salmonidae*). Evolution 57: 328–344.

Crane, P.A., Lewis, C.J., Kretschmer, E.J., Miller, S.J., Spearman, W.J., DeCicco, A.L., Lisac, M.J. & Wenberg, J.K. 2004. Characterization and inheritance of seven microsatellite loci from Dolly Varden, *Salvelinus malma*, and cross-species amplification in Arctic char, *S. alpinus*. Conservation Genetics 5: 737–741.

DeHaan, P.W. & Ardren, W.R. 2005. Characterization of 20 highly variable tetranucleotide microsatellite loci for bull trout (*Salvelinus confluentus*) and cross amplification in other *Salvelinus* species. Molecular Ecology Notes 5: 582–585.

Department of the Interior, U. S. Fish and Wildlife Service. 1999. Determination of Threatened Status for Bull Trout in the Coterminous United States; Final Rule Notice of Intent to Prepare a Proposed Special Rule Pursuant to Section 4(d) of the Endangered Species Act for the Bull Trout; Proposed Rule. Federal Register November 1, Vol. 64, No. 210. Rules and Regulations pg. 58909–58933. Office of the Federal Register, National Archives Records Administration, Washington D.C.

Dingle, H. 1996. Migration: The Biology of Life on the Move. Oxford, UK: Oxford University Press.

Docker, M.F. & Heath, D.D. 2003. Genetic comparisons between sympatric anadromous steelhead and freshwater resident rainbow trout in British Columbia, Canada. Conservation Genetics 4: 227–231.

Downs, C.C., Horan, D., Morgan-Harris, E. & Jakubrowski, R. 2006. Spawning Demographics and Juvenile Dispersal of an Adfluvial Bull Trout Population in Trestle Creek, Idaho. North American Journal of Fisheries Management 26: 190–200.

Dunham, J., Peacock, M., Tracy, C.R., Nielsen, J. & Vinyard, G. 1999. Assessing extinction risk: integrating genetic information. Conservation Ecology [online] 3(1): 2 Available from the Internet. URL:http://www.ecologyandsociety.org/vol3/iss1/art2/

Dunham, J., Young, M.K., Gresswell, R.E. & Rieman, B.E. 2003. Effects of fire on fish populations: landscape perspectives on persistence of native fishes and nonnative fish invasions. Forest Ecology and Management 178: 183–196

Foote, C.J. 1989. Female mate preference in Pacific salmon. Animal Behaviour 38: 721–723.

Foote, C.J., Wood, C.C. & Withler, R.E. 1989. Biochemical genetic comparison of sockeye salmon and kokanee, the anadromous and nonanadromous forms of *Oncorhynchus nerka*. Behavior 106: 43–62.

Fraley, J. J. & Shepard, B. B. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Science 63: 133–143.

Groot, C. & Margolis, L. 1991. Pacific Salmon Life Histories. Vancouver, B.C., Canada: UBC Press.

Gross, M.R. 1991. Salmon breeding behavior and life history evolution in changing environments. Ecology 72: 1180–1186.

Hendry, A.P., Wenburg, J.K., Bentzen, P., Volk, E.C. & Quinn, T.P. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. Science 290: 516–518.

Jackson, D.A., Peres-Neto, P.R. & Olden, J.D. 2001. What controls who is where in freshwater communities- the role of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58: 157–170.

Jakober, M.J., McMahon, T.E., Thurow, R.F. & Clancy, C.G. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society 127: 223–235.

Jonsson, B. & Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3: 348–365.

Kaitala, A., Kaitala, V. & Lundberg, P. 1993. A theory of partial migration. The American Naturalist 142: 59–81.

Kanda, N. & Allendorf, F. W. 2001. Genetic population structure of bull trout from the Flathead River Basin as shown by microsatellites and mitochondrial DNA markers. Transactions of the American Fisheries Society 130: 92–106.

Charles, K., Guyomard, R., Hoyheim, B., Ombredane, D. & Baglinièr, J. 2005. Lack of genetic differentiation between anadromous and resident sympatric brown trout (*Salmo trutta*) in a Normandy population. Aquatic Living Resources 18: 65–69.

Leary, R. F., Allendorf, F. W. & Forbes, S. H. 1993. Conservation genetics of bull trout in the Columbia and Klamath River drainages. Conservation Biology 7: 856–865

Leimar, O. 2005. The evolution of phenotypic polymorphism: randomized strategies versus evolutionary branching. The American Naturalist 165: 669–681.

Lichatowich, J. 1999. Salmon Without Rivers: A History of the Pacific Salmon Crisis. Washington D.C.: Island Press.

Lynch, M., Pfrender, M.E., Spitze, K., Lehman, N., Allen, D., Hicks, J., Latta, L., Ottene, M., Bogues, F. & Colbourne, J. 1999. The quantitative and molecular genetic architecture of a subdivided species. Evolution 53: 100–110.

Maekawa, K., Nakano, S. & Yamamoto, S. 1994. Spawning behaviour and size- assortative mating of Japanese charr in an artificial lake-inlet stream system. Environmental Biology of Fishes 39: 109–117.

Mahoney, B. 2002. Walla Walla basin summer steelhead and bull trout radio telemetry project: 2002 Annual Report to the Bonneville Power Administration. Confederated Tribes of the Umatilla Indian Reservation, Milton-Freewater, OR.

Mahoney, B. 2001. Walla Walla basin summer steelhead and bull trout radio telemetry project: 2001 Annual Report to the Bonneville Power Administration. Confederated Tribes of the Umatilla Indian Reservation, Milton-Freewater, OR.

McDowall, R.M. 2001. Anadromy and homing: two life history traits with adaptive synergy in salmonid fishes?. Fish and Fisheries 2: 78–85.

McLaughlin, R.L. 2001. Behavioral diversification in brook charr: adaptive responses to local conditions. The Journal of Animal Ecology 70: 325–337.

McPhail, J.D. & Murray, C.B. 1979. The Early Life-History and Ecology of Dolly Varden (Salvelinus Malma) in the Upper Arrow Lakes. Vancouver, BC: University of British Columbia, Department of Zoology and Institute of Animal Resources . 113P.

McPhee, M.V., Utter, F., Stanford, J.A., Kuzishchin, K.V., Savvaitova, K.A., Pavlov, D.S. & Allendorf, F.W. 2007. Population structure and partial anadromy in *Oncorhynchus mykiss* from Kamchatka: relevance for conservation strategies around the Pacific Rim. Ecology of Freshwater Fish 16: 539–547.

Narum, S. R., Contor, C., Talbot, A. & Powell, M. S. 2004. Genetic divergence of sympatric resident and anadromous forms of *Oncorhynchus mykiss* in the Walla Walla River, U.S.A. Journal of Fish Biology 65: 471–488.

Neraas, L. P. & Spruell, P. 2001. Fragmentation of riverine systems: the genetic effects of dams on bull trout (*Salvelinus confluentus*) in the Clark Fork River system. Molecular Ecology 10: 1153–1164.

Nordeng, H. 1983. Solution to the "char problem" based on Arctic char (*Salvelinus alpinus*) in Norway. Canadian Journal of Fisheries and Aquatic Sciences 40: 1372–1387.

Northcote, R.G. 1992. Migration and residency in stream salmonids- some ecological considerations and evolutionary consequences. Nordic Journal of Freshwater Research 67: 5–17.

Olsson, I.C., Greenberg, L. A., Bergman, E. & Wysujack, K. 2006. Environmentally induced migration: the importance of food. Ecology Letters 9: 645–651.

Osinov, A.G. 1984. Zoogeographical origins of brown trout, *Salmo trutta* (Salmonidae): data from biochemical genetic markers. Journal of Ichthyology 24: 10–23.

Pfrender, M.E., Spitze, K., Hicks, J., Morgan, K., Latta, L. & Lynch, M. 2000. Lack of concordance between genetic diversity estimates at the molecular and quantitative-trait levels. Conservation Genetics 1: 263–269.

Pigeon, D., Chouinard, A. & Bernatchez, L. 2006. Multiple modes of speciation involved in the parallel evolution of sympatric morphotypes of lake whitefish (*Coregonus clupeaformis, Salmonidae*). Evolution 51: 196–205.

Pritchard, J. K., Stephens, M. & Donnelly, P. 2000. Inference of population structure using multilocus genotype data. Genetics 155: 945–959.

Raymond, M. & Rousset, F. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity, 86: 248–249. GENEPOP on the web version 3.4 stable URL: http://wbiomed.curtin.edu.au/genepop/

Reiss, Y. 2003. Genetic Variability Within Bull Trout (Salvelinus Confluentus) Populations in the Yakima River Basin. Masters thesis, Washington: Central Washington University.

Rice, W.R. & Hostert, E.E. 1993. Laboratory experiments on speciation: What have we learned in 40 years? Evolution 47: 1637–1653.

Rieman, B.E. & Dunham, J.B. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. Ecology of Freshwater Fish 9: 51–64.

Rieman, B.E. & McIntyre, J.D.1993. Demographic and Habitat Requirements for Conservation of Bull Trout. General Technical Report INT-302. U.S. Forest Service, Intermountain Research Station, Ogden, UT.

Shaklee, J. 2003. In Washington Department of Fish and Wildlife Annual Report 2003: 191–207. Longview, WA. Sequences available online at stable URL: http://www.usbr.gov/pn/programs/srao_misc/bulltrout/reports/2003-annualreport-burnspaiute.pdf

Shepard, B., Pratt, K. & Graham, P. 1984. Life Histories of Westslope Cutthroat and Bull Trout in the Upper Flathead River Basin, Montana. Kalispell, MT: Montana Department of Fish, Wildlife, and Parks. 85pp.

Skulason, S., Snorrason, S.S., Noakes, D.L.G. & Ferguson, M.M. 1996. Genetic basis of life history variations among sympatric morphs of Arctic char, *Salvelinus alpinus*. Canadian Journal of Fisheries and Aquatic Sciences 53: 1807–1813.

Smith, J.M. 1970. Genetic polymorphism in a varied environment. The American Naturalist 104: 487–490.

Spruell, P., Rieman, B.E., Knudsen, K.L., Utter, F.M. & Allendorf, F.W. 1999. Genetic population structure within streams: microsatellite analysis of bull trout populations. Ecology of Freshwater Fish 8: 114–121.

Spruell, P., Hemmingsen, A. R., Howell, P. J., Kanda, N. & Allendorf, F. W. 2003. Conservation genetics of bull trout: geographic distribution at microsatellite loci. Conservation Genetics 4: 17–29.

Sunnucks, P. & Hales, D.F. 1996. Numerous transposed sequences of mitochondrial cytochrome oxidase I-II in aphids of the genus *Sitobium* (*Hemiptera: Aphididae*). Molecular Biology and Evolution 13: 510–524.

Swanberg, T.R. 1997. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. Transactions of the American Fisheries Society 126: 735–746.

Taylor, E.B., Foote, C.J. & Wood, C.C. 1996. Molecular genetic evidence for parallel life history evolution within a Pacific salmon (sockeye salmon and kokanee, *Oncorhynchus nerka*). Evolution 50: 401–416.

Taylor, E.B., Pollard, S. & Louie, D. 1999. Mitochondrial DNA variation in bull trout (*Salvelinus confluentus*) from northwestern North America: implications for zoogeography and conservation. Molecular Ecology 8: 1155–1170.

Theriault, V., Bernatchez, L. & Dodson, J. J. 2007. Mating system and individual reproductive success of sympatric anadromous and resident brook charr, *Salvelinus fontinalis,* under natural conditions. Behavioral Ecology and Sociobiology 62: 51–65.

USFWS. 2002. Draft Bull Trout Recovery Plans for the Columbia and Klamath Basins, and the Coastal-Puget Sound. Chapter 1, page v of Executive Summary Region 1, US Fish and Wildlife Service, Portland, Oregon.

USFWS (U.S. Fish and Wildlife Service) 2004. Bull Trout Recovery Plan- Chapter 10. Region 1, US Fish and Wildlife Service, Portland, Oregon. Available online at stable URL: http://www.fws.gov/pacific/bulltrout/colkla/recovery/Default.htm

WDFW (Washington Department of Fish and Wildlife). 1997. 1997 Washington salmonid stock inventory. Appendix: bull trout and Dolly Varden. Washington Department of Fish and Wildlife, Olympia, Washington.

Westgaard, J.I., Klemetsen, A. & Knudson, R. 2004. Genetic differences between two sympatric morphs of Arctic Charr confirmed by microsatellite DNA. Journal of Fish Biology 65: 1185–1191.

Whiteley, A.R., Spruell, P., Rieman, B.E. & Allendorf, F.W. 2006. Fine-scale genetic structure of bull trout at the southern limit of their distribution. Transactions of the American Fisheries Society 135: 1238–1253.

Wofford, J.E.B., Gresswell, R.E. & Banks, M.A. 2005. Influence of barriers to movement on within-watershed genetic variation of coastal cutthroat trout. Ecological Applications 15: 628–637.

Wood, C.C. & Foote, C.J. 1996. Evidence for sympatric genetic divergence of anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*). Evolution 50: 1265–1279.

Zimmerman, C. E. & Reeves, G. H. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss:* evidence from spawning surveys and otolith microchemistry. Canadian Journal of Fisheries and Aquatic Sciences 57: 2152–2162.