

Bull trout population assessment in northeastern Oregon: a template for recovery planning

Annual Progress Report for 2010

by

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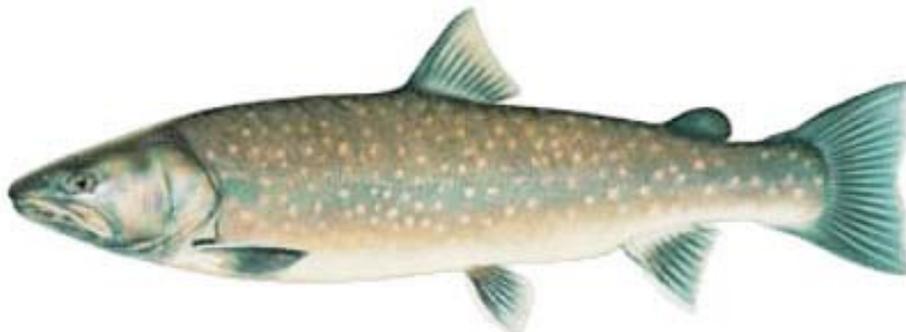


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PREFACE

This report contains one primary chapter focusing on the continuing, long-term monitoring and evaluation work by Utah State University along with three appendices. Appendix 3 is part of Tracy Bowerman's on-going PhD dissertation work, and a later draft is "in review" at *North American Journal of Fisheries Management*.

EXECUTIVE SUMMARY

There are critical gaps in information that potentially limit our ability to effectively manage bull trout and ensure their continued persistence (Porter and Marmorek 2005; Al-Chokhachy et al. 2008). These gaps include quantification of population abundance and trend for all but a few populations, estimates of larval and juvenile survival rates, estimates of dispersal rates between populations, and life-history-specific information, such as the contribution of migratory versus resident fish to overall population growth and persistence. Our research seeks to address some of these knowledge gaps through long-term monitoring of a relatively large bull trout population in the South Fork Walla Walla River (SFWW). We provide essential information on abundance, trend, vital rates, habitat needs, and information on the potential for improving survival at one or more life stages. In addition, we gather information related to population structure (e.g., age, life history, and genetic components). We provide a template against which different strategies for monitoring and evaluation can be assessed in terms of accuracy, precision, cost/effort, and limiting factors. Our goal is to provide the data and conservation assessment tools to aid in the efforts of the US Fish and Wildlife Service, to determine the necessary management actions for recovery of bull trout populations throughout the study area and the rest of the species' range. The project was initiated in 2002 and has continued through 2010, with plans to continue work through 2012 (10 years). To meet our goals, we have developed and implemented a comprehensive mark-recapture program conducted yearly, which includes two tag types, multiple capture techniques (both passive and active) and systematic sampling of two large study areas (SFWW and North Fork Umatilla rivers) with a high degree of effort. 2008 marked the fifth and final year of sampling and study in the North Fork Umatilla River.

The efforts of this project have been part of a completed PhD dissertation (Al-Chokhachy 2006) and Master's thesis (Homel 2007) and are currently part of an ongoing PhD dissertation (Bowerman, *in preparation*; Appendix 3) conducted through Utah State University. Results and syntheses of different components of the project are available in previous annual reports (Budy et al 2003, 2004, 2005, 2006, 2007, 2008, 2009, and herein) as well as in the peer-reviewed manuscripts: Al-Chokhachy et al. 2005; Al-Chokhachy and Budy 2007; Homel and Budy 2008; Homel et al. 2008; Al-Chokhachy and Budy 2007; Al-Chokhachy and Budy 2008; and Al-Chokhachy et al. 2009; and Al-Chokhachy et al. 2010.

2010 Field Season

We sampled 22 reaches during the 2010 field season (late June to mid August) which accounted for approximately 26% of the study area. Over the summer, we handled 633 bull trout including 31 young-of-year (YOY; age-0; 40 – 69 mm TL) bull trout. In 2010, the average bull trout captured was 163 mm (1 SE = 3.3) and 91.6 g (1 SE = 10.8). The smallest bull trout captured was 40 mm and the largest bull trout caught was 623 mm TL (614 mm FL). Length-frequency distributions of captured bull trout in the SFWW have varied little from 2002 through 2010, with most captured fish in the 100 – 200 mm size range.

Of the 633 bull trout we handled in 2010, 579 were marked with PIT tags and 172 of those were also tagged with bicolored, T-bar anchor tags. In 2010, as in all years since 2003, most bull trout were tagged upstream of Burnt Cabin Creek. Similar to 2009, we tagged the highest number of bull trout in reach 78, just upstream of the confluence with Skiphorton Creek.

In 2010, condition of juvenile (< 120 mm; $K_{TL} \pm 1 \text{ SE} = 0.86 \pm 0.006$) and small bull trout (120 – 370 mm TL; $K_{TL} \pm 1 \text{ SE} = 0.87 \pm 0.003$) were slightly below the 9-year average, while condition of large adult (> 370 mm) bull trout ($K_{TL} \pm 1 \text{ SE} = 1.00 \pm 0.015$) was slightly higher than the 9-year average and similar to the condition of large adults in 2006 (Figure 6). Across size groupings, condition in 2010 was close to the 9-year average for the SFWW ($K_{TL} \pm 1 \text{ SE} = 0.87 \pm 0.003$; Figure 7).

The 2010 population estimate for bull trout > 120 mm was 15,289 (95% CI = 12,105 – 20,475), which was greater than any population estimate from previous years. The 2010 estimated abundance of bull trout > 220 mm was 2,437 (95% CI = 1,712 – 3,878), similar to the highest previous estimate in 2002 of 2,695 (95% CI = 2,244 – 3,456). The 2010 estimated abundance of bull trout > 370 mm, was 1,224 (95% CI = 618 – 2,376), higher than the previous three years and similar to the estimate of 1,460 (95% CI = 1,009 – 3,180) in 2002. The population growth rate (λ) in the SFWW from 2002 – 2010 was relatively consistent among estimates obtained using the linear regression approach with different subsets of data, each of which suggested a stable population trend (e.g., λ approximately = 1).

Stream temperatures in the SFWW in 2010 were warmest at the downstream site near Harris Park Bridge (range 0.3 – 15.5 °C) and coldest at the site furthest upstream at the confluence with Reser Creek (range = –0.2 – 9.3 °C). High flows occurred in the SFWW on four separate occasions during 2010. Brief periods of high discharge occurred in January and April, and extended spring run-off kept flows high from the end of April through mid-June, with a large spike at the beginning of June. During the summer sampling period, which lasted from 28 June through 13 August, discharge in the SFWW remained at a steady base flow.

Future

Our annual mark-recapture study in the SFWW will continue in 2011. In addition, between 2011 and 2012, we will be working to best inform the bull trout Recovery Monitoring and Evaluation Technical Group (RMEG) technical exercises based on the information we have gathered from this long-term project and the conclusions we have drawn. In doing so, we are currently working within RMEG to: 1) assign uncertainty scores to likely threats, 2) aid in building a gaming tool to identify strengths and weaknesses of the “Natureserv” scoring approach to assessing threat removal effectiveness, and 3) build a meta-population viability assessment (PVA) to better understand the sensitivities and risk of using the former approach. In 2012, we will complete a comprehensive synthesis of all population data to date. This will include rerunning all survival models for as many age classes as possible, updating and rerunning the Pradel population trend model, and building an integrated population model (e.g., White and Lubow 2002) for evaluating the potential effectiveness of management actions and recovery planning. Integrated population modeling will allow the incorporation of multiple data sources into a matrix-based PVA model. Empirical data with greater variance has less influence, vital rates that have low variance have more influence, and missing vital rates are backed out accordingly (survival for a missing age class, e.g., age-1) using the most robust analytical approach currently available.

Monitoring and evaluation of bull trout populations in the South Fork Walla Walla River, Oregon

INTRODUCTION

Conservation of endangered species requires an understanding of key factors driving and limiting populations. Therefore, estimates of population abundance and trend are necessary to evaluate present and future population status (Soulé 1987). Additionally, because the health of a population is ultimately determined by the fitness of its individuals, estimates of vital rates such as survival and growth are important for identifying factors that potentially limit the population (Morris and Doak 2003). As such, quantification of these key demographic parameters can help inform decisions geared toward recovering and sustaining wild populations of imperiled organisms.

Identifying limiting factors and assessing population trends have become increasingly important for bull trout (*Salvelinus confluentus*), a species of char native to western North America. Bull trout have experienced dramatic declines in both distribution and abundance across much of their range, resulting in the species being listed as “threatened” under the Endangered Species Act (USFWS 1999). Bull trout were once distributed from northern California northward to the headwaters of the Yukon River in western Canada (Cavendar 1978). Today, however, they have been extirpated from the southernmost extent of their historical range (Goetz 1989), and are now considered extinct in the state of California (Rode 1988). Bull trout require cold, clean water, and are thought to prefer complex physical habitat (Fraleley and Shepard 1989; Goetz 1989; Al-Chokhachy and Budy 2007). Numerous factors have contributed to the decline of bull trout populations, including habitat degradation (Fraleley and Shepard 1989), barriers to migration (Rieman and McIntyre 1995), competition with introduced species (McMahon et al. 2007), and active eradication (Parker et al. 2007). Bull trout populations may be further impacted by environmental changes such as climate warming (Rieman et al. 2007).

Bull trout exhibit complex life-history strategies, and are known to exhibit multiple life-history forms that can coexist within a single population (Rieman and McIntyre 1993; Al-Chokhachy and Budy 2008; Homel et al. 2008). Resident fish may spend their entire lives in a single stream system, while migratory bull trout may be fluvial, adfluvial, or anadromous (McPhail and Baxter 1996; Brenkman and Corbett 2005), moving between headwater spawning streams out into larger rivers, lakes, or the ocean, according to the respective life-history type. This diversity of life-history forms further highlights the need

for large-scale, long-term studies that can evaluate populations that occupy a range of habitats ranging from small spawning streams in high-elevation headwaters to large rivers used for migratory corridors and overwintering adult habitat (Watson and Hillman 1997).

The goal of bull trout recovery planning by the U.S. Fish and Wildlife Service (USFWS) is to describe courses of action necessary for the ultimate delisting of this species under the Endangered Species Act, and to ensure the long-term persistence of self-sustaining, complex interacting groups of bull trout distributed across the species' native range (Lohr et al. 1999). To meet this goal, the USFWS has identified several objectives which require the type of information provided by this project: (1) maintain current distribution of bull trout within core areas in all recovery units and restore distribution where needed to encompass the essential elements for bull trout to persist, (2) maintain stable or increasing trends in abundance of bull trout in all recovery units, and (3) restore and maintain suitable habitat conditions for all bull trout life-history stages and strategies. The USFWS recovery-planning document emphasizes conserving core areas within conservation units to preserve genotypic and phenotypic diversity represented in different geographic locations, and to conserve bull trout populations across a range of habitats. The continued survival and recovery of individual core area populations is thought to be critical to the persistence of conservation units and in overall recovery of the Columbia River distinct population segment (Whitesel et al. 2004).

Recent research has contributed to our knowledge of bull trout populations in various parts of the species' range (e.g., Al-Chokhachy et al. 2010), as well as issues managers face in trying to recover bull trout populations (Al-Chokhachy et al. 2008). However, there are still critical gaps in information that potentially limit our ability to effectively manage bull trout and ensure their continued persistence (Porter and Marmorek 2005; Al-Chokhachy et al. 2008). These gaps include quantification of population abundance and trend for all but a few populations, estimates of larval and juvenile survival rates, estimates of dispersal rates between populations, and life-history-specific information, such as the contribution of migratory versus resident fish to overall population growth and persistence. In addition, the relative contribution of different threats (e.g., passage versus water quality) is only poorly understood and documented.

Our research seeks to address some of these knowledge gaps through long-term monitoring of a relatively large bull trout population in the South Fork Walla Walla River (SFWW). Each year, we use mark-recapture/resight data from this watershed to estimate population size and structure, population trend, vital rates, and movement patterns (Al-Chokhachy and Budy 2008; Homel and Budy 2008). Previous research on this population has allowed us to evaluate and compare different monitoring techniques

(Al-Chokhachy et al. 2005; Al-Chokhachy et al. 2009), assess genetic differentiation between resident and migratory life-history types (Homel et al. 2008), and compare demographic parameters and habitat use among several distinct populations (Al-Chokhachy and Budy 2007; Budy et al. 2007). We provide a template against which different strategies for monitoring and evaluation can be assessed in terms of accuracy, precision, and cost per effort (Al-Chokhachy et al. 2009) in addition to focused research on specific components of the project, which has included research on other populations (e.g., Wenaha, John Day, and Umatilla rivers). To date, our work includes nine years (2002 - 2010) of population monitoring data and vital-rate statistics from the SFWW. The data and conservation assessment tools provided by this project will ultimately help guide the USFWS in determining the necessary management actions for recovery of bull trout populations throughout the range of bull trout. For example, demographic data generated from this research and documented by Al-Chokhachy and Budy (2008) are currently being used by the USFWS Bull Trout Recovery Monitoring and Evaluation Technical Group (RMEG) to create a model to assess viability of bull trout populations and the potential for improvements to bull trout status and distribution based on the hypothetical removal of a variety of different threats. This information will be used to help inform bull trout recovery planning led by the USFWS.

In previous years, we have conducted research on several rivers, which allowed us to compare population abundance and distribution, as well as vital rate statistics and habitat use, between populations of bull trout in the John Day, Umatilla, and Walla Walla river systems. In 2009 and 2010, our research focused solely on the South Fork Walla Walla River, located in Northeastern Oregon (Figure 1). The SFWW was initially selected as the comprehensive study area for this research because it contains a relatively high abundance of both resident and migratory fish and a diversity of habitat types, which allows us to study differences in such metrics as movement and survival in relation to life-history strategy. In addition, this watershed is the focus of numerous complex water management issues associated with fish protection, and thus provides an opportunity to apply research to active management decisions. Long-term research in this watershed has allowed us to monitor the bull trout population in the SFWW for nine years, providing one of the most comprehensive and continuous capture-recapture studies on fluvial bull trout in the region.

STUDY AREA

The South Fork Walla Walla River

The Walla Walla River in northeastern Oregon and southeastern Washington is a tributary of the Columbia River that drains an area of 4,553 km² (Walla Walla Subbasin Summary Draft 2001). The tributaries of the Walla Walla River originate in the Blue Mountains at elevations near 1800 m. Primary tributaries to the main stem Walla Walla River include the North and South Fork Walla Walla Rivers in Oregon, and Mill Creek and Touchet River, which enter the main stem after it flows northward into Washington state.

The Walla Walla River historically contained a number of native anadromous and resident salmonid populations including: bull trout, redband trout (*Oncorhynchus mykiss* subpopulation), summer steelhead (*O. mykiss*), mountain whitefish (*Prosopium williamsoni*), and, spring and fall Chinook salmon (*Oncorhynchus tshawytscha*), chum salmon (*O. keta*), and coho salmon (*O. kisutch*), although the extent of fall Chinook, chum, and coho salmon within the system is not known; (Walla Walla Subbasin Summary Draft Plan 2001). Today, steelhead represents the only native anadromous salmonid still present in the Walla Walla River system. However, since 2000 there has been annual supplementation of adult Chinook salmon in the SF Walla Walla River by the Confederated Tribes of the Umatilla Indian Reservation (CTUIR), and observations indicate that natural reproduction occurs in addition to ongoing supplementation (Mike Lambert, CTUIR, personal communication). Populations of native redband trout, bull trout, mountain whitefish, sculpin (*Cottus* spp.), and dace (*Rhinichthys* spp.) still persist in the Walla Walla River, as well as introduced brown trout (*Salmo trutta*), which are found in the lower portions of the basin.

Little documentation exists on the historical distribution of bull trout in the Walla Walla Subbasin prior to 1990. Anecdotal evidence suggests that large fluvial bull trout were found to utilize the Columbia River. Telemetry studies in the mid-Columbia River region have shown bull trout to use both primary and secondary tributaries for spawning (FERC Project 2145 Draft 2002). Therefore, it is presumed that bull trout had access to the Columbia River and all of its tributaries prior to the impoundment of the Columbia River (Buchanan et al. 1997). Today, resident and fluvial forms of bull trout exist in the Walla Walla (Walla Walla Subbasin Summary Draft 2001), and both life-history forms spawn in the tributaries and headwaters of the Walla Walla River. Recent data demonstrate that bull trout travel throughout the Walla Walla River system and into the Columbia River (see Results below; Budy et al. 2010).

Within the Walla Walla River Basin, bull trout are arbitrarily divided into four populations (core areas) based on geography: North Fork Walla Walla River, SFWW, Mill Creek, and the Touchet River (Buchanan et al. 1997). Ratliff and Howell (1992) described the population status of bull trout as “low risk” in the SFWW and Mill Creek, and “of special concern” in the North Fork Walla Walla River. Since that report, the status of the SFWW population has remained at low risk, but both the North Fork Walla Walla River and Mill Creek populations have been upgraded to “high risk” and “of special concern” respectively (Buchanan et al. 1997). Alterations to migratory corridors linking these populations have occurred, but the degree of genetic and geographical isolation is unknown, although we have documented connectivity between these populations. Two individuals were PIT tagged in Mill Creek and moved up the SFWW during spawning season (one in 2008, and a second in 2010 [see Results below]), and one fish PIT tagged in the upper SFWW was detected in upper Mill Creek during spawning (in 2009; Budy et al. 2010).

The long-term study site on the SFWW spans nearly 21 km in length. The upper boundary was set at the confluence with Reser Creek (117.7 km upstream of the Columbia River; Reach 103), and the lower boundary was set above Harris Park Bridge (97 kilometers upstream of the Columbia River; on public, county land; Budy et al. 2003). In order to account for spatial variation of the study area and the distribution of bull trout, the study site was divided into 103 reaches, each approximately 200 m in length, using Maptech mapping software (Figure 1).

An initial site was randomly selected from the list of reaches, and thereafter every fifth reach (an approximate 20% sample rate) was systematically designated for sampling; these reaches have been sampled annually since 2002. The UTM coordinates from the mapping software were used to locate the general location of the bottom of each reach, and the closest pool tail to the coordinates was set as the true reach boundary. The reach continued upstream for at least 200 m and the top was set at the first pool-tail above the 200-m mark. Total length was recorded for each reach. Location coordinates (UTM using GPS) were recorded at the boundaries of each reach.

METHODS

Size designations

The following size designations have been used since the onset of this bull trout population assessment in northeastern Oregon in 2002. Bull trout smaller than 220 mm represent subadult, not sexually mature fish (Al-Chokhachy and Budy 2008) and bull

trout 220 mm or larger represent both resident and migratory sexually mature fish (Al-Chokhachy et al. 2005; Al-Chokhachy and Budy 2007). Considering bull trout that are 220 mm or greater (hereafter termed adult) to be sexually mature is a conservative estimate, as smaller adults have been found in the study area, as well as in other systems (WDFW 2000; Dunham et al. 2008). Additional size categories are used for population growth rate estimates and survival estimates. For the purposes of this study, immature bull trout are 70 - 119 mm, small adults are 220 - 369 mm, and large, likely migratory, adults are ≥ 370 mm; this latter designation is based on the percent of fish within that age class found to be migratory by Al-Chokhachy and Budy (2008) and others (Rieman et al. 1993; Shephard 1989). Not all bull trout > 370 mm are migratory, but there is a presumption that larger fish are migratory and observations of movement patterns support this presumption (Budy et al. 2009). The size categories > 220 mm and > 370 mm are considered the most important for adult trend and population analyses. In 2010, we updated age-at-length estimates calculated from otolith analysis to define the following age classes: < 70 mm = age-0 (young of year, YOY), 70 - 120 mm = age-1, 120 - 170 mm = age-2, 170 - 220 = age-3, 220 - 370 mm = age-4 and age-5, and > 370 mm = \geq age-6 and older (Figure 12).

Fish sampling

Capture.—We captured bull trout using multiple sampling techniques including angling, snorkel herding, and electrofishing downstream to a seine. 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 calculate condition (Fulton's $K_{TL} = W / L^3 * 100,000$) and determine length-to-weight regressions and annual growth. 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 adults to estimate fecundity, sex ratio, age, and diet. Tissue samples may be used for future stable isotope analysis.

Marking.— In all study reaches, each bull trout ≥ 70 mm TL captured was marked with a unique PIT tag as well as an external mark, the latter of which was used to identify marked individuals during snorkel surveys (recapture sampling). In previous years, the ≥ 120 mm TL size minimum was chosen as a safe size for inserting anchor tags and 23-mm PIT tags. In 2010, the weight of 23-mm PIT tags increased due to a switch in tag manufacturer. To accommodate the increase in weight relative to fish body weight, bull trout from 70 to 169 mm TL were tagged with 12-mm PIT tags and fish ≥ 170 mm are tagged with 23-mm PIT tags. In addition to an internal PIT tag, all bull trout were given an external mark by either clipping the adipose fin on bull trout < 170 mm TL or inserting a T-bar anchor (Floy) tag, unique to year and stream, on the right side, adjacent to the dorsal fin on bull trout ≥ 170 mm TL. In 2009, we increased the minimum size of fish

tagged with anchor tags from ≥ 120 to ≥ 170 mm TL, and we retained this protocol in 2010. The fin clip was saved for later genetic analysis. Prior to tagging, bull trout were anesthetized with tricaine methanesulfonate (MS-222) until they exhibited little response to stimuli. A PIT-tag was then inserted into a small incision on the ventral side of the fish, anterior to the pelvic fins. After tag implant, scales were taken from the right side at the base of the dorsal fin for aging and growth information. During recovery, all anesthetized fish were placed in a flow-through recovery container within the channel, monitored until full equilibrium was restored, and returned to slow-water habitat near individual capture locations.

Resighting.—We used daytime snorkel surveys to resight marked bull trout within study reaches (mean reach length = 250 m). To avoid double-counting fish that were migrating upstream to the headwaters to spawn, we began surveys in the upper-most reaches of the study area and worked downstream. Snorkel surveys were conducted on consecutive days until the sampling was complete. We used this approach to minimize the incidence of counting the same fish twice in different reaches. Within each reach, two snorkel observers proceeded in an upstream direction while scanning for fish across their assigned lane, such that the entire stream channel was surveyed. Water temperature and sampling time were recorded for each reach snorkeled. All bull trout (tagged and untagged), *O. mykiss* spp., and mountain whitefish were enumerated and placed into 50-mm size classes. Additionally, all juvenile and adult Chinook salmon encountered were enumerated. Accurate identification of fish species and size estimation was emphasized.

Recapture.—During our capture sampling, described above, we also recaptured previously-tagged bull trout (2002 to present). All actively captured bull trout were passed over a handheld PIT-tag reader and visually checked for anchor tags from previous years. Any recapture was weighed (nearest 0.1 g) and measured (both total length and fork length to the nearest mm) for estimates of annual growth. Recapture location was recorded for movement analysis. Recapture events provide critical information for estimates of bull trout survival, annual population estimates, and the data needed to parameterize the Pradel population trend, mark and recapture model.

Passive fish detection.—Two PIT-tag passive in-stream antenna (PIA or detectors) are located within the study area that continuously collect information on tagged bull trout. One detector is located at Harris Park Bridge (river km 97; UTM coordinates: 110408261 E, 5076370 N) at the bottom of the study site, and the second detector is located just above the confluence with Bear Creek (river km 105.6; UTM coordinates: 110414281 E, 5077108 N). The Harris Park Bridge detector (WW1) has been operational since mid-September 2002, and the Bear Creek detector (WW2) has been

operational since mid-October 2002; however, there were periods of time in 2010 when both did not operate due to mechanical failure. WW1 washed out during high flows in June 2010, and was inoperable between 8 June 2010 and 22 July 2010. WW2 was inoperable or operated only during daylight hours for periods of a few days in March, May, July and August, but otherwise collected data continuously. Additional detectors are located downstream in the main stem Walla Walla River at Nursery Bridge, Burlingame Diversion, and Oasis Road Bridge (see Figure 1). Having additional detectors downstream of the study area allows us to monitor fish migrations and connectivity within the Walla Walla River drainage. All detectors are linked either through phone or satellite, and data are uploaded to the PTAGIS website on a regular basis (Website: <www.psmfc.org/pittag/Data_and_Reports/index.html> under "Small-scale Interrogation Site Detections -Query").

Growth

Growth information was obtained from bull trout previously tagged in the study area in 2009 and recaptured during the 2010 summer field season. This data was added to previous years of growth information to estimate average annual growth in total length (mm) and weight (g), which was determined from bull trout recaptured the field season one year after initial tagging or previous recapture. We scaled this growth by the number of days between initial capture and recapture events (approximately one year).

Diet, age, and fecundity

A small subsample of bull trout, ten or fewer individuals per year, have been collected from 2002-2010 for diet, age, and fecundity analysis. In 2010, we collected stomachs, sagittal otoliths, and gonads from five sacrificed bull trout. Stomach contents were partitioned into groups (i.e., macroinvertebrates, *Oncorhynchus* spp., etc.; see Figure 11) and each group was quantified as percentage of diet by wet weight (g). Sagittal otoliths were used to estimate bull trout age by embedding, sanding, and polishing the otoliths, then viewing them under a microscope to count otolith annuli. We estimated fecundity of sacrificed bull trout by counting eggs from ripe females and then relating number of eggs per female to that individual's weight (g) and total length (mm).

Population estimates

We used tagging and snorkeling data to parameterize mark-resight population estimates using a Lincoln-Petersen bias-adjusted estimator (Chapman 1951). We estimated population size and 95% confidence intervals (Krebs 1999) for three size groupings of bull trout: ≥ 120 mm, ≥ 220 mm, and ≥ 370 mm. We expanded these

reach-based population estimates to estimate abundance for the subpopulation within the entire study area.

Population growth rate

Obtaining reliable estimates of population growth rate or trend to determine population trajectory is a particularly challenging task that requires multiple years of data. We estimated population trend using two different methods and three data types. Because each methodology has different sources of bias associated with it, comparison of different approaches can help improve confidence in the direction of the trend. First, we estimated trend via linear regression of log-transformed annual changes in population growth rate (λ) as a function of time step (Morris and Doak 2002; Budy et al. 2007) based on 1) redd count data (1994 - 2010) obtained from the USFWS and the Oregon Department of Fish and Wildlife (ODFW) and 2) population estimates from the mark-resight data (2002 - 2010). We compared these results with an estimate of trend using a temporal symmetry model (Pradel 1996; Nichols and Hines 2002) based on capture-recapture data from 2002 - 2009. For both approaches, we estimated trend for fish \geq 220 mm, because this size class corresponds to the adult population within the SFWW (Al-Chokhachy and Budy 2008) and directly corresponds to bull trout recovery goals. Additionally, we performed separate trend analyses using both approaches for large bull trout ($>$ 370 mm), because this size class contains the greatest proportion of individuals exhibiting migratory patterns within the SFWW and those individuals with the greatest fecundity (Al-Chokhachy and Budy 2008).

Survival

Survival estimates will not be updated again until 2012. See the 2007 annual report (Budy et al. 2008) for survival estimates.

Temperature

We monitored temperature at four sites in the SFWW from August 2009 to August 2010 using in-stream temperature loggers programmed to record temperatures at 90-minute intervals. Temperature was recorded at the top of the study area, just below Reser Creek (River km 117.7), in the middle of the upper portion of the study area near Skiphorton Creek (River km 112.9), the middle of the lower part of the study area near Bear Creek (River km 105.6), and just below the bottom of the study area, near Harris Park (River km 97).

RESULTS

Fish sampling

We sampled 22 reaches during the 2010 field season (late June to mid August) which accounted for approximately 26% of the study area. We handled 633 bull trout including 31 young-of-year (YOY; 40 – 69 mm TL) bull trout (Figure 2). In 2010, the average length of bull trout captured was 163 mm TL (1 SE = 3.3) and 91.6 g (1 SE = 10.8). The smallest bull trout captured was 40 mm (weight unknown) and the largest bull trout captured was 623 mm TL (614 mm FL, weight unknown). YOY bull trout were not anaesthetized; after capture, they were immediately measured (TL) with a hand ruler then returned to the stream to avoid predation by larger bull trout in the holding tanks. Length-frequency distributions of captured bull trout in the SFWW have varied little from 2002 through 2010, with most captured fish in the 100 – 200 mm size range (Figure 2).

Of the 633 bull trout we handled in 2010, we tagged 579 with PIT tags and 172 of those were also tagged with bicolored (purple/green) anchor tags (Figure 3). In 2010, as in all years since 2003, the majority bull trout were caught upstream of Burnt Cabin Creek (Figure 3). Similar to 2009, we tagged the highest number of bull trout in reach 78, near Skiphorton Creek (Figure 3).

We developed a strong weight-at-length relationship for bull trout weighed and measured in 2010 ($R^2 = 0.98 - 0.99$; Figure 4). A solid fork length-to-total length relationship was also apparent for bull trout measured in 2010 ($R^2 = 0.99$; Figure 5).

Condition.—Condition (Fulton's K_{TL}) of bull trout captured from 2002 - 2010 varied by size grouping and year; in general, condition was lowest for juvenile (< 120 mm; 9-year mean = 0.87) and small adult bull trout (120 - 370 mm; 9-year mean = 0.89) and highest for large bull trout (>370 mm; 9-year mean = 0.95; Figure 6). These results are consistent when compared to growth data over the same period, where larger fish put on more weight but less length resulting in higher condition values (Figures 6 and 10). In 2010, condition of juvenile (< 120 mm; $K_{TL} \pm 1 \text{ SE} = 0.86 \pm 0.006$) and small adult bull trout (120 – 370 mm TL; $K_{TL} \pm 1 \text{ SE} = 0.87 \pm 0.003$) were slightly below the 9-year average, while condition of large adult (> 370 mm) bull trout ($K_{TL} \pm 1 \text{ SE} = 1.00 \pm 0.015$) was slightly higher than the 9-year average and similar to the condition of large adults in 2006 (Figure 6). Across size groupings, condition in 2010 was similar to the 9-year average ($K_{TL} \pm 1 \text{ SE} = 0.875 \pm 0.015$) for the SFWW (Figure 7).

Snorkel surveys.—We performed snorkel surveys in each of the 22 study reaches in 2010, and observed bull trout in all 22 reaches. We sighted a total of 582 bull trout; the majority of bull trout sighted were estimated to be in the 120 - 170 mm and 170 - 220 mm size classes (n = 164 and n = 123, respectively); however, bull trout as large as the 620 - 670 mm category and as small as the 0 - 70 mm category were sighted, and previously marked fish in nearly all of the size classes were re-sighted during snorkel surveys (Figure 8). Reaches 68 and 58 had the highest counts of bull trout (87 and 47 individuals, respectively) and reaches 3 and 8 had the lowest counts of bull trout (7 and 8 individuals, respectively; Figure 9).

Active recaptures in 2010

During 2010 active sampling, we physically recaptured a total of 17 bull trout, of which one had been PIT tagged in 2007, three had been tagged in 2008, and twelve in 2009. Eight of these fish were recaptured in the same reach in which they had initially been captured and marked (two from 2008 and seven from 2009). One fish was recaptured that had been caught and marked in 2008 near Nursery Bridge.

Passive fish detection in 2010

As in previous years, throughout the 2010 calendar year, bull trout were detected at various Passive In-stream Antennae (PIA) within the SFWW and main stem Walla Walla River system (Figure 1). Data from PIA detections were summarized by unique monthly detections such that if a PIT-tagged fish was detected numerous times at the same PIA in one month, it was recorded only once. The greatest number of unique monthly detections occurred in April and May, and the largest number of detections occurred at the WW2 PIA, located at the confluence with Bear Creek (Figure 10). During summer months and into the spawning seasons, detections occurred only at PIA systems located higher in the river system (Oasis Bridge, WW1, and WW2), whereas in late autumn and winter, fewer fish were detected at WW1 and WW2 compared to other months, and fish were detected moving past the Burlingame Diversion and Oasis Bridge PIA. Four bull trout that had been PIT tagged in the upper portion of the SFWW study area were detected passing the Oasis Bridge PIA in November and December; according to the length-at-age relationship (Figure 13), all of these fish were approximately age-3 when they were detected at Oasis Bridge, indicating potential use of the Columbia River for subadult rearing habitat. One fish PIT tagged in Mill Creek was detected at the WW2 and WW1 PIA in October, suggesting evidence of dispersal between the two populations.

Growth of recaptured fish

Since 2002 we have recaptured 84 bull trout in the SFWW for estimates of annual growth in total length (mm; Figure 11). We first began PIT tagging bull trout < 120 mm in 2007 and continued tagging these small fish through 2010, thus explaining why this size category has the fewest observations (Figure 11). Average annual growth in total length of tagged bull trout varied between subadults and adults. The two smallest bull trout size classes (< 120 mm and 120 - 219 mm) exhibited similar annual growth in total length, 64.7 mm/year (± 2 SE = 16.4 mm/year) and 64.5 mm/year (± 2 SE = 9.4 mm/year), respectively (Figure 10). These juvenile and subadult fish exhibited higher annual growth in total length than small adults (220 - 370 mm), 44.9 mm/year (± 2 SE = 9.3 mm), and much higher growth in total length than large adults (> 370 mm), 17.3 mm/year (± 2 SE = 3.9 mm; Figure 11).

We have recaptured 80 bull trout for estimates of annual growth in weight (g; Figure 11). In terms of body mass, the trend was opposite of total length. Small (220 - 370 mm) and large (> 370 mm) adults exhibited higher mass (as weight gain) growth rates, 125.3 g/year (± 2 SE = 27.3 g/year) and 160.5 g/year (± 2 SE = 83.5 g/year), respectively, than subadult bull trout (120 - 220 mm) and juvenile (<120 mm), 69.0 g/year (\pm SE = 13.5 g/year) and 29.9 g/year (± 2 SE = 6.9 g/year), respectively (Figure 11). However, growth in weight was extremely variable for bull trout in the largest size class.

Diet, age, and fecundity

We sacrificed five bull trout in 2010 to collect stomach contents for diet analysis, sagittal otoliths for aging purposes, and gonads for fecundity analysis. Bull trout diet data are available from fish sacrificed from 2003 - 2010. Diet analysis showed that bull trout sacrificed in 2010 were primarily consuming *Oncorhynchus* spp. (96.6%) which includes both *O. mykiss* and *O. tshawytscha* (Figure 12). However, this percentage is skewed by a single bull trout that had one complete and parts of a second *Oncorhynchus* in its stomach. Three of the remaining four bull trout had no fish and only a few macroinvertebrates in their stomachs, and one had a completely empty stomach. Accordingly, a small percentage of bull trout diet in 2010 was composed of macroinvertebrates and eggs (1.6% and 1.7%, respectively). Prey items extracted from bull trout stomachs have varied in content and proportion among years. In previous years, a large percentage of bull trout diet was composed of macroinvertebrates (Figure 12). However, diet inference from these data is limited due to the extremely small sample size available.

Since 2002, 55 bull trout otoliths have been aged from individuals ranging from 90 - 674 mm TL. The estimated age of sacrificed bull trout ranged between 1 and 10 years (Figure 13). Length-at-age estimates increase at a rate consistent with observed yearly growth (Figure 11); however, there was high variability between fish estimated at age-10, with an extremely small sample size of two.

Bull trout fecundity was estimated by counting eggs from sacrificed female fish. We have estimated fecundity from 19 female bull trout from 2002 - 2010. The number of eggs per female was then compared to that individual's weight (g, $R^2 = 0.83$; Figure 14) and total length (mm, $R^2 = 0.84$; Figure 15). In general, the number of eggs per female increased as weight and length increased (Figures 14 and 15).

Population estimates

Estimated abundance of bull trout in the SFWW varied among size groups. The 2010 population estimate for bull trout > 120 mm was 15,289 (95% CI = 12,105 – 20,475), which was greater than any population estimate from previous years (Figure 16). The 2010 estimated abundance of bull trout > 220 mm was 2,437 (95% CI = 1,712 – 3,878), similar to the highest previous estimate in 2002 of 2,695 (95% CI = 2,244 – 3,456). The 2010 estimated abundance of bull trout > 370 mm, was 1,224 (95% CI = 618 – 2,376), higher than the previous three years and similar to the estimate of 1,460 (95% CI = 1,009 – 3,180) in 2002 (Figure 16).

Population growth rate

The population growth rate (λ) or population trend in the SFWW from 2002 – 2010 was relatively consistent among estimates obtained using the linear regression approach with different subsets of data, each of which suggested a stable population trend (Table 1). A λ value > 1 indicates positive population trend, a value of $\lambda = 1$ indicates no change in population growth rate, and a λ value < 1 indicates that the population is declining. Estimates based on the linear regression approach were slightly higher using redd count data from 1994 - 2010 ($\lambda = 1.102$, 95% CI = 0.899 – 1.350) than estimates using redd count data from only 2002 - 2010 ($\lambda = 0.931$, 95% CI = 0.751 – 1.154; Table 1). These estimates were similar to those using the linear regression method for the population estimates of bull trout > 220 mm ($\lambda = 1.132$, 95% CI = 0.767 – 1.671; Table 1). The small number of bull trout > 370 mm resulted in large confidence intervals around the growth rate using population estimates for this size group ($\lambda = 1.367$, 95% CI = 0.702 – 2.662; Table 1).

Using the mark-recapture temporal symmetry model (Pradel), we obtained similar but slightly lower estimates of population growth rate for bull trout > 220 mm ($\lambda = 0.931$, 95% CI = 0.893 – 0.971) and > 370 mm ($\lambda = 0.931$, 95% CI = 0.878 – 0.996; Table 1). While this approach is generally considered less biased than the regression-based approach, it can likewise be affected by sparse data (Hines and Nichols 2002). We did not update this estimate to include 2010 data, but the precision of population growth rate estimates using the temporal symmetry model will likely improve when we update this analysis in 2012 with two additional years of data collection.

Table 1. Population growth rate estimates with 95% confidence intervals (CI) in the South Fork Walla Walla River from 2002 – 2010, based on linear regression of the log-transformed annual changes in population growth using redd count data from all index reaches combined (Redds) and population abundance estimates for bull trout > 220 mm and > 370 mm (Pop Est), as well as the population growth estimates (\pm 95% CI) obtained using a temporal symmetry model (Pradel) based on mark-recapture data for bull trout > 220 mm and > 370 mm for the same time period.

Estimate source	Lambda	Lower 95% CI	Upper 95% CI
Redds 1994 – 2010	1.102	0.899	1.350
Redds 2002 – 2010	0.931	0.751	1.154
Pop Est > 220 mm, 2002 – 2010	1.132	0.767	1.671
Pop Est > 370 mm, 2002 – 2010	1.367	0.702	2.662
Pradel > 220 mm, 2002 – 2009	0.931	0.893	0.971
Pradel > 370 mm, 2002 – 2009	0.931	0.878	0.997

Temperature and flow

We collected temperature data at four sites from mid August 2009 to mid August 2010 using temperature loggers at four sites along the longitudinal gradient of the study area. Over this one-year period, stream temperatures were warmest and most variable at the downstream site at Harris Bridge (range = 0.3 – 15.5 °C) and generally colder, but less variable, at the site furthest upstream at the confluence with Reser Creek (range = 1.98 – 9.4 °C; Figure 17).

High flows occurred in the SFWW on four separate occasions during 2010. Brief periods of high discharge occurred in January and April, and extended spring run-off kept flows high from the end of April through mid-June, with a large spike at the beginning of June (USGS). During the summer sampling period, which lasted from 28 June through 13 August, discharge in the SFWW remained at a steady base flow.

DISCUSSION

Data gathered in the SFWW is some of the most comprehensive population-level data that has been collected on a fluvial population of bull trout in the United States. Despite the high quality and large quantity of data gathered in the SFWW system, we occasionally encountered sampling issues that may affect some of our analyses. While collecting data in the SFWW, researchers take care to avoid electro-seining for bull trout around Chinook salmon and *Oncorhynchus mykiss* redds. Because it appears that the number of Chinook salmon spawning in the SFWW study area has increased during our sampling season in the past two years, it is possible that we could be sampling a slightly smaller portion of riverine habitat than we have in the past.

The collection of otoliths from a wide size range (99 – 720 mm TL) of bull trout has allowed us to estimate age (age-1 to age-10) for multiple ages of bull trout in the SFWW. This is the most accurate measure of age available; however, counting annuli on otoliths can be imprecise, particularly for bull trout, which have very small otoliths relative to many other species. Annuli become harder to discern in older fish, leading to greater variability for older age estimates. There may also be a difference in the rate of bone accumulation between migratory and resident fish, which could result in older estimates for migratory fish which likely have more defined growth rings compared to resident fish. Above all, the amount of confidence given to age estimates from otoliths should reflect the sample size, which is still relatively small, albeit valuable, for this dataset (n = 55).

Long-term datasets allow us to examine trends and natural variability in a population. The data gathered from nine years (2002 - 2010) of research in the South Fork Walla Walla River, Oregon, has enabled us to assess demographic and vital rates for bull trout that exhibit both migratory and resident histories, and co-occur within the study area. Using this extensive dataset, we have monitored trends in the relative frequency of size classes, condition, distribution, and growth rate of fish within the SFWW study area. This dataset has also allowed us to estimate population abundance and growth rate

across years. This information is pertinent to bull trout restoration efforts as mandated by the Endangered Species Act (1973), and will help inform managers in the recovery planning process for the species.

Based on this data, demographic rates for the bull trout population in the SFWW appears to be stable. The size structure of bull trout sampled within the study area is similar to other migratory bull trout populations (e.g., Fraley and Shepard 1989) and is consistent from one year to the next, suggesting stable recruitment into larger size classes. Moreover, in 2010, bull trout condition (K_{TL}) was similar to the 9-year average for the two smaller size classes (< 120 mm and 120 - 370 mm) and higher than the 9-year average for the largest size class (> 370 mm) also generally indicating good population health.

Estimates of abundance and trend in 2010 are similar to estimates of previous years, suggesting a stable population growth rate (i.e., trend) in the study area. Our data suggest that the abundance of subadult bull trout (> 120 mm) in the SFWW has increased in the past few years. This is likely a real trend and is consistent with increased trends in both adult size groupings; however, a change in methodology could potentially have contributed to a positive bias of abundance estimates for subadult fish. In 2009, we increased the minimum size of fish that were marked with an external anchor tag from 120 mm to 170 mm. All PIT-tagged fish < 170 mm were marked by an adipose fin clip, but this latter marking was more difficult to observe during snorkel counts than the previously used anchor tags. This change in methodology could have led us to undercount marked fish relative to unmarked fish in the small size class (120 – 170 mm), which would have resulted in higher population estimates. We do not include abundance estimates for fish < 120 mm because snorkel observations of fish in this size range are uncommon due to the cryptic nature of small bull trout (Figure 9; Thurow 1997).

Attaining accurate population trend estimates requires multiple years of data. The population trend estimates we calculated using the linear regression approach all have 95% confidence intervals that overlap 1.0, suggesting a stable population growth rate in the SFWW. However, these values were estimated based on linear regression, which can easily be affected by a single population abundance estimate from a given year. Thus, a single year can have a disproportionate influence on the resulting estimate of lambda (λ). With only nine years of data, an estimate of the population growth rate may be skewed by a single particularly low or high year and therefore, should be viewed with caution. However, given overall similarity in population trend estimates (λ) near 1 among different sampling and analytical methods, we feel reasonably confident the population is currently stable.

The combination of information gathered from this ongoing, long-term study and additional research conducted on this bull trout population (e.g., Al-Chokhachy et al. 2009; Homel and Budy 2008) will provide the USFWS with important information on factors that affect population growth and stability. Additionally, it provides vital rate information specific to migratory and fluvial life-history strategies (Al-Chokhachy and Budy 2008; Homel et al. 2008). Information in this report is currently being used by the Bull Trout Recovery, Monitoring, and Evaluation Technical Group (RMEG) to assess the potential effect of various threats on long-term population viability of several bull trout populations, which will ultimately help inform decisions made in recovery planning for bull trout.

LITERATURE CITED

- Al-Chokhachy, R., and P. Budy. 2007. An assessment of the transferability of bull trout microhabitat relationships across three streams in eastern Oregon. *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 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., P. Budy, and M. Conner. 2009. Detecting changes in bull trout population abundance: understanding the accuracy, precision, and costs of our efforts. *Canadian Journal of Fisheries and Aquatic Sciences* 66:649-658.
- Al-Chokhachy, R., W. Fredenberg, and S. Spalding. 2008. Surveying professional opinion to inform bull trout recovery and management decisions. *Fisheries* 33:18-28.
- 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.
- Brenkman, S.J., and S.C. Corbett. 2005. Extent of anadromy in bull trout and implications for conservation of a threatened species. *North American Journal of Fisheries Management* 25:1073-1081.
- Buchanan, D.V., M.L. Hanson, and R.M. Hooten. 1997. Status of Oregon's bull trout. Oregon Department of Fish and Wildlife. October 1997. Portland, Oregon.
- Buckman, R.C., W.E. Hosford, and P.A. Dupee. 1992. Malheur River bull trout investigations. Pages 45-47 in P. Howell and D. V. Buchanan, editors. *Proceedings of the Gearhart Mountain bull trout workshop*. Oregon Chapter of the American Fisheries Society, Corvallis.
- 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 pages.
- 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 pages.
- 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. *UTC FWRU* 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 US Fish and Wildlife Service. *UTC FWRU* 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.
- 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.
- Cavender, T.M. 1978. Taxonomy and distribution of the bull trout, *Salvelinus confluentus* from the American Northwest. California Fish and Game 64:139-174.
- Chapman, D.G. 1951. Some properties of the hypergeometric distribution with applications to zoological censuses. University of California Publications in Statistics 1:131-160.
- Colpitts, G. 1997. Science, streams, and sport: trout conservation in southern Alberta 1900-1930. M.A. thesis, Department of History, University of Calgary, Alberta, Canada.
- Dunham, J. B., C.V. Baxter, K.D. Fausch, W. Fredenberg, S. Kitano, I. Koizumi, K. Morita, T. Nakamura, B.E. Rieman, K.A. Savvaitova, J. Stanford, E.B. Taylor, and S. Yamamoto. 2008. Evolution, ecology, and conservation of Dolly varden, white-spotted Char, and bull trout. Fisheries 33:537-550.
- FERC Project 2145 Draft. 2002. Movement of bull trout within the Mid-Columbia and its tributaries 2001-2002. Prepared for Public Utility District 1 of Chelan County, Wenatchee, Washington. Bioanalysts, Inc., 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 63:163-143.
- Goetz, F. 1989. Biology of the bull trout, *Salvelinus confluentus*: A literature review. Willamette National Forest, Eugene, Oregon.
- Goetz, F. 1991. Bull trout life history and habitat study. U.S. Department of Agriculture, Forest Service, Deschutes National Forest, Bend, Oregon.
- 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.
- Hines, J.E., and J.D. Nichols. 2002. Investigations of potential bias in the estimation of λ using Pradel's (1996) model for capture-recapture data. Journal of Applied Statistics 29(1/4):573-587.
- Homel, K., and P. Budy. 2008. Temporal and spatial variability in the migration patterns of juvenile and subadult bull trout (*Salvelinus confluentus*) in Northeast 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.
- Johnston, F.D., J.R. Post, C.R. 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.
- Kershner, J.L., C.M. Bischoff, and D.L. Horan. 1997. Population, habitat, and genetic characteristics of Colorado River Cutthroat trout in wilderness and non-wilderness stream sections in the Uinta Mountains of Utah and Wyoming. *North American Journal of Fisheries Management* 17:1134-1143.
- Krebs, C.J. 1999. *Ecological Methodology*, second edition. Addison-Wesley Educational Publishers, Inc., U.S.A.
- 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.
- Lichatowich, J. 1999. *Salmon without rivers: A history of the pacific salmon crisis*. Island Press. Washington D.C.
- Lohr, S., T. Cummings, W. Fredenberg, and S. Duke. 1999. Listing and recovery planning for bull trout. U.S. Fish and Wildlife Service publication. Boise, Idaho.
- Mahoney, B. 2001. Walla Walla basin summer steelhead and bull trout radio telemetry project: 2001 Annual Report. Prepared by the Confederated Tribes of the Umatilla Indian Reservation for the Bonneville Power Administration. Portland, Oregon.
- Mahoney, B. 2002. Walla Walla basin summer steelhead and bull trout radio telemetry project: 2002 Annual Report. Prepared by the Confederated Tribes of the Umatilla Indian Reservation for the Bonneville Power Administration. Portland, Oregon.
- McMahon, T.E., A.V. Zale, F.T. Barrows, J.H. Selong, and R.J. Danehy. 2007. Temperature and competition between bull trout and brook trout: A test of the elevation refuge hypothesis. *Transactions of the American Fisheries Society* 136:1313-1326.
- McPhail, J.D., and C.B. Murray. 1979. The early life-history and ecology of Dolly Varden (*Salvelinus malma*) in the Upper Arrow Lakes. University of British Columbia, Department of Zoology and Institute of Animal Resources, Vancouver, BC.
- 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.
- Morris, W.F., and D.F. Doak. 2002. *Quantitative conservation biology: theory and practice of population viability analysis*. Sinauer Associates, Sutherland, Massachusetts.
- Nichols, J.D., and J.E. Hines. 2002. Approaches for the direct estimation of λ , and demographic contributions to λ , using capture-recapture data. *Journal of Applied Statistics* 29(1):539-568.
- Northcote, R.G. 1992. Migration and residency in stream salmonids- some ecological considerations and evolutionary consequences. *Nordic Journal of Freshwater Research* 67:5-17.

- ODFW (Oregon Department of Fish and Wildlife). 1995. Bull trout spawning ground surveys Umatilla and Walla Walla basins. September 1, 1995 to October 31, 1995. Progress Report (Preliminary). Umatilla Fishery District, Pendleton, Oregon.
- ODFW (Oregon Department of Fish and Wildlife). 1996. Bull trout spawning ground surveys. Umatilla and Walla Walla basins. September 1, 1996 to October 31, 1996. Progress Report. Umatilla Fish District, Pendleton, Oregon.
- 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.
- 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 pages.
- 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. 1992. Bull trout investigations in the Metolius River-Lake Billy Chinook system. Pages 37-44 in P. Howell and D. V. Buchanan, editors. *Proceedings of the Gearhart Mountain bull trout workshop*. Oregon Chapter of the American Fisheries Society, Corvallis, Oregon.
- Ratliff, D.E., and P.J. Howell. 1992. The status of bull trout populations in Oregon. *In Proceedings of the Gearhart Mountain Bull Trout Workshop*. Oregon Chapter of the American Fisheries Society.
- Riehle, M.D. 1993. Metolius Basin water resources monitoring. Progress report 1988-1992. US Forest Service. Deschutes National Forest, Bend, Oregon.
- Rieman, B.E., and F.W. Allendorf. 2001 Effective population size and genetic conservation criteria for bull trout. *North American Journal of Fisheries Management* 21:756-764
- Rieman, B.E., and K.A. Apperson. 1989. Status and analysis of salmonid fisheries. Westslope cutthroat trout symposium and analysis of fishery information. Project F-73-R-II. Subproject Number 2. Job Number 1. Idaho Department of Fish and Game, Boise, Idaho.
- Rieman, B.E., and J.D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. USDA 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.
- Rieman, B.E., D.J. Isaak, S. Adams, D. Horan, D. Nagel, C. Luce, and D. Myers. 2007. Anticipated climate warming effects on bull trout habitats and populations across the interior Columbia River basin. *Transactions of the American Fisheries Society* 136:1552-1565.
- Reist, J.D., G. Low, J.D. Johnson, and D. McDowell. 2002. Range extension of bull trout, *Salvelinus confluentus*, to the central Northwest Territories, with notes on identification and distribution of Dolly Varden, *Salvelinus malma*, in the western Canadian Arctic. *Arctic* 55:70-76.

- Rode, M. 1988. Bull trout, *Salvelinus confluentus* (Suckley), in the McCloud River, status and recovery recommendations (draft). Inland Fishing Administration Report, California Department of Fish and Game, Sacramento, California.
- Schlosser, I.J. 1991. Stream fish ecology: A landscape perspective. *Bioscience* 41:704-712.
- Soule, M.E. 1987. Viable populations for conservation. Cambridge University Press. New York, New York.
- Thiesfeld, S.L., J. C. Kern, A.R. Dale, M.W. Chilicote, and M.A. Buckman. 1999. Lake Billy Chinook sockeye salmon and kokanee research study 1996-1998. Contract Completion Report. FERC Number 2030. 153 pages.
- Thurrow, 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.
- Underwood, K.D., S.W. Martin, M.L. Schuck, and A.T. Scholz. 1995. Investigations of bull trout (*Salvelinus confluentus*), steelhead trout (*Oncorhynchus mykiss*), and spring chinook salmon (*O. tshawytscha*) interactions in southeast Washington streams. BPA report. Project Number 90-053. Contract Number DE-B179-91BP17758. 173 pages.
- USFWS (US Fish and Wildlife Service). 1998. Endangered and threatened wildlife and plants; determination of Threatened Status for the Klamath River and Columbia River Distinct Population segments of bull trout.
- USFWS (US Fish and Wildlife Service). 1999. Determination of threatened status for bull trout in the coterminous United States. Pages 58910-58933 in Federal Register 64.
- Walla Walla Subbasin Plan. 2004. Prepared for the Northwest Power Planning Council, submitted by Walla Walla County (on behalf of the Walla Walla Watershed Planning Unit) and the Walla Walla Basin Watershed Council.
- 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.
- Washington Department of Wildlife. 2000. Final bull trout/Dolly Varden management and recovery plan. Washington Department of Wildlife, Fisheries Management Division, Olympia, Washington.
- Whitesel, T.A., and 7 coauthors. 2004. Bull trout recovery planning: a review of the science associated with population structure and size. Science Team Report # 2004-01, U.S. Fish and Wildlife Service, Regional Office, Portland, Oregon. Website: <http://columbiariver.fws.gov/scienceteam.htm#product>
- Ziller, J.S. 1992. Distribution and relative abundance of bull trout in the Sprague River subbasin, Oregon. Pages 18-29 in P. Howell and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain bull trout workshop. Oregon Chapter of the American Fisheries Society, Corvallis, Oregon.

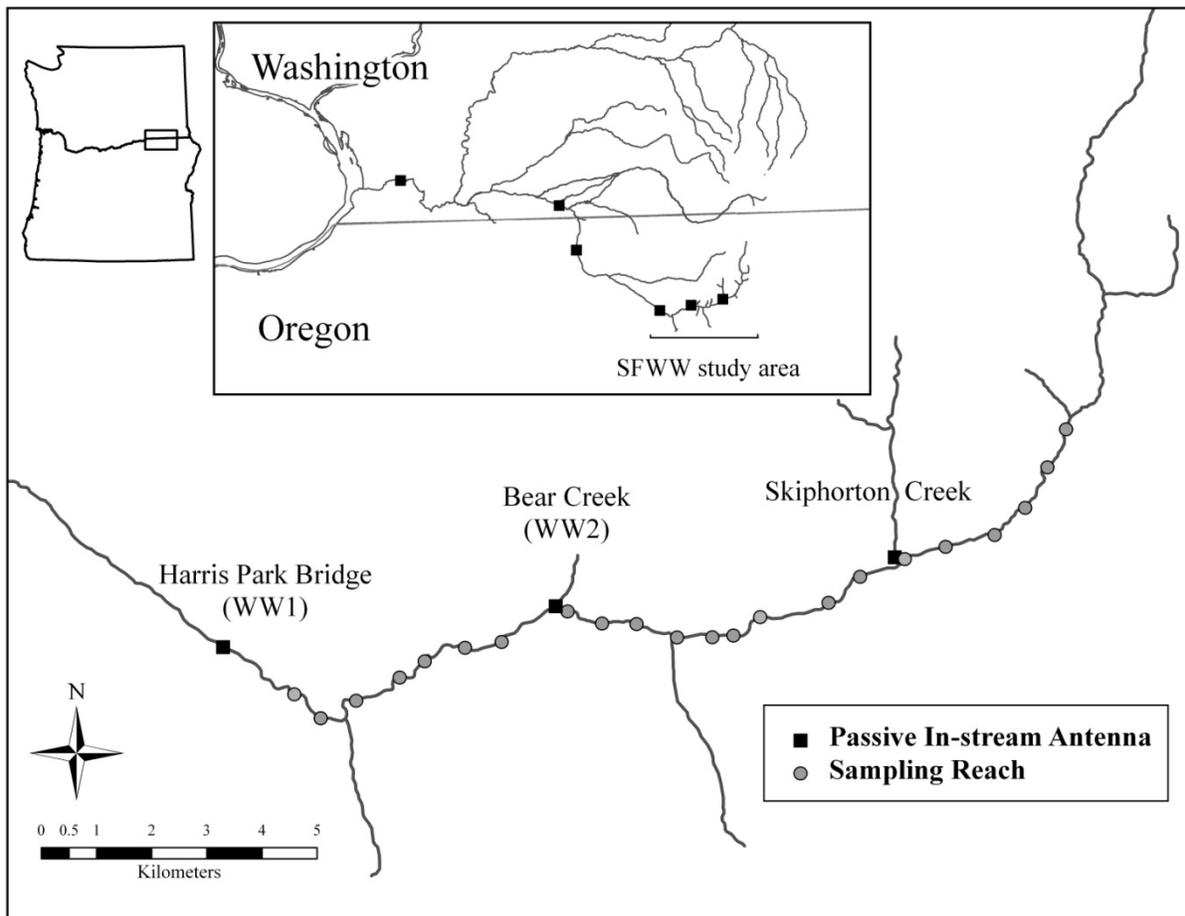
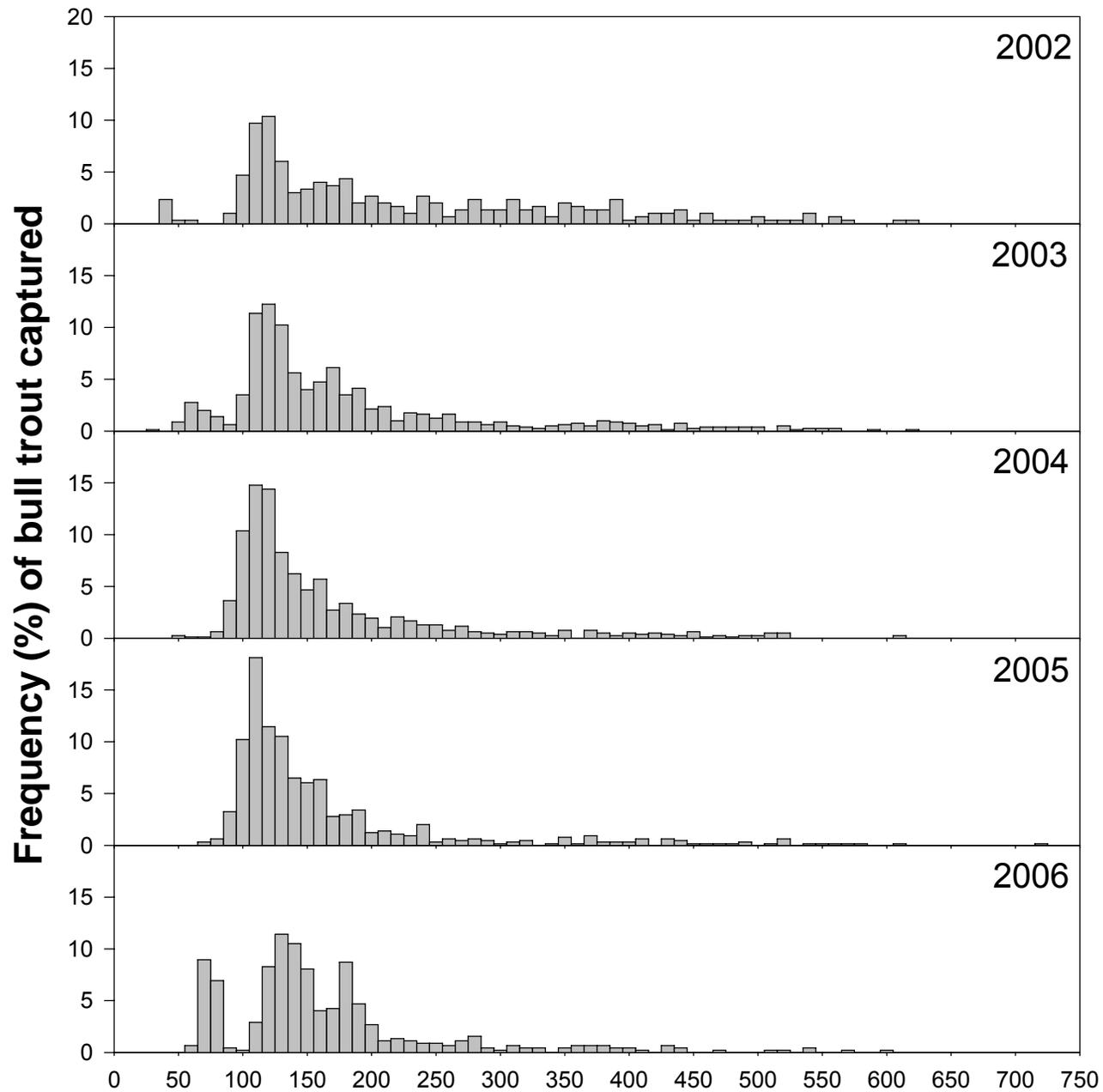


Figure 1. Map of the South Fork Walla Walla (SFWW) River, Oregon, showing original 22 study reaches (gray circles) and passive in-stream antenna (PIA or detectors) locations (black squares) within our primary study area. Inset shows location of three other PIA in the Walla Walla and Columbia rivers.



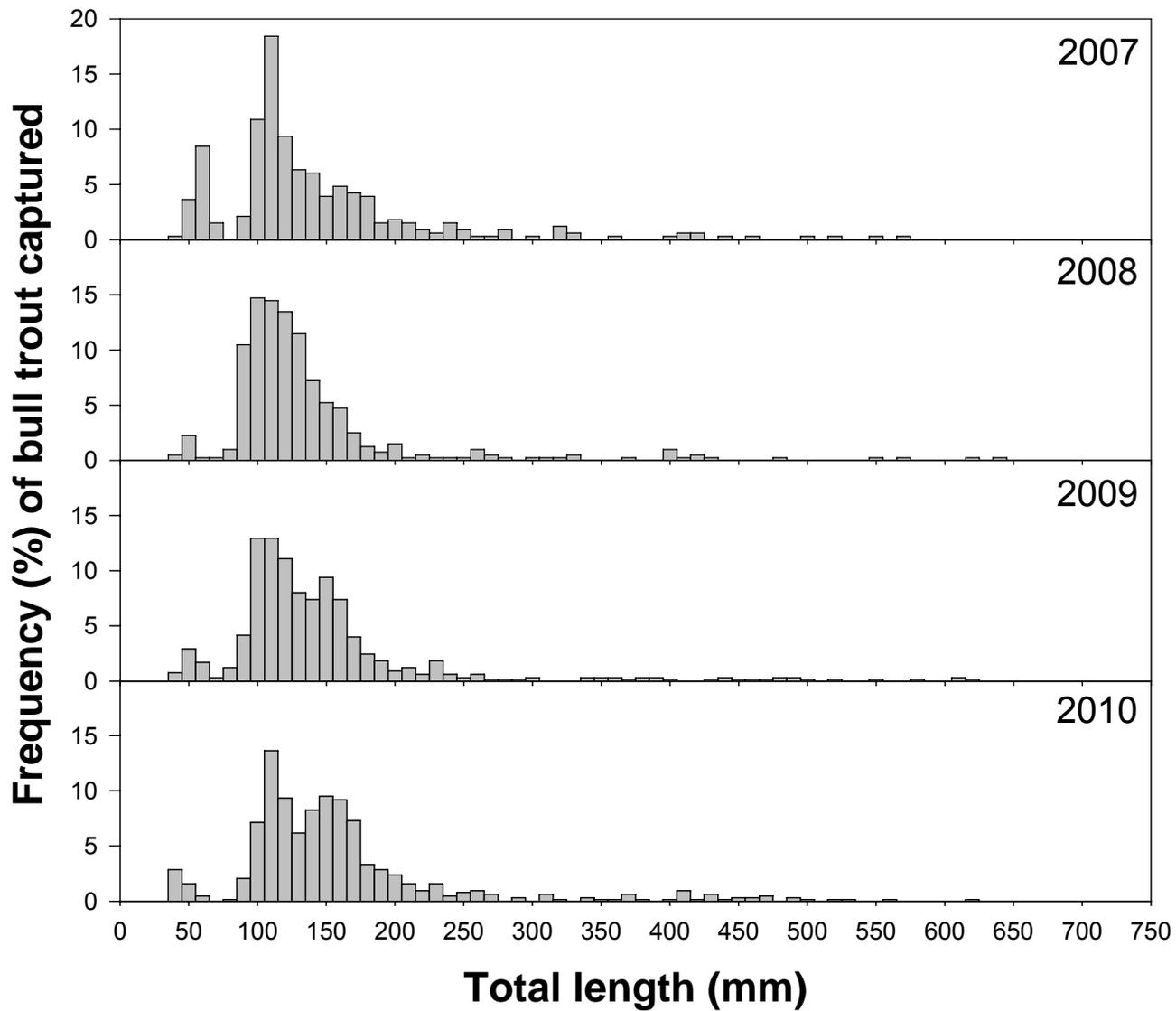
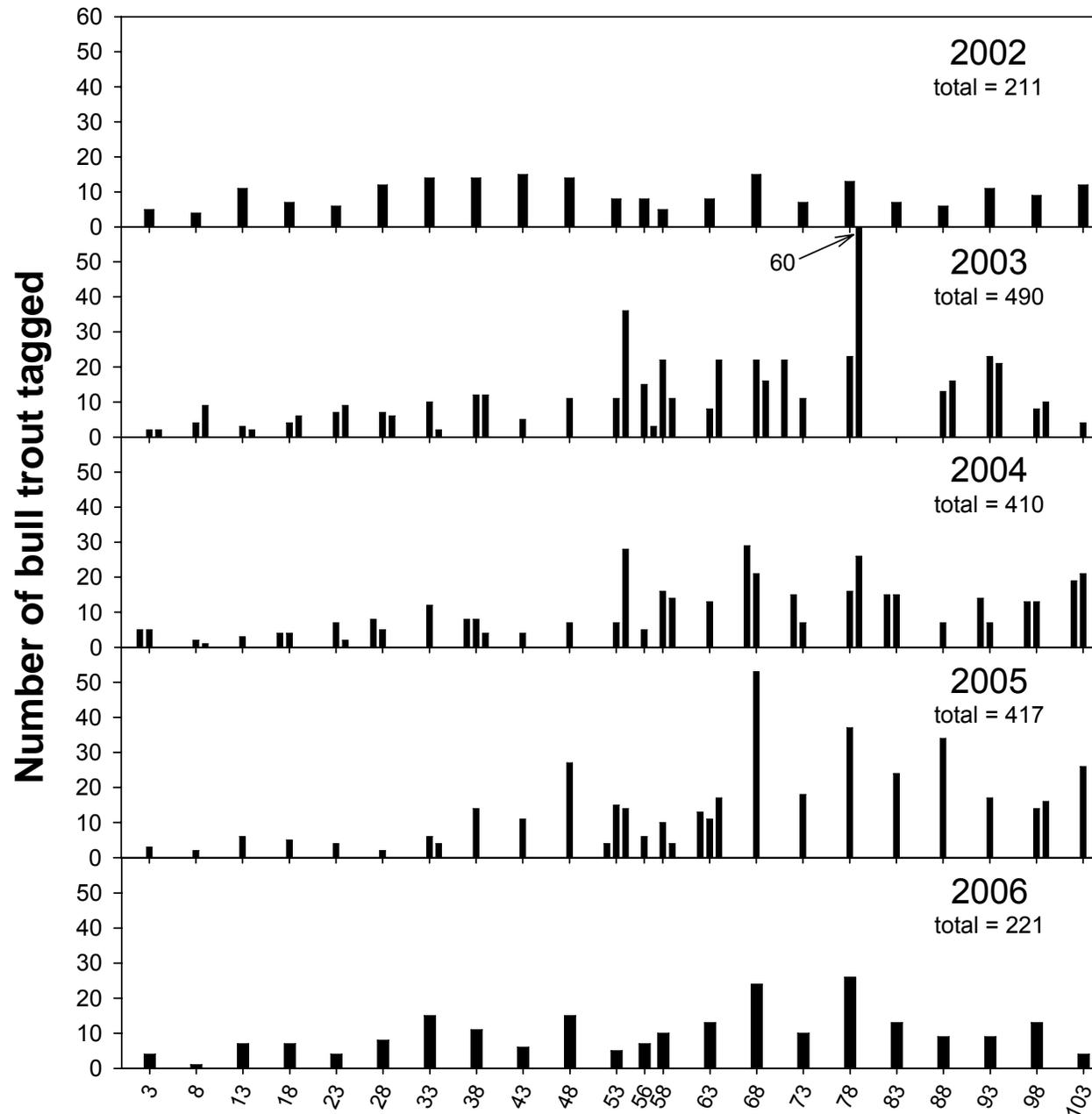


Figure 2. Length-frequency (% of total catch) distribution of bull trout captured and handled in the South Fork Walla Walla River, Oregon, 2002 – 2010. Note, figure spans two pages.



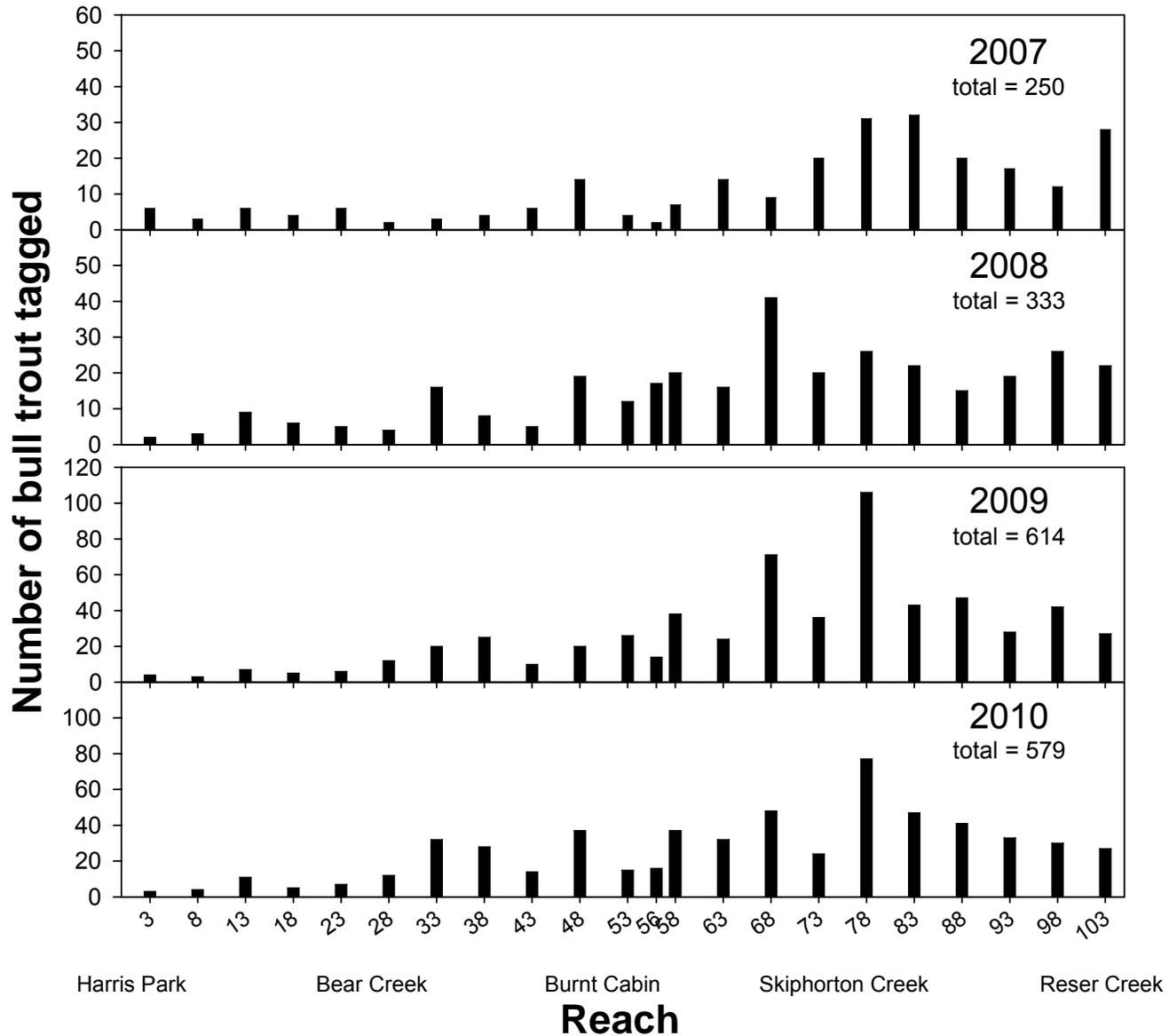
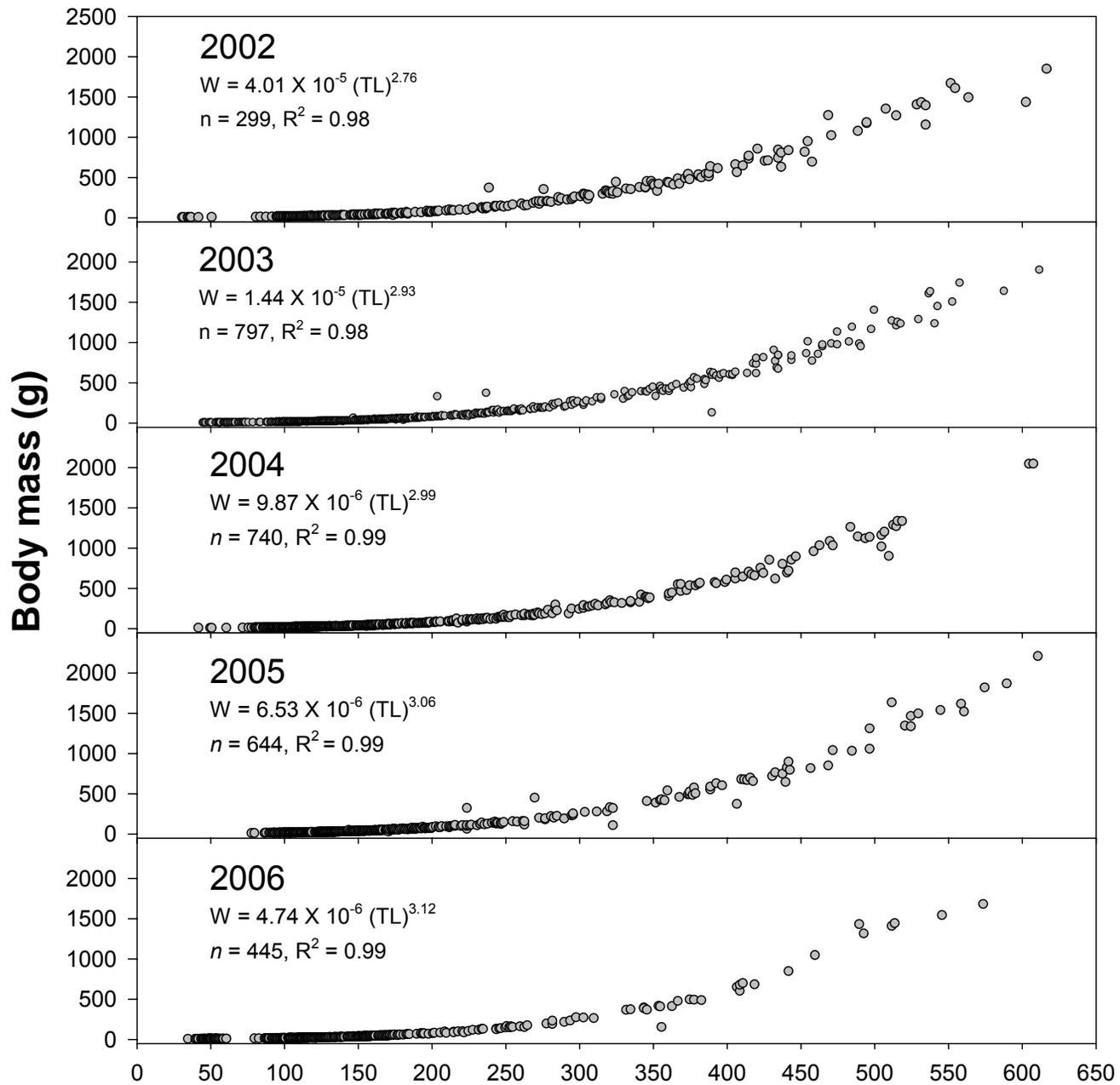


Figure 3. Number of bull trout tagged by reach in the South Fork Walla Walla River, Oregon, 2002 - 2010. Reaches are numbered from bottom (0 at Harris Park) to top of the study site (103 at Reser Creek). Total numbers tagged are given below sample year. Note scale change in 2009 and 2010 panels, and figure spans two pages.



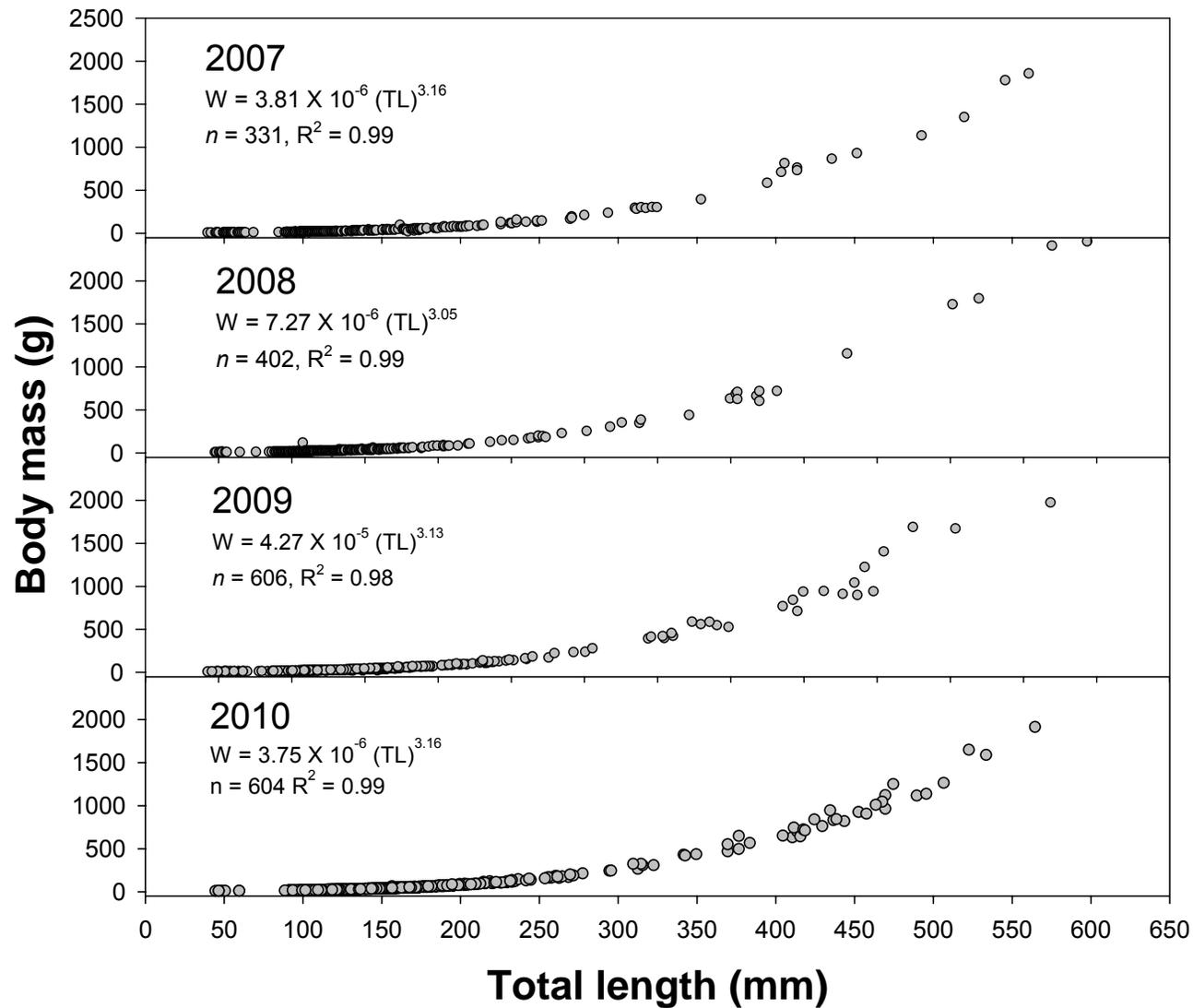


Figure 4. Length-weight regression for bull trout captured in the South Fork Walla Walla River, Oregon from 2002 – 2010. Regression equation, sample size (n), and R² values are given on each panel. Note figure spans two pages.

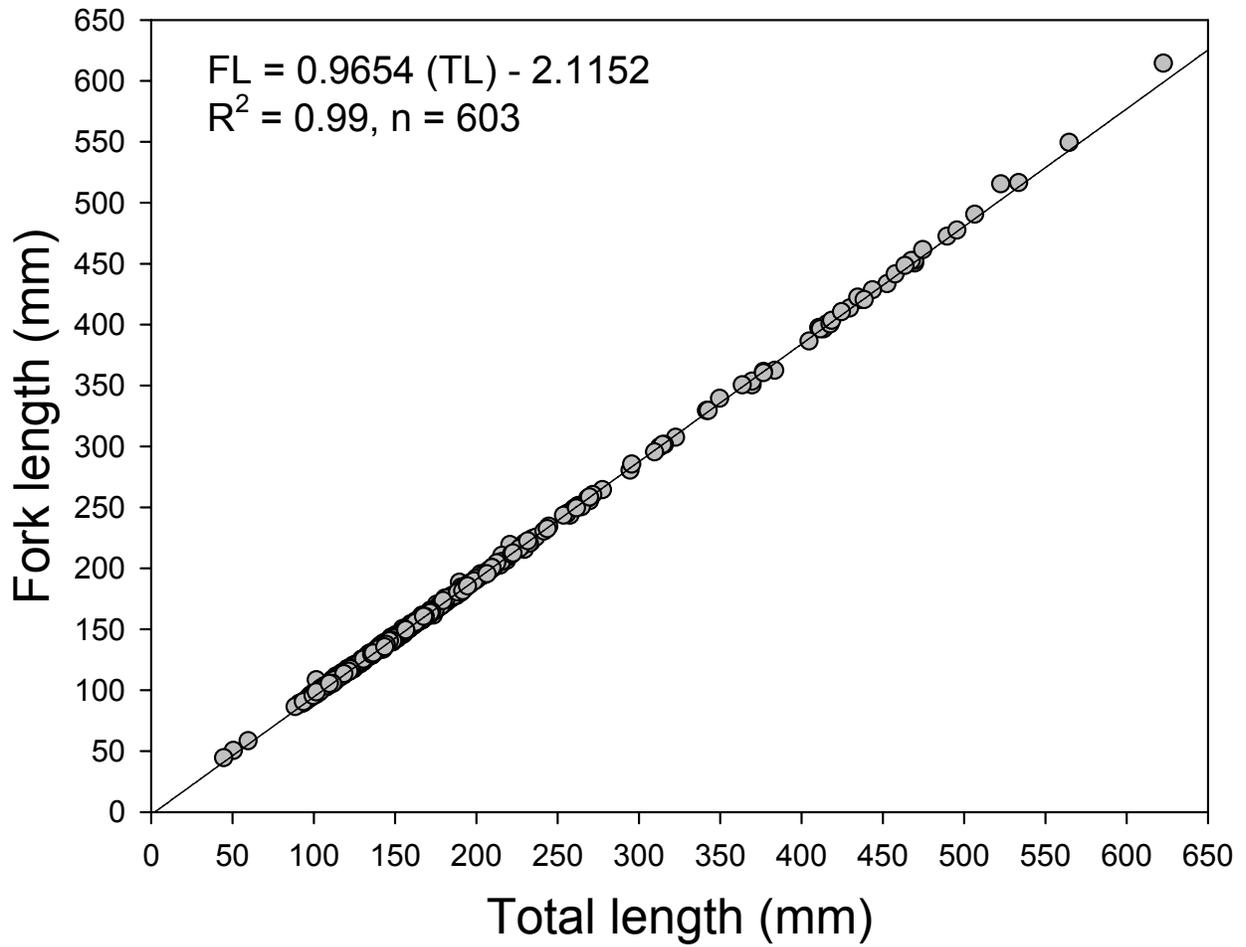


Figure 5. Relationship between total length (TL) and fork length (FL) for bull trout tagged in the South Fork Walla Walla River, Oregon, 2010. Linear regression equation, R^2 value, and sample size (n) are given.

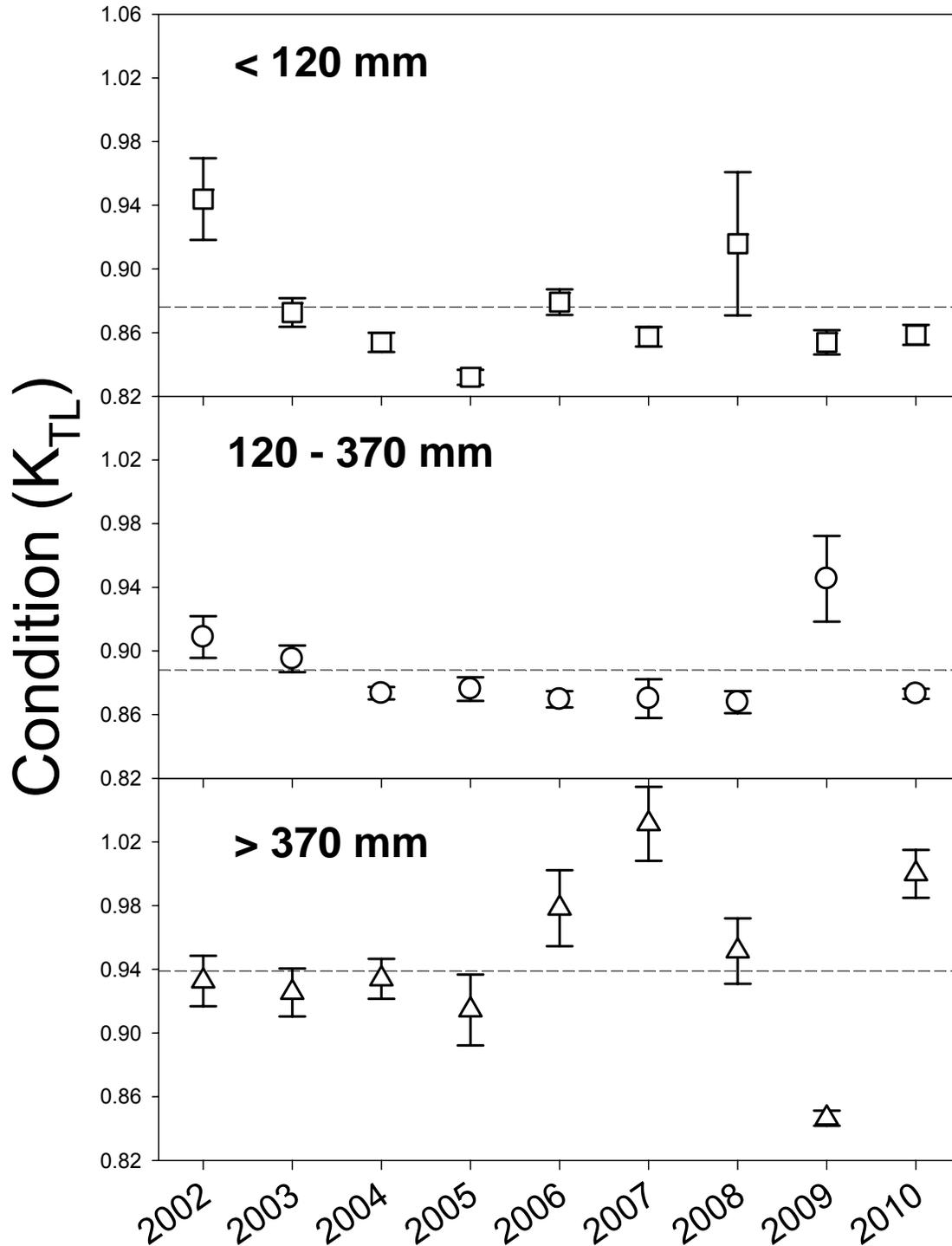


Figure 6. Condition (Fulton's $K_{TL} \pm 1$ SE) of three different size classes of bull trout handled in the South Fork Walla Walla River, Oregon, 2002 - 2010. Dashed line represents size-specific, 9-year average K_{TL} .

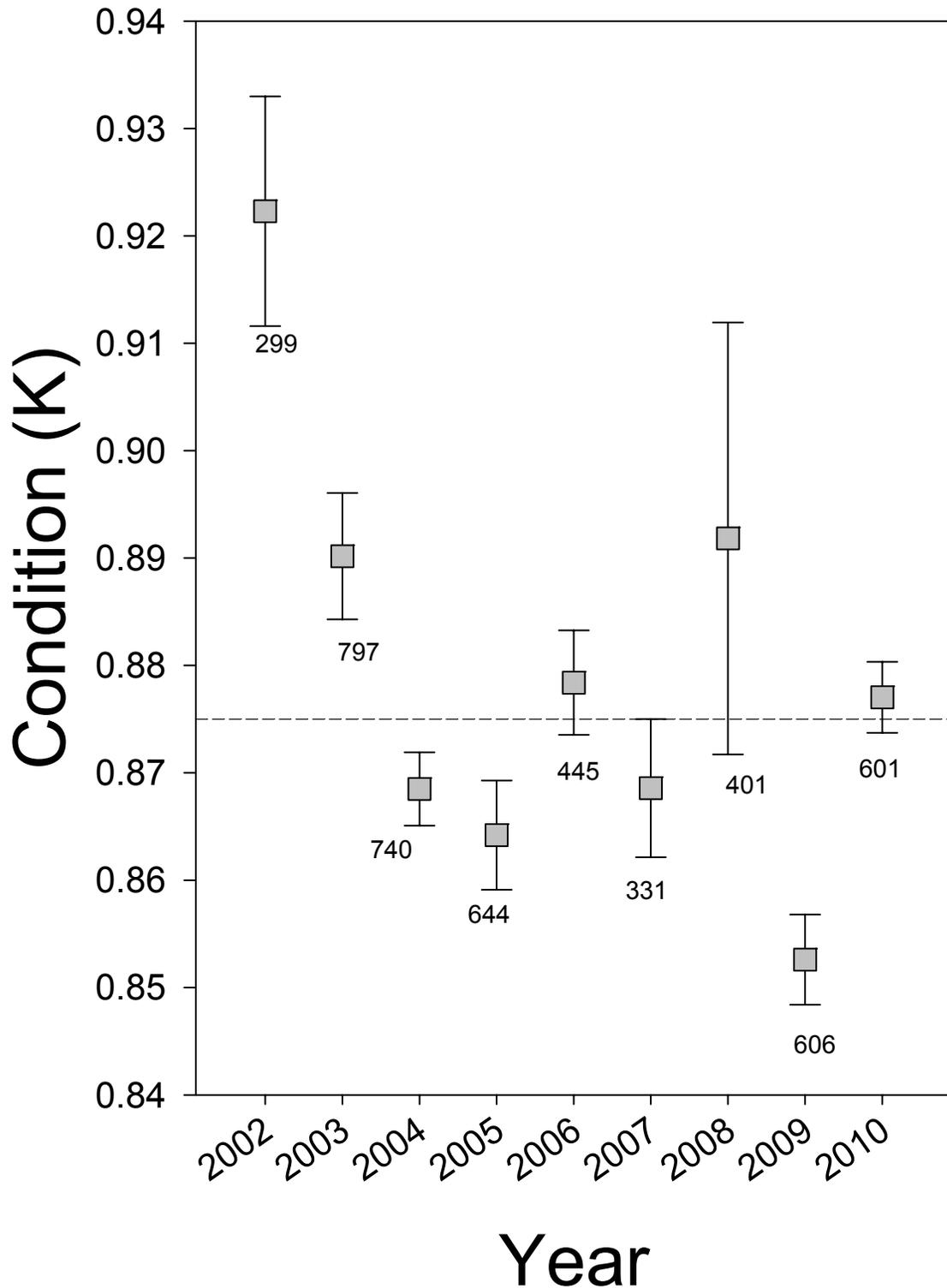


Figure 7. Average annual condition (Fulton's $K_{TL} \pm 1$ SE) of bull trout (all sizes combined) sampled in the South Fork Walla Walla River, Oregon (2002 – 2010). Sample size is given for each year. Dashed line represents nine-year average K_{TL} .

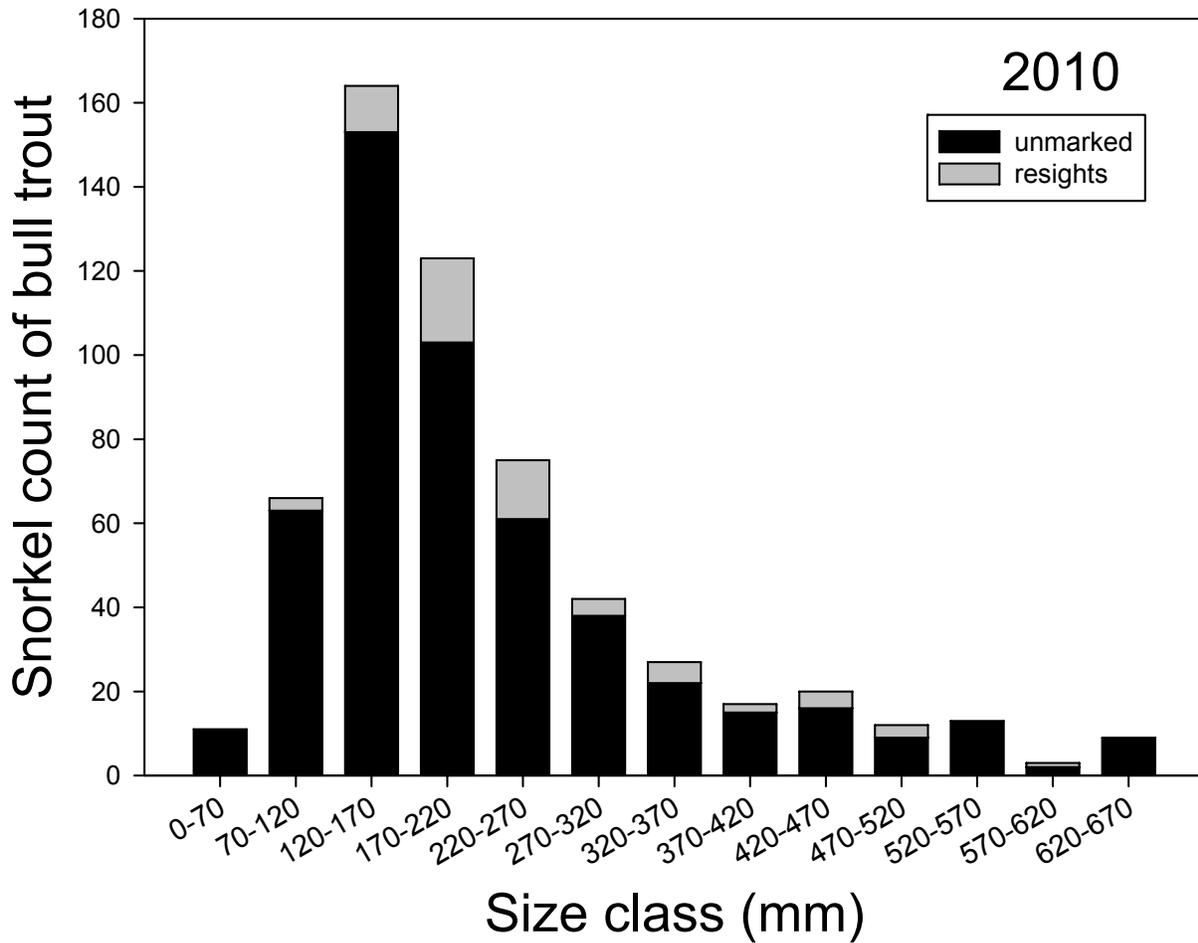
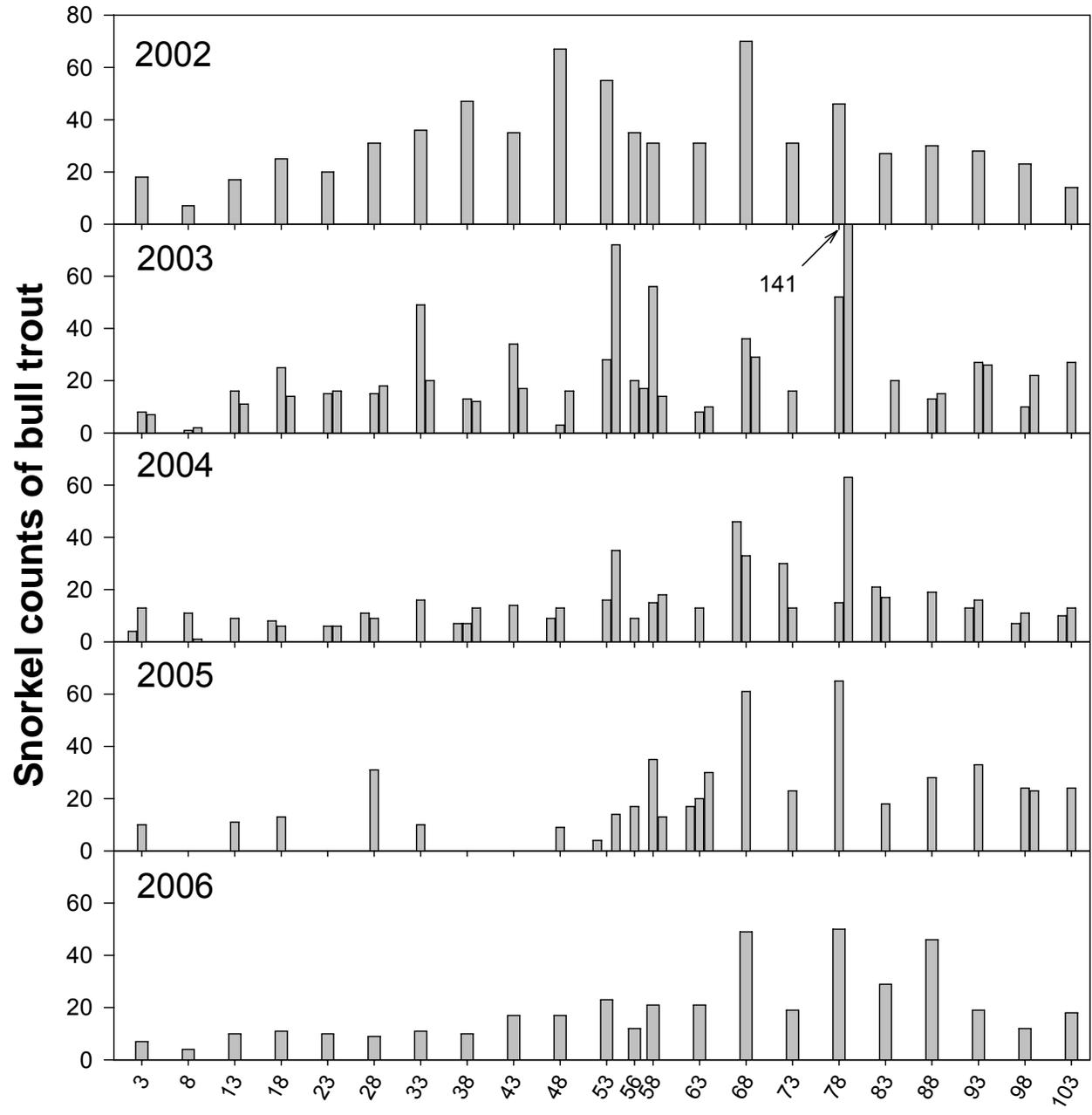


Figure 8. Number of bull trout in 50-mm size bins observed during snorkel-count surveys in the South Fork Walla Walla River, Oregon in 2010: black bars are newly sighted fish and gray bars are resighted (previously marked) fish.



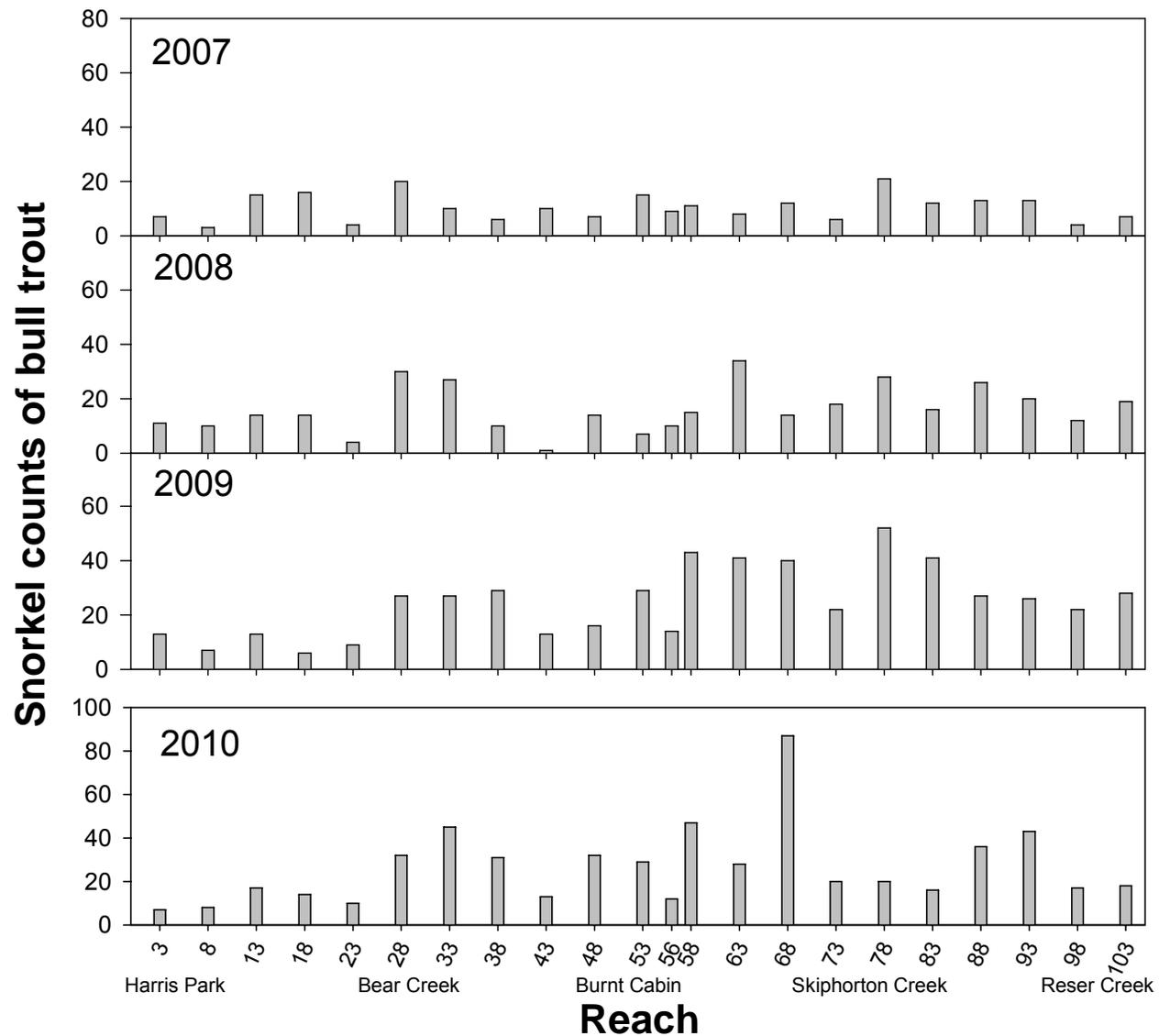


Figure 9. Number of bull trout counted during snorkel surveys in sample reaches of the South Fork Walla Walla River, Oregon, 2002 - 2010. Reaches are numbered from bottom (0 at Harris Park) to top of the study site (103 at Reser Creek). No bar implies that no sampling was conducted in that particular reach. Percentage of stream sampled in 2003 and 2004 and 2005 changed to approximately 47%, 47% and 30% of study area, respectively. Note scale change in 2010.

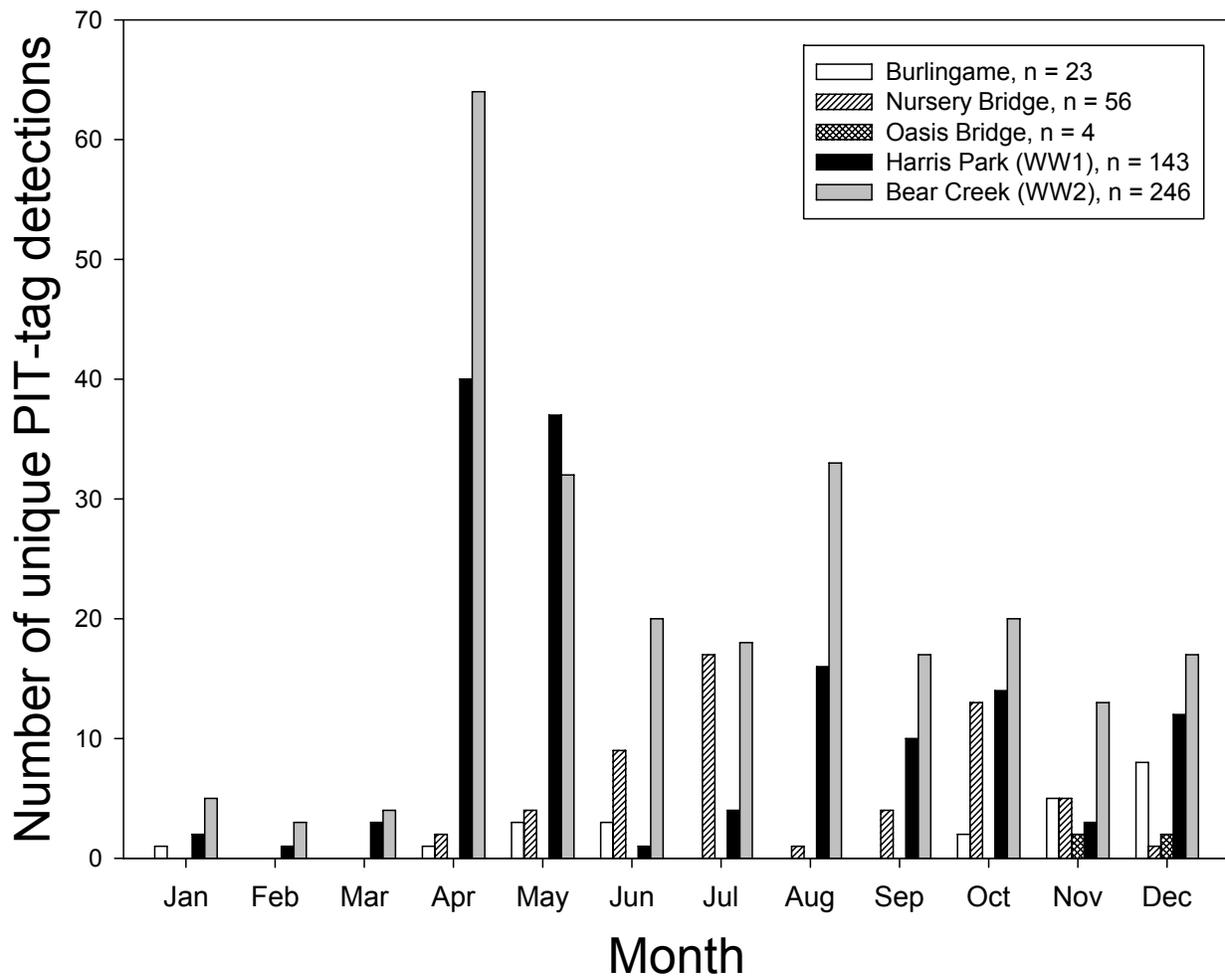


Figure 10. The number of unique PIT-tag detections per month in 2010 at each of the five passive in-stream antenna (PIA) arrays located in the South Fork Walla Walla River and main stem Walla Walla River system, Oregon. Total detections (n) by PIA are given in legend.

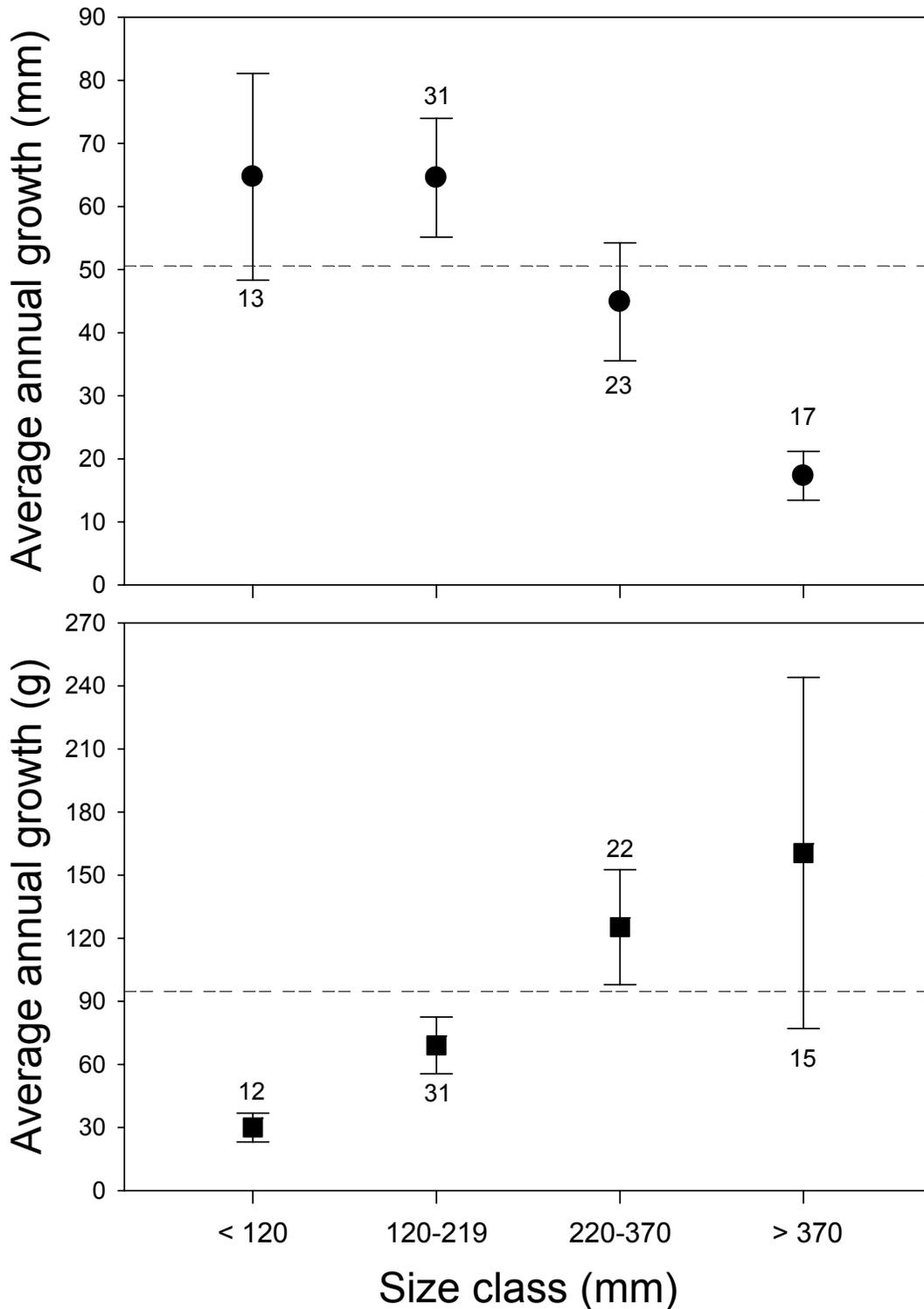


Figure 11. Average annual growth (± 2 SE) in total length (mm, top panel) and mass (g, bottom panel) for four size classes of bull trout tagged and recaptured in the South Fork Walla Walla River, Oregon, 2002 – 2010. Sample sizes are given above or below error bars. Dashed lines indicate mean across all size classes.

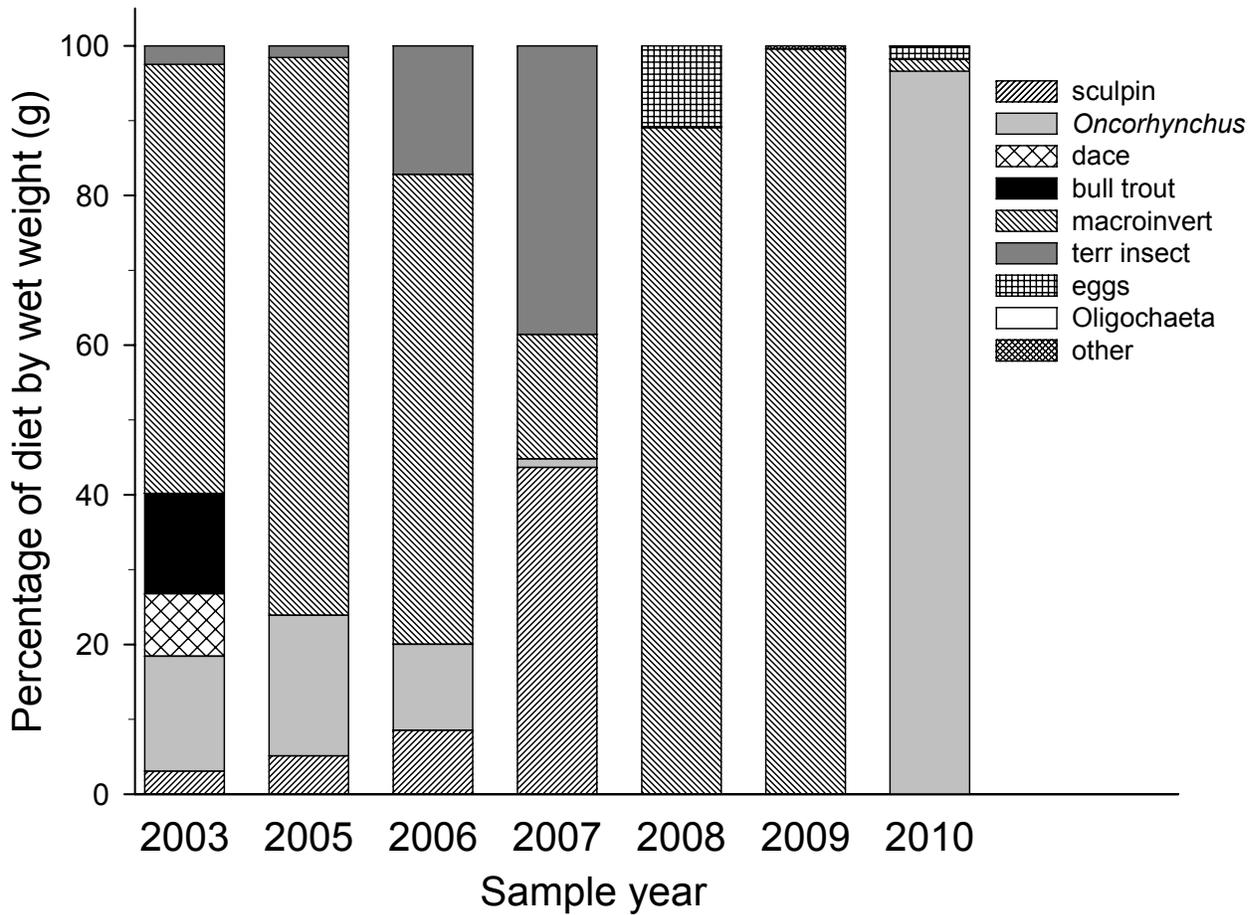


Figure 12. Bull trout diet composition from sacrificed bull trout in the South Fork Walla Walla River, Oregon, 2003 and 2005 - 2010. “macroinvert” = aquatic macroinvertebrates. “terr insect” = terrestrial insects. “other” = vegetation.

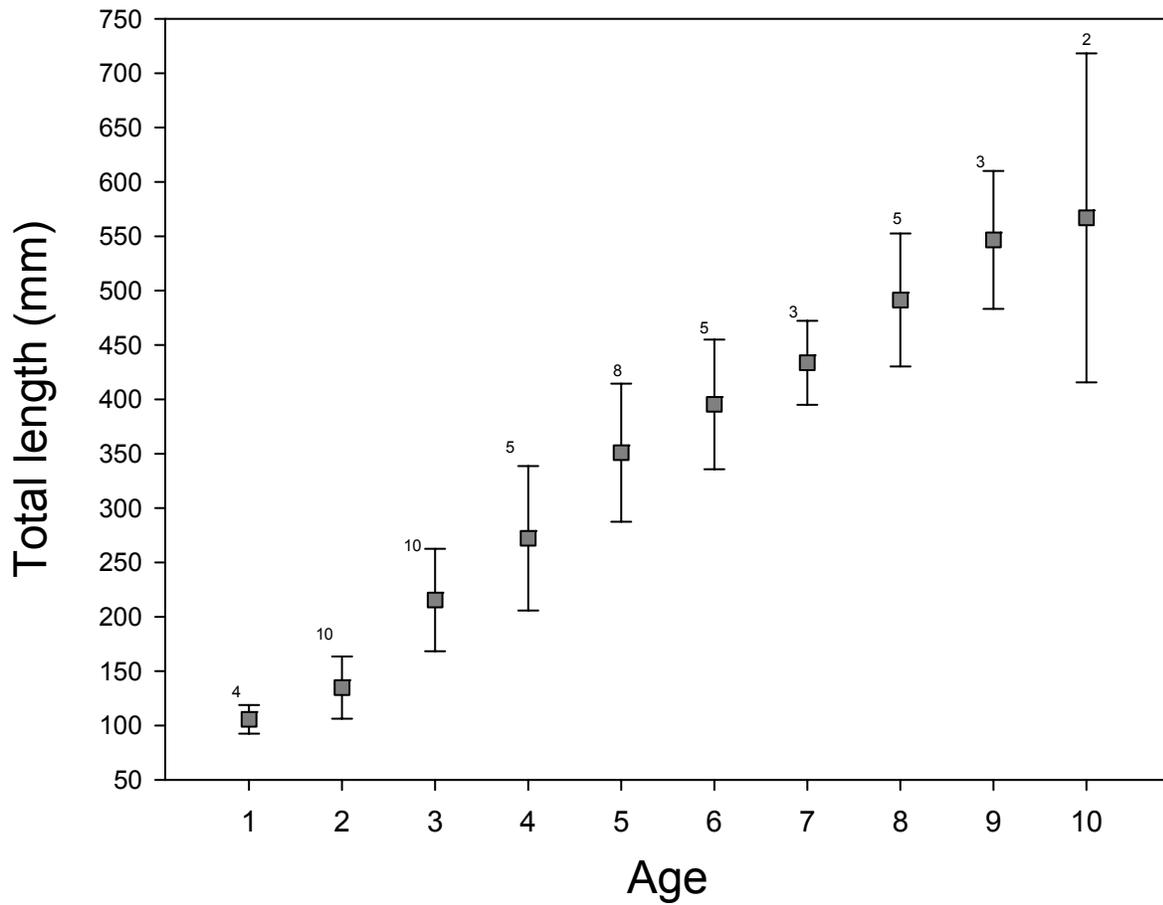


Figure 13. Bull trout total length (mean \pm 1 SD) and corresponding age estimated from otoliths of sacrificed bull trout in the South Fork Walla Walla River, Oregon, 2002 - 2010. Sample size is given above error bars.

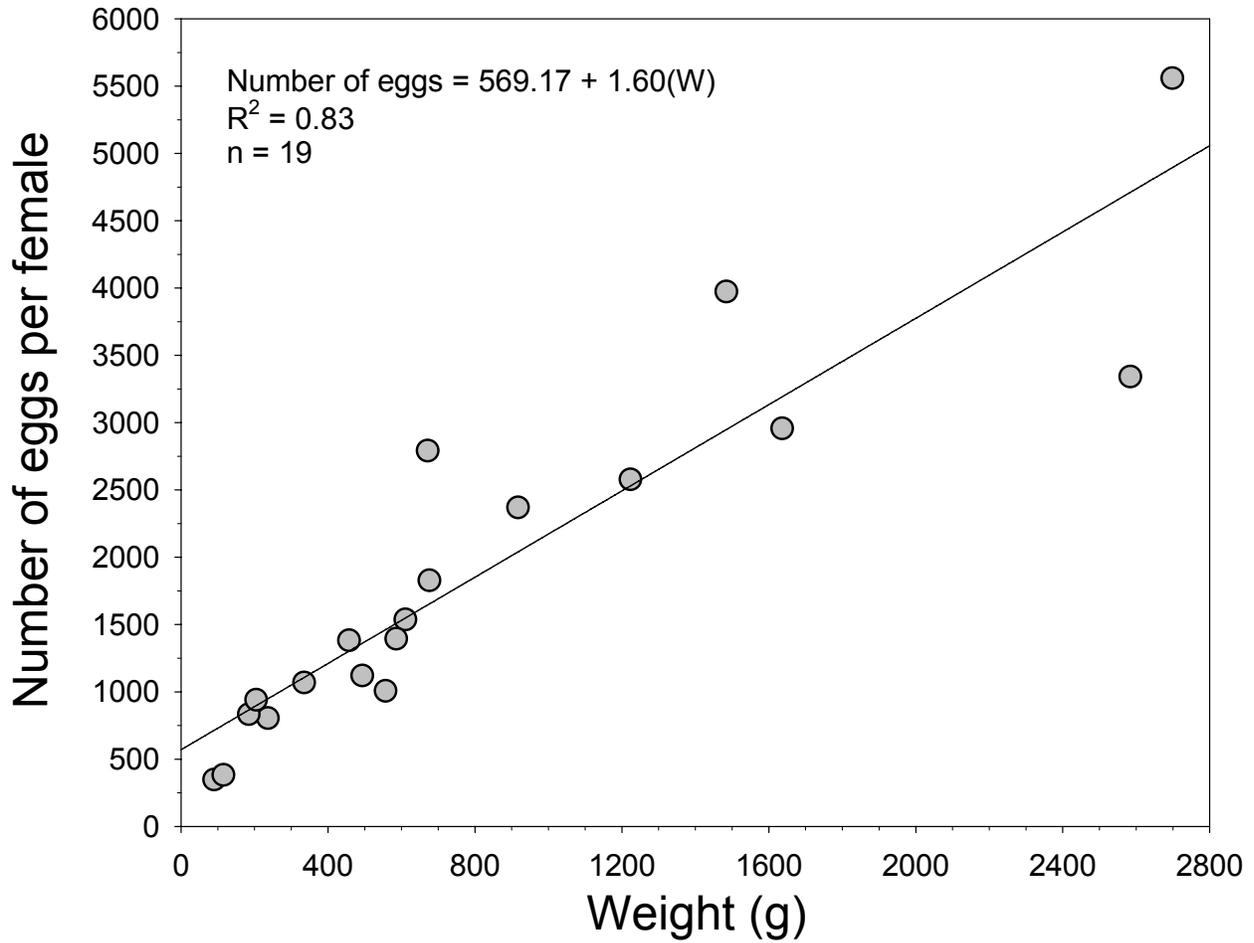


Figure 14. Female bull trout fecundity by weight for sacrificed bull trout in the South Fork Walla Walla River, Oregon, 2002 - 2010. Linear regression equation, R^2 -value, and sample size (n) are given.

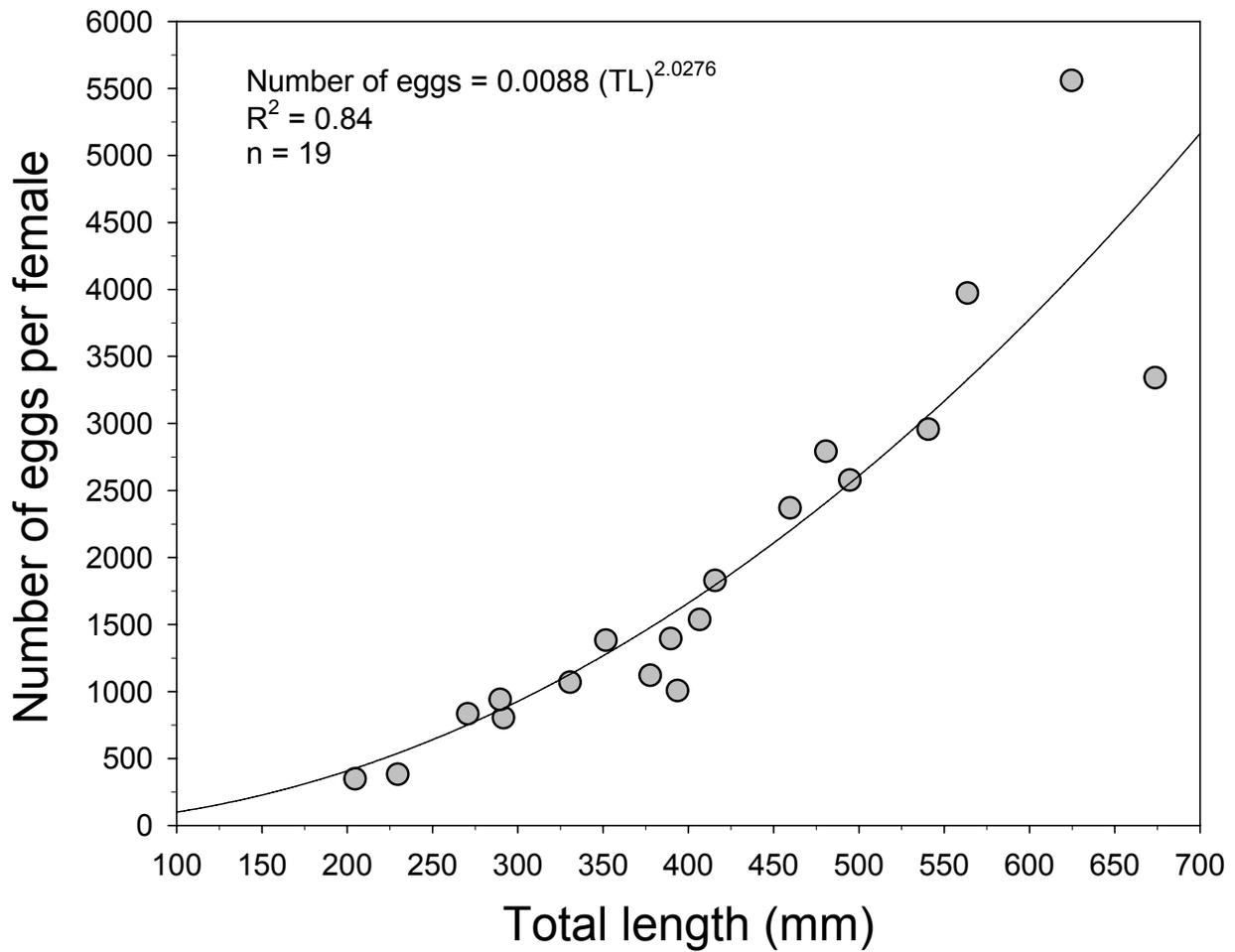


Figure 15. Female bull trout fecundity by total length for sacrificed bull trout in the South Fork Walla Walla River, Oregon, 2002 - 2010. Regression equation, R²-value, and sample size (n) are given.

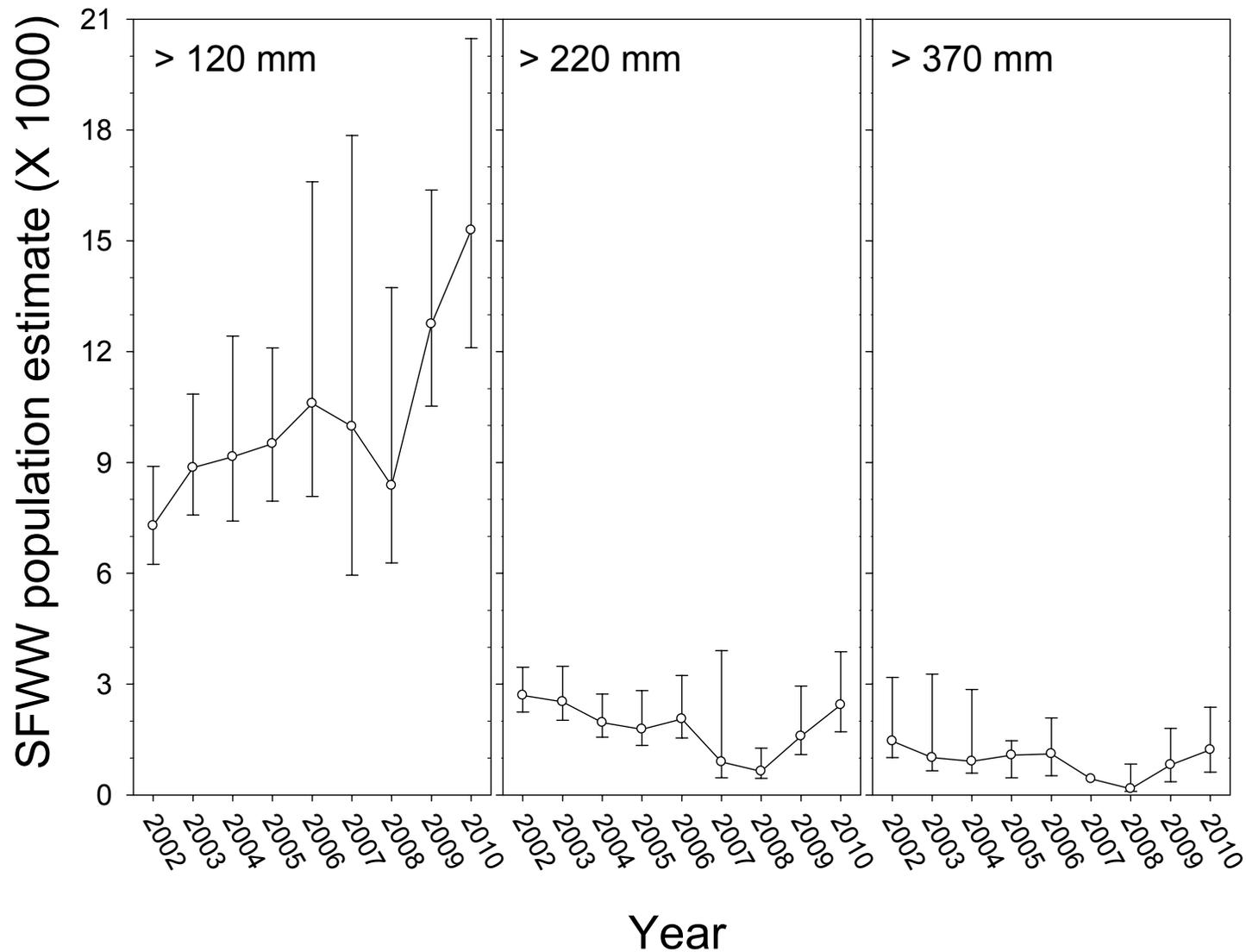


Figure 16. Annual population estimates (\pm 95% CI) for three size groupings of bull trout in the South Fork Walla Walla River, Oregon, 2002 - 2010. Due to low sample size, no CI were obtainable for the bull trout population component > 370 mm in 2007. Population size was estimated for the entire study area from Harris Park bridge to Reser Creek.

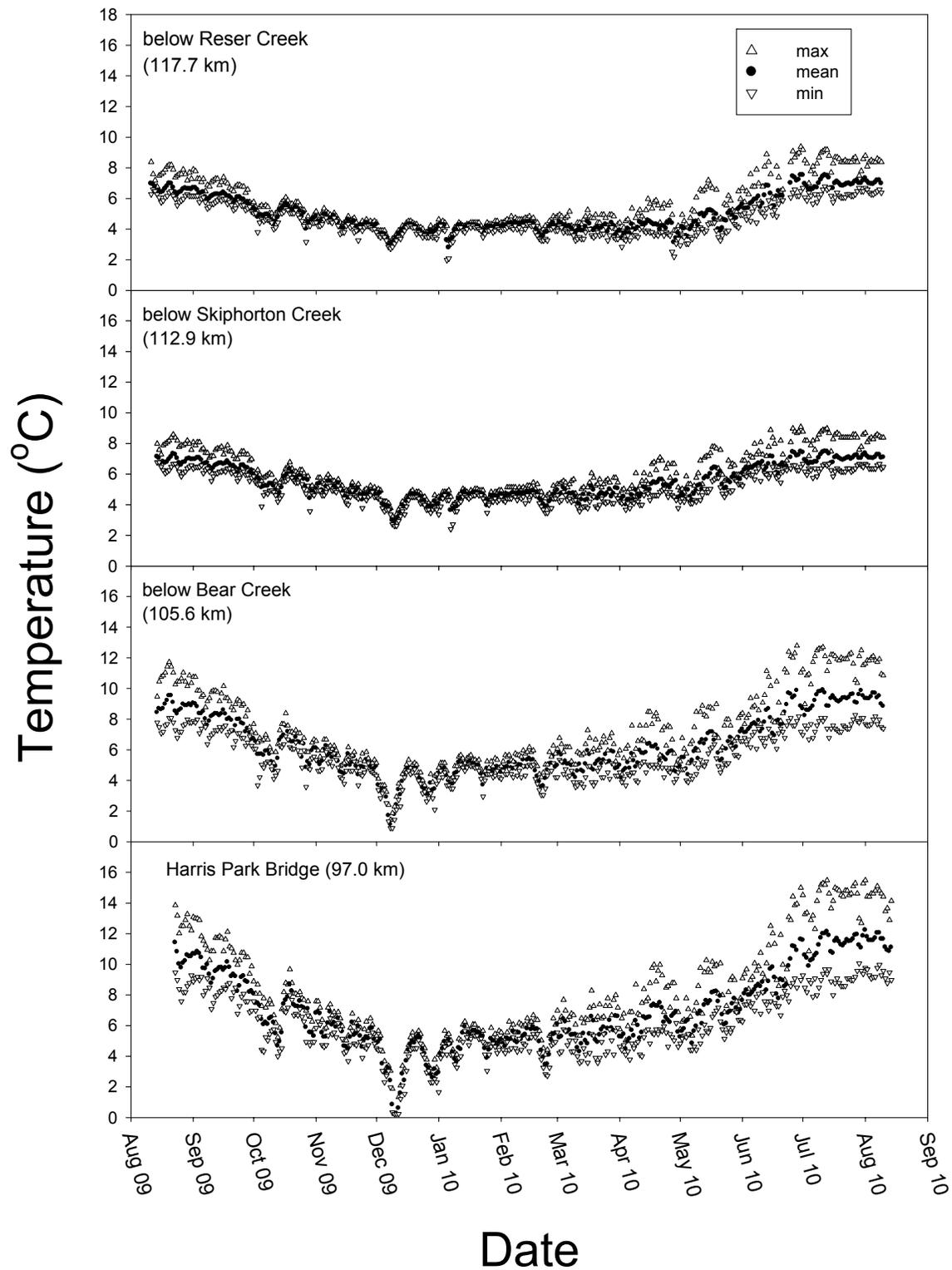


Figure 17. Daily temperatures (maximum, mean, minimum) recorded at four locations in the South Fork Walla Walla River, Oregon, from August 2009 to August 2010. River km describe the distance of the location upstream from the confluence of the Walla Walla and Columbia rivers. Our study area is located between river km 97.0 and 117.7.

APPENDIX 1

Revised objectives and tasks specified to meet the annual project goals

Objective 1. Comprehensive bull trout population assessment and monitoring (annual):

- Task 1.1 Marking.
- Task 1.2 Recapture.
- Task 1.3 Snorkel surveys for juvenile densities.
- Task 1.4 Adult and egg information, egg-to-parr survival.

Objective 2. Innovative pass-through PIT-tag monitoring system (Annual):

- Task 2.1 Tagging, detection, and fish movement.
- Task 2.2 Working with USFWS, CRFPO, develop and maintain tagging database
- Task 2.3 Synthesis of eight years of tagging, recapture, movement, migration, and life-history patterns. **2010.**

Objective 3. Population vital rate data analysis: Based on information gathered as part of Objectives 1-2 above (Annual):

- Task 3.1 Analysis of mark/recapture data: population estimates and movement.
- Task 3.2 Analysis of additional population-level data (e.g., snorkel, redd counts etc.)
- Task 3.3 Analysis of key vital rates and demographic characteristics: age, size, growth, survival, fecundity, cohort size estimates by size class, and life history expression.

Objective 4. Early life history and habitat variability study (2007 - 2010):

- Task 4.1 Field work associated with this task is complete (in 2007 we initiated a 3-year comprehensive study of early-life stage survival in relation to natural and anthropogenic-influenced (land use) variation in habitat type and quality)
- Task 4.2 Analyze and synthesize two years of 'early life history and habitat variability data' already collected. ONGOING: **2010 - 2011.**

Objective 5. Using comprehensive data and information described in Objectives 1-4 above, build a comprehensive (and transferrable) template for evaluating recovery options for bull trout and informing the RMEG NatureServ risk categorization process (2010 - 2012)

- Task 5.1 Build, update, and improve population viability and persistence model.
- Task 5.2 Connectivity and patch dynamics: Build and use predictive models to assess the importance of riverscape connectivity on the distribution of an imperiled fish species given habitat fragmentation and climate change. **(2008 - 2010)**
- Task 5.3. Assess options for including indices of connectivity as a RMEG NatureServ ranking criteria

APPENDIX 2

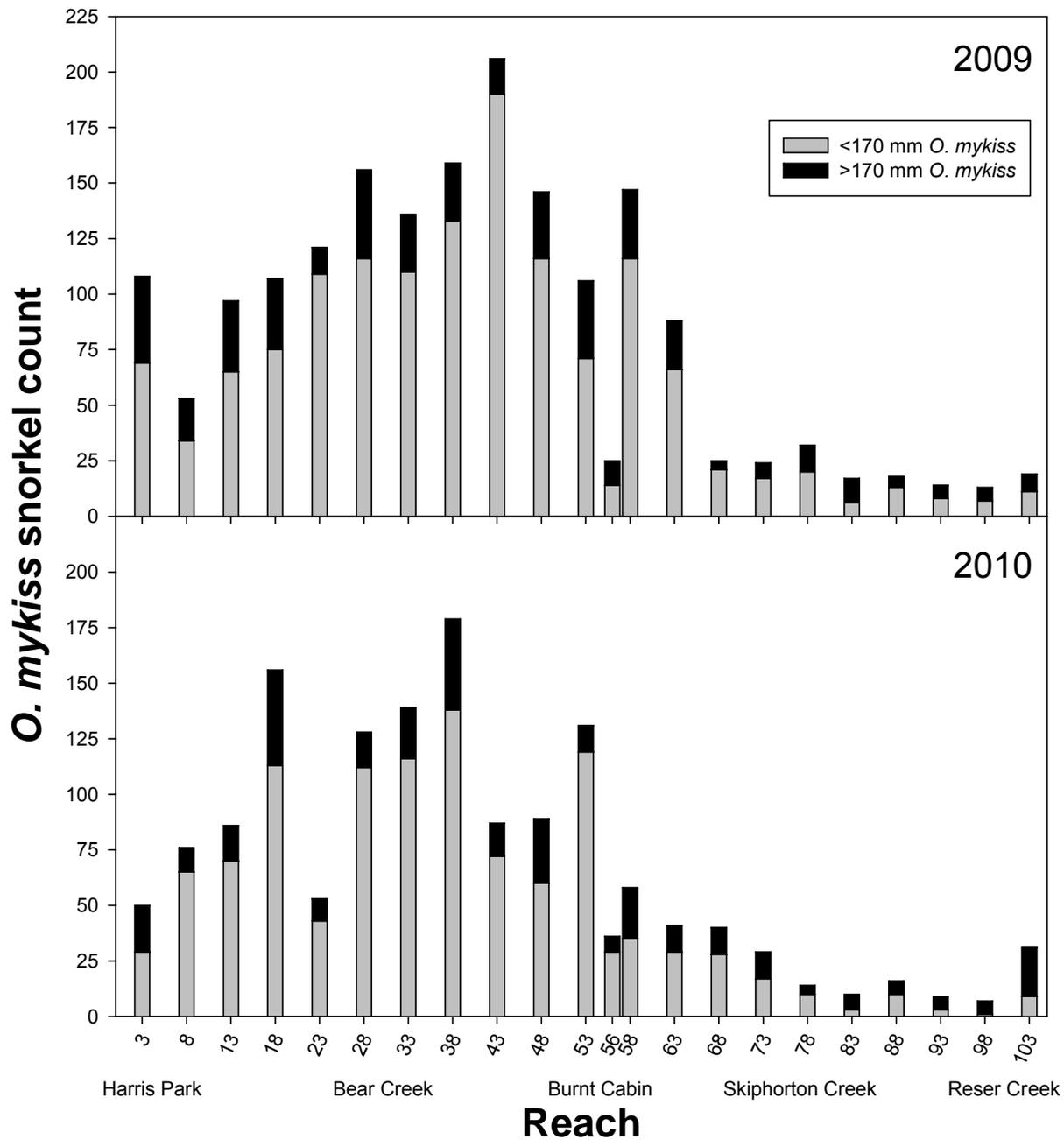


Figure A2.1. *Oncorhynchus mykiss* (by size class) snorkel counts in the South Fork Walla Walla River in 2009 and 2010.

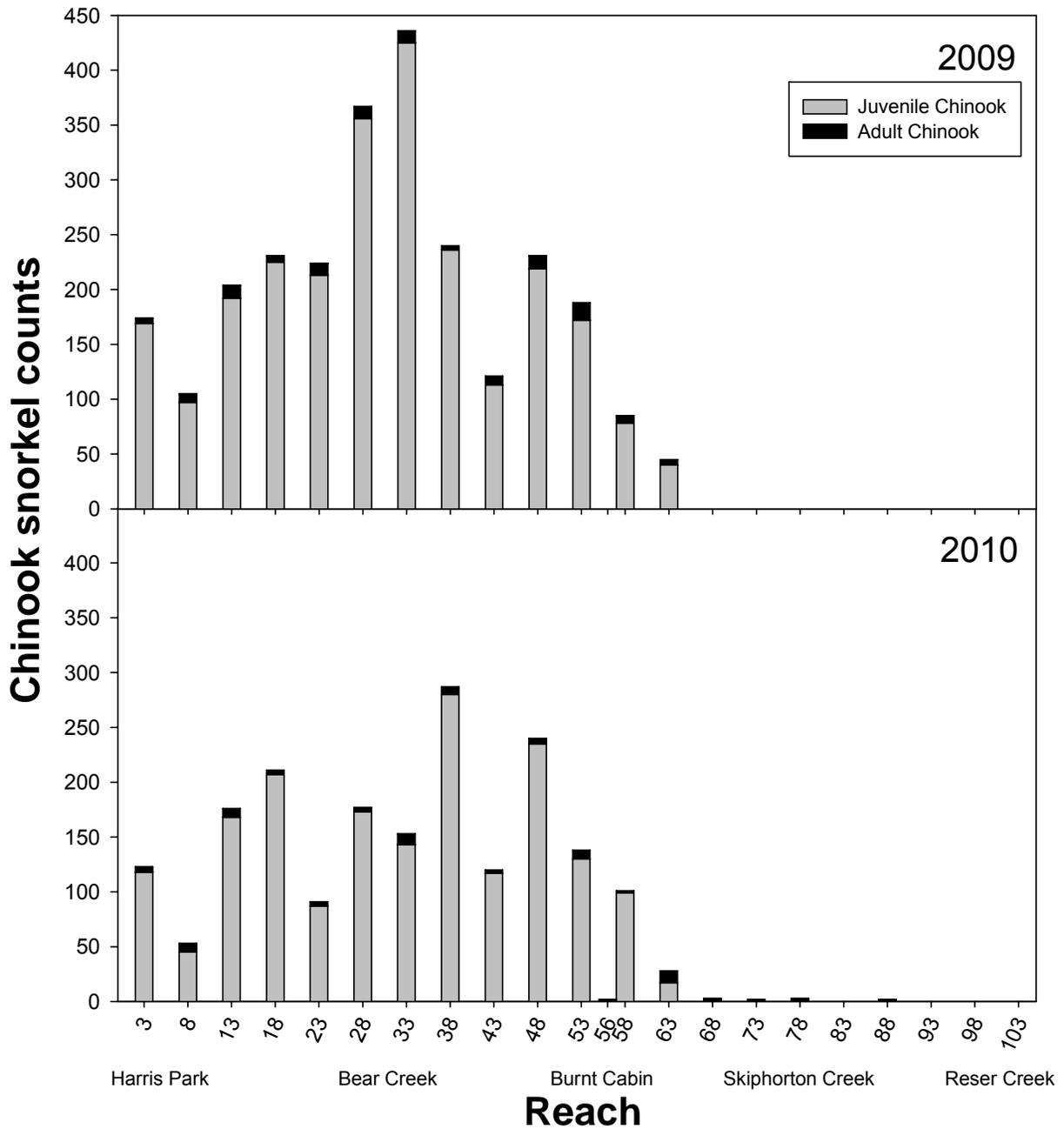


Figure A2.2. Chinook salmon snorkel counts in the South Fork Walla Walla River, 2009 and 2010. Lack of bars in reaches 83, 93, 98, and 103 indicate that no Chinook salmon were observed there.

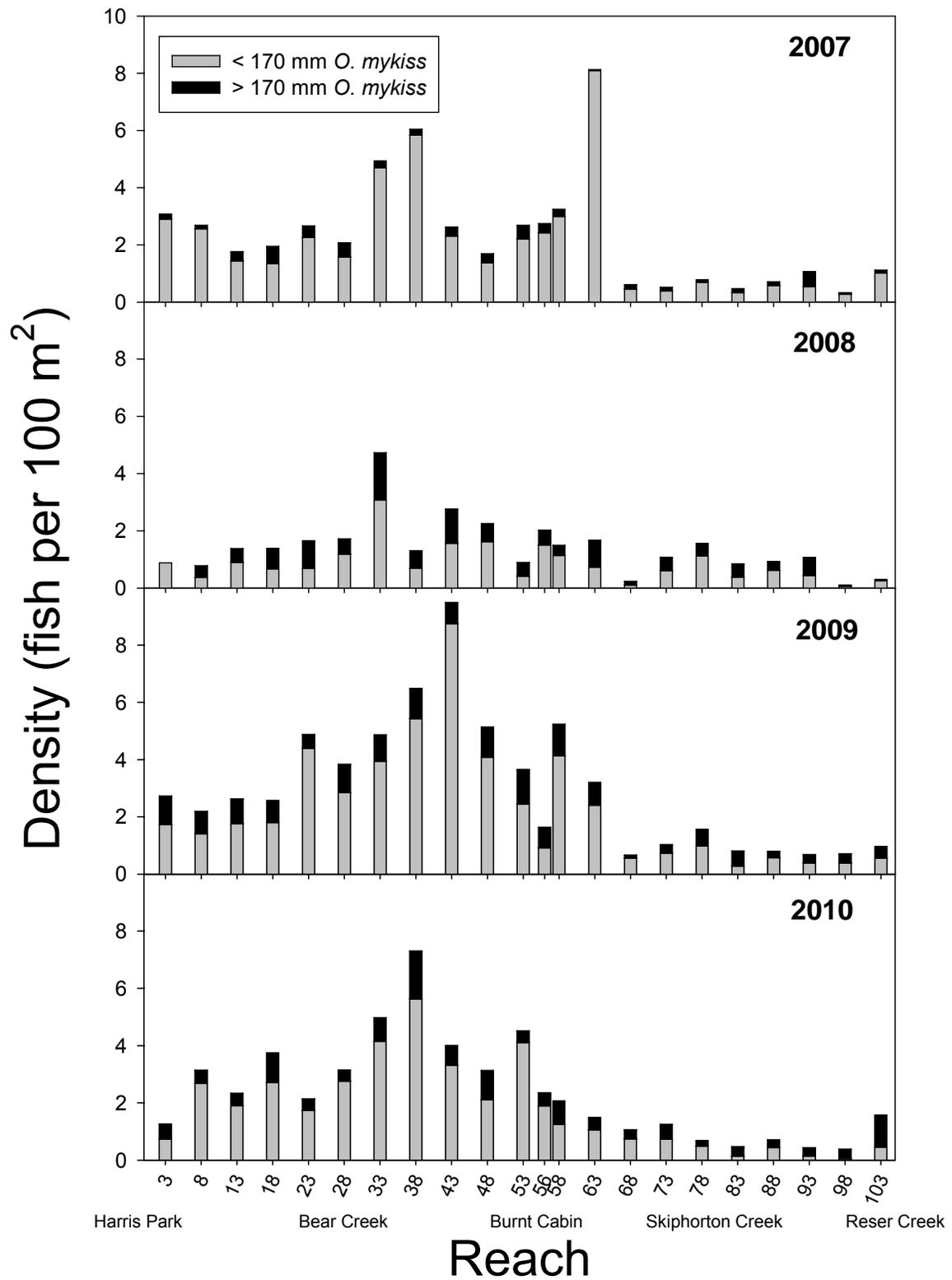


Figure A2.3. Density estimates (fish per 100 m²) for *Oncoryhnchus mykiss* (by size class) from snorkel surveys in the South Fork Walla Walla River from 2007 - 2010.

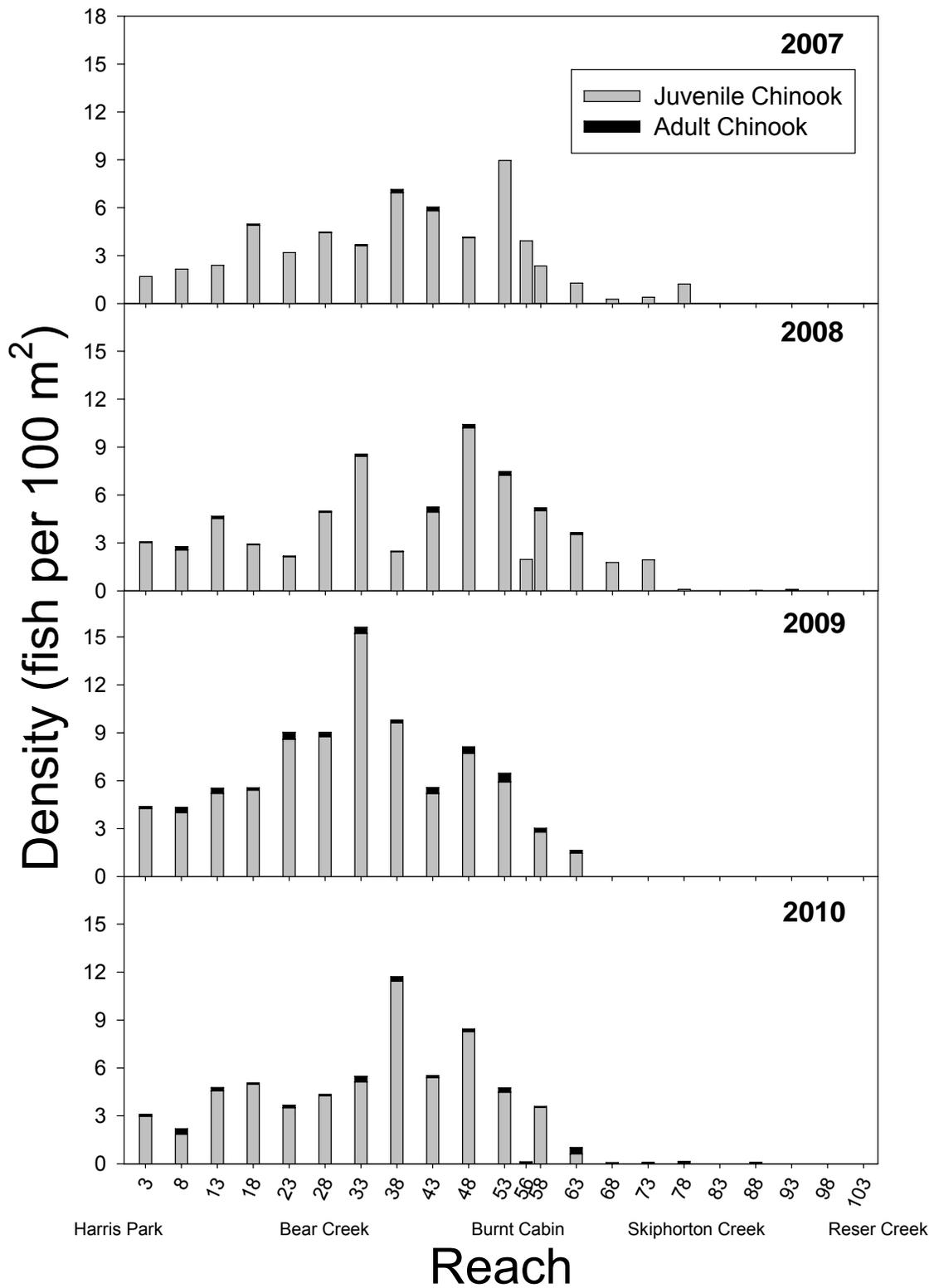


Figure A2.4 Density estimates (fish per 100 m²) for Chinook salmon from snorkel surveys in the South Fork Walla Walla River from 2007 - 2010.

APPENDIX 3

Use of multiple recapture techniques leads to increased understanding of movement patterns and improved estimates of survival for juvenile bull trout, *Salvelinus confluentus*

INTRODUCTION

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; Hillborn et al. 2007). However, demographic rates are often difficult to assess between egg deposition and subadult stages, in part because survival rates during early stages are often relatively low and can be highly variable (Bradford 1995). Although they can be costly to obtain, 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, in relation to anthropogenic influences (e.g., Johnston et al. 2007). As such, obtaining precise estimates of survival specific to individual life stages should be a priority for conservation of imperiled species.

Mark-recapture studies provide a means to estimate survival and other key demographic information specific to individual 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 survival estimates and interpretation of observed patterns (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 (S) and site fidelity (F), the probability that an animal remains available for recapture within the study area (Burnham 1993; White and Burnham 1999). Using the CJS model, it is therefore impossible to distinguish permanent emigration from mortality, or temporary emigration from capture probability in CJS estimates (Barker et al. 2004; Horton and Letcher 2008). As such, an understanding of migration patterns is necessary to correctly interpret parameters, and emigration must be incorporated into mark-recapture analysis in order to parse out true survival and capture probabilities. The difficulty in quantifying movement rates to distinguish between emigration and mortality has previously limited studies that sought to estimate survival of stream-dwelling fishes, particularly for populations with variable emigration rates (Paul et al. 2000; Letcher and Gries 2002). However, recent advances in technology have allowed researchers to improve recapture and resighting probabilities, while simultaneously, 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, accompanied by innovations in PIT-tag readers, including mobile PIT-tag

detectors and stationary in-stream antennas, which 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 detector through a study site. In contrast, a passive in-stream antenna (PIA) detects fish marked with PIT tags as they swim past a stationary location in the stream, and can be operated continually. Both of these methods allow detection of marked individuals without handling or harassment.

Although PIT-tag data acquired at PIAs can help describe fish movement 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, recaptures must take place over a short time period relative to the time between captures to ensure that survival probability is constant among individuals (Lebreton et al. 1992). In contrast, a model developed by Barker (1997) also requires recaptures during discrete sampling occasions, but in addition, can also incorporate resight data collected during the intervals between discrete sampling occasions. Whereas discrete sampling is conducted in a specific study area, the continual sampling between discrete occasions is assumed to take place throughout the range of the population. This assumption allows for direct estimation of true survival and site fidelity as distinct parameters (Barker and White 2001; Barker et al. 2004). This model has rarely been used in the fisheries literature (*but see* Al-Chokhachy and Budy 2008; Horton and Letcher 2008), but appears promising either for studies that include numerous data types (Barker et al. 2004) or for fishes that exhibit diverse movement patterns (Horton and Letcher 2008).

Salmonid fishes are particularly well known for high migration rates (Peterson and Fausch 2003), long distance movement, and diverse life-history strategies (Quinn 2005). In particular, bull trout, *Salvelinus confluentus*, is a species of stream-dwelling char that exhibits variability in life-history forms, migration patterns, and maturation schedules (Bahr and Shrimpton 2004; Johnston and Post 2009). Bull trout occur as a number of different life-history forms that can coexist within a single population, including migratory and non-migratory (resident) life-history types (McPhail and Baxter 1996; Al-Chokhachy and Budy 2008; Homel et al. 2008). Adults typically spawn in cold, headwater streams which also serve as rearing habitat for juveniles (Fraley and Shepard 1989; McPhail and Baxter 1996). Resident adult bull trout may inhabit upper portions of a watershed throughout their lives, whereas migratory individuals typically move downstream during their third or fourth summer to larger river systems and lakes where they may reside for several years before returning to natal waters to spawn (Fraley and Shepard 1989; Rieman and McIntyre 1993). As such, high within-population variability and behavioral plasticity make it challenging to quantify movement patterns and obtain precise survival estimates for bull trout. Estimation of demographic parameters is even more challenging for populations that inhabit large rivers and migrate to smaller headwaters to spawn (fluvial life-history form) because there is no distinct end-point to downstream movements, and migrations may vary between years and can range in distance from several to more than 200 kilometers (McPhail and Baxter 1996; Bahr and Shrimpton 2004; Hogen and Scarnecchia 2006).

Considerable research has been conducted to describe migratory behavior and habitat use for individual bull trout populations (e.g., Swanberg 1997; Bahr and Shrimpton 2004; Watry and Scarnecchia 2008), but the majority of these studies have focused on adult migration patterns.

Information about bull trout life-history requirements and vital rates is still relatively sparse, particularly regarding early life stages. Much of the research specific to juvenile bull trout has described microhabitat use and behavior (Goetz 1997; Sexauer and James 1997; Spangler and Scarnecchia 2001; Al-Chokhachy and Budy 2007); very few studies have assessed rates of survival and environmental factors affecting survival. Paul et al. (2000) generated finite yearly survival rates by comparing the relative abundance of juvenile age classes between years. They found evidence of a negative relationship between juvenile fish densities and age-specific annual survival, but these survival estimates were relative, rather than absolute. Likewise, Johnston et al. (2007) assessed juvenile survival by comparing relative abundance of age classes, but were unable to distinguish between survival and migration. Al-Chokhachy and Budy (2008) developed stage-specific survival estimates for bull trout > 120 mm in total length (TL), but did not include smaller subadult sizes < 120 mm in their analysis. To our knowledge, reliable empirical estimates of survival for smaller size classes (< 120 mm TL) are generally lacking for bull trout.

The objectives of this study were to (1) quantify and better understand movement patterns exhibited by juvenile bull trout (70 - 170 mm TL), and (2) incorporate knowledge of juvenile migration rates to obtain the most precise estimate of survival for bull trout in this size range. We uniquely marked individual fish with PIT tags, and used a combination of recapture and resighting techniques to detect marked fish on subsequent occasions, which allowed us to describe movement patterns and evaluate individual survival. Because bull trout are federally listed as a threatened species, we used sampling techniques that improved the likelihood that a fish was encountered, while simultaneously minimizing handling of fish and disturbance to

stream habitat. We assessed movement rates by combining recapture and resight data from our immediate study site with ancillary resight data collected at PIA located throughout the surrounding watershed. To establish the best survival estimates possible, we compared the relative performance of two different types of survival models. We compared estimates of apparent survival using the common CJS model, which included only data from discrete mark-recapture events, with estimates of true survival using Barker's model type, which utilized additional resight data from PIA. Our results 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.

METHODS

Study area.—We marked and recaptured fish in Skiphorton Creek, a tributary stream that bull trout use primarily for spawning and juvenile rearing. Skiphorton Creek originates in the foothills of the Blue Mountains in northeastern Oregon and enters the South Fork Walla Walla River (SFWW) approximately 113 kilometers upstream from the Columbia River (Figure 1). Skiphorton Creek is a step-pool stream with a mean width of approximately 5 m and mean water depth of 0.24 m. The stream is characterized by complex habitat, including numerous small side channels, pools, undercut banks, large woody debris and log jams. During the summer, the fish assemblage is composed of juvenile or small resident bull trout (primarily < 170 mm TL) and rainbow and/or juvenile steelhead trout *Oncorhynchus mykiss*. 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 captured, marked, and resighted juvenile bull throughout approximately 600 m of Skiphorton Creek directly upstream from the confluence with the

SFWW; this section was divided into 10 contiguous reaches of approximately 60 m in length, and we surveyed the study entire area during each sampling event.

We gathered additional resight and recapture information at multiple locations throughout the South Fork Walla Walla River and main-stem Walla Walla River (Figure 1). Bull trout spawn throughout approximately 20 km of the upper SFWW and tributaries such as Skiphorton Creek, and utilize the entire lower SFWW and Walla Walla River system for migration and overwintering habitat (Anglin et al. 2008). The population of bull trout in the SFWW exhibits both migratory and resident life-history forms (Homel et al. 2008), and migration timing and distance can be highly variable (Homel and Budy 2008). We used several different types of capture and resighting methods to characterize the timing and geographic range of bull trout movement, as well as to increase the probability of detecting a marked individual.

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 two or three per summer (depending upon the year) to minimize stress to juvenile fish, and we gathered data on all captured fish between 70 and 170 mm total length (TL). We anaesthetized fish and weighed each to the nearest 0.1 grams, measured total length to the nearest millimeter, and calculated fish condition, a measure of relative health (Fulton’s $K_{TL} = W/L^3 \cdot 100,000$). We identified recaptures by scanning all fish with a hand-held PIT-tag detector, and recorded the PIT- tag code. We marked all previously untagged fish by making a small surgical incision and

inserting a small PIT tag (11.5 mm long) into the peritoneal cavity, anterior to the pelvic fins; we clipped adipose fins to determine PIT-tag loss during subsequent recaptures. After handling, all fish were placed in a flow-through recovery container within the channel and released to slow-water habitat near the point of capture after full equilibrium was restored. Fish were “marked” with a PIT tag upon initial capture and marked fish caught during subsequent electroseine sampling events were termed “recaptures”.

Mobile antenna resights.—In 2008 and 2009, in addition to the mark-recapture sampling events, we also used a mobile PIT-tag antenna and receiver to detect previously marked fish in Skiphorton Creek. We called this type of sampling “mobile antenna resight” to remain consistent with literature on Barker models, in which the term “resight” has been used to refer to any method of obtaining observations of marked animals other than physical live recaptures during discrete mark-recapture sampling events (and may include some other kind of physical capture; Barker 1997). The mobile antenna (Biomark BP portable) consisted of a backpack-mounted tuner and receiver, which was connected to a 0.35 by 0.35 m triangular antenna at the end of an extendable pole (see Roussel et al. 2000; Cucherousset et al. 2005; Keeler et al. 2007). The antenna’s maximum vertical PIT-tag detection distance ranged between 0.15 and 0.35 m, depending on the size and orientation of the tag and the antenna’s tuning. Lateral read-range was extremely limited, such that a PIT-tagged fish had to be directly below the antenna to be identified.

During each mobile antenna resight survey, the antenna operator waded upstream throughout the entire Skiphorton study area, moving the antenna slowly through the water, passing over all areas

of the streambed at a height that would allow for PIT-tag detection. The antenna operator recorded the date, time, and exact location of each PIT tag within the same sampling reaches used in electroseine sampling to reference the location of marked individuals. Each mobile antenna sampling period took approximately eight hours, and all surveys were conducted by the same person to minimize sampling variability. We performed mobile antenna resight surveys both during the day and at night and compared the recapture probability between the two. Where possible, we attempted to sample at regular intervals, alternating between electroseine mark-recapture and mobile antenna resight sampling (Table 1). In addition to regular surveys during each summer, we also conducted one mobile antenna resight sampling event during September of 2008 and two surveys during September and October 2009.

Mobile-antenna tag recoveries.—One limitation of detecting PIT tags without actually seeing fish during the mobile antenna resight surveys was that we could not immediately be certain whether the tag was (a) in a live fish, (b) the PIT tag had been shed from a fish that was still alive, or (c) the marked fish had died but the tag was still in the river. We addressed the first possibility by double marking all fish to estimate PIT-tag retention probability. Because the observed rate of PIT-tag retention was high (see results), we considered found tags to represent dead fish. During mobile antenna surveys, we distinguished between a live resight and a “tag recovery”, which we determined in the following manner: after detecting a PIT tag with the mobile antenna, the operator tapped on the substrate directly adjacent to the tag location to startle the fish. If the operator could not relocate the PIT tag or if the tag was in a different location following the disturbance, the observation was considered a live resight. During daytime sampling, live fish almost always moved immediately. During night sampling, however, the

antenna operator often had to disturb the substrate repeatedly before a fish moved. Therefore, to be considered a tag recovery, a PIT tag had to be found immobile in the same location during two consecutive mobile antenna surveys. Although we did not actually observe dead fish, we used the term “recovery” to describe when immobile PIT tags were found using the mobile antenna, to be consistent with previous research in which the terms “ring recovery” and “dead recovery” have been used (Burnham 1993; Barker et al. 2004). During resight surveys, the substrate was not disturbed enough to dislodge PIT tags, which were usually buried in areas of the stream bed composed of fine grains, and were found in the same location during every sampling event subsequent to initial detection, even after high flow events. Where possible, gravel surrounding immobile PIT tags was removed and sieved, but we found no dead fish and were unable to extract tags from the gravel.

Passive in-stream antenna arrays and ancillary resight data.—In addition to sampling within the Skiphorton Creek study area, we also collected continuous resight data of marked fish as they swam past passive in-stream PIT-tag antenna arrays (PIAs). As part of a large-scale, multi-year research project (see Al-Chokhachy and Budy 2008), five PIAs operated in the Walla Walla River system, located approximately 7, 16, 38, 52, and 103 km downstream from the Skiphorton Creek study area (Figure 1). The date, time, and PIT-tag number was recorded as a marked fish swam past a PIA; the devices operated continually, except for short-term occasions when maintenance was required, and enabled us to gather resight data throughout the year at multiple sites located throughout the Walla Walla River system.

In 2008 and 2009, we installed an additional PIA at the downstream end of Skiphorton Creek (Figure 1) to identify when fish moved downstream out of the study area. We used a solar panel to generate power for the remote site, but because of limited sunlight, the PIA only operated between July 24 through September 28, 2008, and June 8 through September 30, 2009. The estimated detection efficiency of the antenna was 0.85-1.0, depending upon how well the antenna remained tuned.

Bull trout marked in Skiphorton Creek could also be recaptured throughout the entire Walla Walla River system via several different methods. Each summer, as part of the greater study described above, approximately 20 kilometers of the SFWW was sampled for bull trout and all recaptures from fish marked in Skiphorton Creek were recorded. Additionally, marked bull trout could also be recaptured at screw traps and via research-related angling at multiple locations throughout the main stem Walla Walla River throughout the year. Marked fish caught using any of these methods were considered ancillary resights, because data was collected during the intervals between discrete mark-recapture sampling periods. Although resights obtained from such sampling made up a very small proportion of total data, this additional sampling allowed us to consider marked fish to be at risk of capture anywhere in the Walla Walla River system.

Juvenile movement patterns.—We evaluated the timing, direction, distance, and frequency of juvenile bull trout movement using data combined from all of the sampling methods described above. Because our observations of fish movement were opportunistic rather than systematic, we did not generate formal statistics to quantify migration patterns. We were, however, able to observe general movement behavior within the study stream and into the South Fork Walla

Walla and mainstem Walla Walla rivers. Any marked fish that was detected outside the Skiphorton Creek study area (in the SFWW or main-stem WW River) or resighted at the PIA located at the downstream end of Skiphorton Creek were considered to have emigrated. We considered the assumption of emigration valid for the duration of our study because we observed no marked fish re-enter Skiphorton Creek after having left. We used movement observations to inform our understanding of emigration timing, and assessed how emigration from the study area impacted survival estimates.

Survival analyses.—We estimated the annual survival probability for two size classes of juvenile bull trout, 70 - 119 mm TL and 120 - 169 mm TL (representing age-1 and age-2 fish, respectively) with two different model types, both using Program MARK (White and Burnham 1999). First, we estimated apparent survival using a Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965), which has been commonly used to assess survival probabilities based on mark-recapture data for a wide range of taxa (e.g., Lebreton et al. 1992; Muir et al. 2001; Letcher and Gries 2002). In the CJS model, data are obtained from discrete mark-recapture sampling occasions, which are conducted over a short time period during which the population is assumed to be closed. To meet this assumption, we used only data collected during electroseine mark-recapture sampling in Skiphorton Creek and mobile antenna resight surveys, both of which were conducted over discrete intervals of one to three days. Because we had too few resights during most mobile antenna surveys to generate unique estimates of apparent survival, mobile antenna resights were incorporated into the previous mark-recapture sampling period. The two parameters estimated in 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, as discussed previously, we conducted a second analysis using an ad hoc method in the CJS model to account for known emigration by removing individual encounter history contributions to parameter estimation after an individual had emigrated from the study site (*see* Horton and Letcher 2008).

We compared estimates of apparent survival from the standard CJS model and the CJS model in which we accounted for emigration with estimates of true survival using the Barker model type (Barker 1997; Barker and White 2001). In addition to data from electroseining mark-recapture sampling during each discrete time period i , used in the CJS model, the Barker model also allowed us to use all resight and tag recovery data obtained during the intervals between discrete sampling events $[i, i + 1)$. As in the CJS model, mobile antenna live resights from within the study area were incorporated into the data from the previous mark-recapture period. Mobile antenna tag recoveries, resights collected continually at PIA, and ancillary resights from throughout the entire Walla Walla River system were included in the interval data. If an individual was recaptured and/or resighted on more than one occasion during the interval $[i, i + 1)$, only a single detection was recorded in the encounter history (Barker et al. 2004). Using the Barker model, the additional complexity necessary to accommodate data obtained during intervals between discrete sampling events and to separate emigration from survival, results in a total of seven parameters (Barker 1997). The parameter S_i is the probability that an animal alive at time i survives to time $i+1$, and p_i is the probability that an animal alive and available for capture at time i is captured. Parameters associated with emigration are 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), and F'_i is 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). Parameters associated with resighting include R_i , the probability that an animal alive at time i is resighted alive in $[i, i+1)$, and R'_i , the probability that an animal is resighted before it dies in $[i, i+1)$. An additional parameter, r_i , the probability that an animal dies and is found dead in the interval $[i, i+1)$, allowed us to incorporate data from tag recoveries. Because we recovered only a relatively small number of tags, we also compared precision of survival estimates using a data set that included tag recoveries and the same data without tag recoveries, for which we set $r = 0$.

Within each of the two model types (CJS and Barker), we constructed models following a “step down” approach (Lebreton et al. 1992), and selected models based on Akaike’s Information Criterion corrected for effective sample size (AICc; Burnham and Anderson 2002). Initially, we retained high dimensionality in our survival parameters (ϕ in the CJS model and \hat{S} in the Barker model), and iteratively modeled parameters less pertinent to the analysis. Data limitations and model parsimony led us to model some parameters as constant across time, and between size classes. After selecting the model structure for these less pertinent parameters, we next focused on modeling survival, the parameter of greatest interest. After selecting the model structure for these less pertinent parameters, we next focused on modeling survival, the parameter of greatest interest (e.g., Doherty et al. 2002; Collins and Doherty 2006). We modeled survival for two different age groups and in relation to factors determined *a priori*, including annual variation and the individual covariates length and condition, both measured at initial capture. In addition, we included models with a marking effect to test the hypothesis that survival rates were lower during the time interval immediately following initial capture and marking. We discarded any

candidate models for which we were not able to estimate parameters due to a lack of data. To facilitate comparison of survival estimates and variance between the CJS and Barker model types, we only present estimates from the single best model from the set of candidate models, using the mean individual covariate value for each of the two size groups. Because our data contained covariates, we were unable to perform goodness-of-fit tests using Program MARK.

We compared survival estimates from the top model from both the CJS and Barker model types with an index of survival, the return rate. 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 anywhere in the geographic range of the population more than nine months after tagging (recaptured in the subsequent field season or later). We estimated a return rate for marked fish (\widehat{RR}) using a simple proportion $\widehat{RR} = \frac{Y}{N}$ and binomial variance $var(\widehat{RR}) = \frac{RR(1-RR)}{N}$ where Y represents the number of marked fish that were resighted within the next field season or afterward, 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 Skiphornton 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 51 in May 2008, and 142 in July 2009 (Table 1). The majority of bull trout captured and PIT tagged were between 90 and 110 mm in length, whereas only 25% of marked individuals were 120 - 169 mm TL (Figure 2).

Table 1. Sampling schedule and methods used to sample juvenile bull trout in Skiphorton Creek, Oregon, and throughout the Walla Walla River. Fish were captured and marked using electroseining (ES) during discrete sampling events. Marked fish were resighted during intervals between discrete events via (1) mobile PIT-tag antenna resights (MAR) within Skiphorton Creek, (2) at five passive in-stream antennae located outside the study area in the larger Walla Walla River (PIA_{WW}), and (3) at the downstream end of the Skiphorton Creek study area (PIA_{SH}).

Sampling date	Resight interval (days)	Marked	Live recaptures	Live resights	Dead recoveries	Sampling method
Jul 10-13, 2007	-	87	0	-	-	ES
	34	-	-	0	0	PIA _{WW}
Aug 14-15, 2007	-	65	14	-	-	ES
	261	-	-	6	0	PIA _{WW}
May 2-3, 2008	-	51	3	-	-	ES
	67	-	-	2	0	PIA _{WW}
Jul 7-8, 2008	-	94	3	-	-	ES
	34	-	-	4	3	PIA _{WW} + PIA _{SH}
Aug 13-14, 2008	-	123	23	-	-	ES + MAR
	298	-	-	62	5	PIA _{WW} + PIA _{SH}
Jun 8-9, 2009	-	107	8	-	-	ES + MAR
	42	-	-	34	0	PIA _{WW} + PIA _{SH}
Jul 21-22, 2009	-	142	32	-	-	ES + MAR
	372	-	-	219	4	PIA _{WW} + PIA _{SH}

Multiple techniques were necessary to obtain sufficient data to track movement patterns of marked individuals and evaluate survival rates, although the efficiency of resighting techniques varied in efficiency. Data obtained using the mobile antenna accounted for 62% of all resight observations, while detections at all PIAs combined comprised 36% of resights, and ancillary resights in the SFWW and main stem WW rivers accounted for 2%. The number of fish resighted during each interval between discrete sampling periods increased over the course 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 study area in 2008 and 2009, PIA resights increased dramatically, and allowed us to document emigration rates and timing during the time this temporary PIA was operating. In addition, we used resights at PIAs located downstream of the study area to infer emigration rates.

The mobile PIT-tag antenna enabled us to resight marked bull trout while minimizing disturbance to the stream and fish, and was particularly effective when used at night. The probability of detecting a PIT-tagged fish was 4.5 times greater when the mobile antenna was used at night compared to during the day and 2.5 times greater than the probability of recapturing a marked fish using electroseine sampling (Table 2). We recaptured only one fish that had shed its PIT tag, resulting in an estimate for retention probability of 98.8%. Given this high rate of tag retention, we considered the 12 tag recoveries found during 2008 and 2009 using the mobile antenna to represent mortalities in our analyses.

Table 2. Methods used to recapture or resight juvenile bull trout in Skiphorton Creek study area, Oregon, 2007 - 2009. Data is based on 7 electroseining, 3 daytime mobile-antenna, and 4 nighttime mobile-antenna events. Sampling hour refers to the total number of hours worked by all members of the sampling crew.

Sampling method	Data type collected	Capture probability (p)	SE	Average recaptures per sampling hour
Electroseining	live only	0.22	0.03	0.76
Mobile antenna - day	live and dead	0.11	0.02	2.29
Mobile antenna - night	live and dead	0.51	0.04	7.55

Juvenile movement patterns.— We used recapture and resight data collected between July 10, 2007 and July 31, 2010 to assess the timing of bull trout movement and distances traveled. Within the Skiphorton Creek study area, juvenile bull trout moved both upstream and down, but the predominant direction of movement was downstream (Figure 3). Movement in the upstream direction occurred at low frequencies throughout the study and the largest upstream movement distance was 0.2 kilometers. We observed numerous juvenile bull trout that remained for more than one month within the same 60 m reach in which they were previously captured, and in many instances, fish were located in the same habitat (e.g., a small pool or eddy) on numerous consecutive sampling occasions. The maximum distance traveled downstream increased over time for both size classes. 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 days. After 9 months post-tagging, most marked fish were resighted in the SFWW, more than 4 km downstream from the study area (Figure 4).

Larger fish traveled farther and with greater frequency; in the 70-119 mm size class, 52% of fish recaptured between four months and one year post-tagging had moved more than 4 km downstream of the study area, compared with 92% of the fish in the 120-169 mm size class. The largest observed movement was 53 kilometers downstream from the study area (Figure 3).

Juvenile bull trout emigrated from the study area throughout the year, and we observed no temporal cue for emigration, nor did we observe a distinct size threshold. Based on a linear relationship between juvenile bull trout growth rate and time, we estimated the length of marked fish for which the exact date of emigration was known (i.e., fish detected passing the PIA just downstream of the study area). Juvenile bull trout emigrated from the study area across a range of sizes exceeding 80 mm, although the majority of emigrants were longer than 100 mm TL, and the proportion of marked fish emigrating increased with length (Figure 2). As a result of high emigration rates, the proportion of marked fish found outside the study area increased steadily with time (Figure 4). Furthermore, no marked fish were detected within the study area more than 18 months after tagging, which meant that a substantial proportion of marked fish were unavailable for recapture during subsequent sampling periods. For example, in 2008, at least 5% of the marked population had emigrated prior to any sampling events, and in 2009, more than 11% of marked individuals had emigrated prior to sampling.

Juvenile survival rates.—Estimates of annual apparent survival from the CJS model type were considerably lower than both the return rate and survival estimates from the Barker model type, which is consistent with the high rates of emigration we observed. Compared to the return rate, estimates of apparent survival from the naïve CJS model were biased extremely low but

improved when emigration was included in the models. Point estimates of annual survival using the Barker model type were higher than the return rate, but the 95% confidence intervals encompassed the return rate. Estimates of annual return rate, calculated from the proportion of fish recaptured, were also higher than estimates of apparent survival from the CJS model type, but similar to annual survival estimates from the Barker model type. Estimates from the Barker model were less biased than the CJS results, and furthermore, provided additional insight into movement patterns of juvenile bull trout.

The calculated return rate based solely on the proportion of marked individuals recaptured or resighted anywhere in the Walla Walla system more than nine months after initial marking (but did not include capture/resight probability) was $\widehat{RR} = 0.171 \pm 0.017$ (estimate \pm SE) for the 70-119 mm size class, and $\widehat{RR} = 0.190 \pm 0.030$ for the 120-169 mm size class (Figure 6). Overall, the variance for estimates of annual survival was greater for the larger size class than for the smaller, regardless of which model type was used, because there were fewer fish marked in the larger size class.

Using the CJS model type, model selection of the less pertinent parameter, recapture probability (p_i) resulted in a set of candidate models for which p_i varied as a function of increasing trend through time plus length as an individual covariate. Apparent survival was modeled as a function of time interval, year, age group, cohort, tag effect, individual covariates length and condition, and interactions among some of these variables. The model that minimized AICc included separate apparent survival estimates for the two size classes with fish length as an individual covariate (Table 3). Based on this model, the estimate of yearly apparent survival for the smaller

size class was $\phi = 0.090 \pm 0.018$ for a fish 100 mm TL, and $\phi = 0.009 \pm 0.009$ for the larger size class using a mean length of 133 mm. Compared to the return rate, CJS estimates were biased extremely low, accounting for only approximately 52% and 5% of the observed survival for the two size classes, respectively. Using the ad hoc CJS approach, which removed the contribution to the maximum likelihood of individuals known to have emigrated, the model selection process resulted in the same best model as the naïve CJS model. With emigration included explicitly in the model, survival estimates were $\phi = 0.142 \pm 0.023$ for the 70-119 mm size class, similar to the return rate, but $\phi = 0.068 \pm 0.030$ for the 120-169 mm size class, which was only approximately 36% of the return rate. Model selection showed little support for the model that included a tagging effect, and a likelihood ratio test also provided no evidence of a difference in survival during the time period immediately following tagging, compared to other time intervals ($X^2_2 = 1.112$, $P = 0.57$).

In contrast to the low survival estimates produced by the CJS model, annual survival estimates from the Barker model were higher than either CJS apparent survival estimates or the return rate (Figure 5). For all candidate Barker models, we modeled p as a function of individual length and r as constant. Because of the variability in resights among intervals (Table 1), we modeled both R (the probability of resighting an individual between discrete sampling intervals) and R' (the probability of resighting an individual prior to its death between sampling intervals) as a function of time, with the first interval set equal to 0, because there were no resights during that period. Model selection demonstrated strong support for a model in which we explicitly modeled permanent emigration by setting $F' = 0$ and F as a function of length as an individual covariate. We modeled survival as a function of the same variables used in the CJS analysis. Model selection produced identical model ranking for data with and without dead recoveries, but

Table 3. Summary of model selection for best mark-recapture models used to estimate apparent survival using the CJS model and survival using the Barker model, for juvenile bull trout captured and marked in Skipthorton Creek, Oregon, 2007-2009. Two age groups were used: 70-119 mm and 120-169 mm total length. Akaike's information criterion corrected for small sample bias (AICc), model weight, model likelihood, number of parameters, and variance are shown.

Survival varies by	AICc	ΔAIC	AICc weights	Model likelihood	Number of parameters
CJS					
age group + length	664.95	0.00	0.84	1.00	7
age group	668.87	3.91	0.12	0.14	5
group + tag effect	673.25	8.30	0.01	0.02	9
age cohort	681.87	16.9	0.00	0.00	6
Barker					
age cohort + condition	1838.23	0.00	0.58	1.00	19
age cohort	1839.63	1.40	0.29	0.50	18
age cohort + length	1841.49	3.27	0.11	0.20	19
age cohort with tag effect	1844.35	6.13	0.03	0.05	20
year	1860.91	22.68	0.00	0.00	19

parameter estimates varied slightly. For both data sets, the model with the greatest support was one in which survival varied between cohort and with fish condition included as an individual covariate, suggesting that survival was related to both age and body size (Table 3).

Incorporating tag recoveries into the model yielded higher estimates of survival but did not improve precision of estimates. Estimated annual survival for the Barker model type including dead recoveries was $\hat{S} = 0.211 \pm 0.029$ for fish 70-119 mm, and $\hat{S} = 0.239 \pm 0.060$ for fish 120-169 mm, based on an average condition of 0.87 for both size classes. Using the data set that did not include dead recoveries (where r was set = 0), the same best-ranking model yielded lower

estimates of $\hat{S} = 0.186 \pm 0.026$ and $\hat{S} = 0.183 \pm 0.057$, respectively. Based on AIC_c weights, there was little support for the model that included annual variability in survival, although this was unsurprising based on only three years of data. There was also little support for a tagging effect based on model selection and no evidence of a tagging effect using a likelihood ratio test ($X^2_2 = 1.768$, $P = 0.41$).

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. Use of multiple recapture and resighting techniques allowed us to incorporate emigration into our analysis, which improved the accuracy of annual survival estimates for juvenile bull trout. Results using the Barker model type appear to be the least-biased estimates of survival based on the model types we considered, and are the most precise field-based estimates available for juvenile bull trout of which we are aware. Data collected via multiple methods both within and outside of the study area allowed us to determine when juvenile fish emigrated from the spawning and rearing tributary, and enabled us to observe bull trout movements throughout the larger river system. Our study demonstrates the importance of incorporating movement patterns into survival analyses for migratory species, and provides an important comparison of contemporary capture techniques and analysis methods.

Marking, recapture, and resight techniques.—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 additional handling. Based on both CJS and Barker models, we observed no evidence of lower survival

rates immediately after tagging compared to subsequent capture occasions. This general finding corresponds with a number of studies of juvenile salmonids which have also observed no discernable 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). In contrast, research by Brakensiek and Hankin (2007) demonstrated evidence of a period of lower survival after tagging juvenile coho salmon, but this was particularly true for fish less than 75 mm fork length, a size smaller than almost all of the fish in our study.

Similarly, we found electroseining to be an effective way to recapture marked individuals while they remained within the study area. However, we still limited the number of electroseining events during the study season to minimize handling, given the status of bull trout as a threatened species. We were able to increase the number of resighting occasions within the study area with use of the mobile antenna, which caused very little disturbance to the stream and fish. The mobile antenna was also an efficient use of sampling time, as it required only one person to operate (compared to three for the electroseine method) and the entire study area could be scanned in 8 hours (Table 2). We do note, however, that while the mobile antenna was effective in our relatively small-sized study stream, as it has been in other small creeks (Roussel et al. 2000; Keeler et al. 2007), it would likely be less efficient in a larger river.

In addition to providing a non-invasive way to obtain resight information, the mobile antenna allowed us to recover PIT tags from dead fish in the study area. We recovered a total of 12 PIT tags over the course of our study, which allowed us to increase our certainty about the fate of those individuals. Although this is a relatively small number of tag recoveries and may not have

been sufficient to improve the precision of survival estimates when dead recovery data were included in the Barker model analysis, it is reasonable to expect that larger number of tag recoveries would yield greater precision in parameters of interest (Barker and Kavalieris 2001). We may have recovered so few PIT tags because not all PIT tags from dead fish persisted in the system—tags may have been washed downstream by the current, buried too deep in the gravel to be detected, or removed from the system in the stomach of a predator. For example, while using the mobile antenna, we found one PIT tag in a pile of mustellid scat on a log near the river.

Immobile PIT tags found using the mobile antenna could also have been shed from a fish that was still alive and thus would not have represented a true mortality. However, based on the high rate of PIT-tag retention we observed, we considered tag loss during the time frame of this study 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, such as of 96.6% after seven months in brown trout (Ombredane et al. 1998) and 99.8% after nine months in Atlantic Salmon (Gries and Letcher 2002). In contrast, lower rates of PIT-tag retention have been reported for larger size classes of fish, including an average of 81.6% for Chinook salmon recaptured between six months and four years after tagging (Knudsen et al. 2009) and 83% for Arctic Grayling after 3 years (Buzby and Deegan 1999). If PIT-tag retention was in fact 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 at six locations stationed across the entire Walla Walla river system allowed us to collect data continually throughout the year, including during the winter

and spring when we could not access our remote field site. Although we were not able to operate every PIA year-round, use of multiple PIAs located throughout the system helped us develop a detailed spatial and temporal understanding of juvenile bull trout movement patterns and emigration rates based on a relatively large number of observations. Further, it was not necessary for PIAs to operate at 100% detection efficiency, as the Barker model type can incorporate data collected opportunistically (Barker 1997). Detection efficiency did vary among PIA and at different discharges, but we did not have sufficient data or an analytical ability to incorporate this variability into our analyses.

Owing to the high emigration rate and variation in emigration timing of juvenile bull trout in this study, a large amount of sampling effort was required to obtain sufficient resight data to estimate survival and to characterize juvenile bull trout movement patterns. Detailed knowledge of individual emigration timing required use of several sampling techniques, and the spatial and temporal scope of this research was possible only because a preexisting infrastructure of PIAs existed within the Walla Walla River system. The 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 estimate survival without the use of additional resight methods both within and outside of the Skiphorton Creek study area. Thus, the price of using various sampling techniques relative to information gain should be weighed carefully within the context of overall study objectives (e.g., Al-Chokhachy et al. 2009).

Mark-recapture models and annual survival estimates.—Our results suggest that understanding and incorporating movement patterns into capture-recapture studies can have important

implications on estimation of survival and other important vital rates (Cilimburg et al. 2002; Horton and Letcher 2008). Migration rates and distances are often difficult to quantify for species like bull trout, as well as fishes such as brook trout, rainbow trout, and coastal cutthroat trout, that exhibit diverse life-history characteristics and variation in both migratory habit and home range size (e.g., Rodriguez 2002; Meka et al. 2003). Migratory behavior is known to vary among different age classes of bull trout and among populations (Goetz 1989; McPhail and Baxter 1996; Monnot et al. 2008). For the population of juvenile bull trout considered here, emigration occurred across a range of sizes, but was more frequent for larger juvenile fish and was permanent within the time frame of this study (i.e., juvenile fish emigrated from the study area and did not return). Continual emigration resulted in a constant loss of marked fish from the study population; thus, models that decoupled survival and site yielded the best survival estimates. The return rate 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 the study area. In contrast, the naïve CJS model used only data collected within the Skiphorton Creek study area, from which marked fish were continually emigrating, resulting in survival estimates that were biased extremely low.

Two primary assumptions of the CJS model are that all individuals have an equal probability of survival and detection (Pollock 1991; Lebreton et al. 1992). Observations of movement patterns for juvenile bull trout in our study demonstrated that the assumption of equal detection probability was clearly violated when individuals emigrated from the study area and were no longer available for capture. The observed heterogeneity in movement timing and fish length at emigration precluded strict assumptions about when fish were available for capture within the

study area. When we incorporated observed emigration directly into encounter histories, we observed a small improvement over the naïve CJS model, but this model still led to a negative bias in estimates of apparent survival. Furthermore, this bias was more pronounced for the larger size class, likely because fish in this size range emigrated from the study area with greater frequency than individuals in the smaller size class. Our results were consistent with results from simulations performed by Horton and Letcher (2008) who also found that the naïve CJS model type yielded negatively biased survival estimates when emigration rates were high. However, they found that when individual emigration was explicitly incorporated into the model, this ad hoc CJS method produced robust survival estimates. Unlike Horton and Letcher's simulation models, we were unable to document every emigrant during our field study, such that survival estimates using the ad hoc CJS approach were still negatively biased.

In contrast, the Barker model allowed us to capitalize on multiple data sources, and to model emigration using two distinct parameters, resulting in an estimate of true survival. We used a combination of mobile antenna resights, resights at PIAs, and additional ancillary resight data from throughout the Walla Walla River system in the Barker model, to meet the assumption that marked bull trout were available for recapture throughout most of the geographic range of the population (Barker et al. 2004). Although the intensity of resighting efforts varied geographically (e.g., were more intense at PIA locations), we believe that this would have minimal effect on our survival estimates, as heterogeneous recovery rates have been shown to have little influence on bias of survival estimates in band recovery models (Nichols et al. 1982; Barker 1992).

In our study, the Barker model type produced estimates of annual survival which were greater than the observed return rate. Although we have no way of knowing true survival rates in the wild, it is a reasonable expectation that true survival rates would be higher than the return rate, which does not account for recapture probability (Martin et al. 1995; Sandercock 2006). Using simulation modeling, Horton and Letcher (2008) found that the Barker model type yielded robust estimates of survival with very little bias, regardless of whether emigration was temporary or permanent. Although uncommon in fisheries literature, the Barker model has been used with great success to estimate survival for fishes with multiple coexisting life-history strategies such as bull trout (Al-Chokhachy and Budy 2008) and Arctic grayling (Buzby and Deegan 2004), and for populations that exhibit complex migration patterns (Barker et al. 2004). Given the robust nature of the Barker model and the relative agreement between annual survival estimates derived from this model and our observed return rates, we believe that the best estimates for juvenile bull trout annual survival from our study are those obtained using the Barker model type.

In addition to providing an analytical comparison of the performance of the CJS model and the newer Barker model, our study also provides an important baseline of field-based annual survival estimates for age-1 bull trout (70-119 mm TL). Prior to our study, survival of this age class represented a significant gap in our understanding of bull trout demography. Our research also corroborates previous estimates of annual survival for age-2 bull trout in similar systems.

Survival estimates for fish marked in Skiphorton Creek were slightly higher than from the larger SFWW River (Al-Chokhachy and Budy 2008), where estimates of annual survival for sub-adult bull trout 120-169 mm TL varied between 0.025 ± 0.009 and 0.154 ± 0.052 , depending on the year. Our results also fall within the high end of estimated return rates for subadult bull trout

(<270 mm TL) in Mill Creek, another tributary to the Walla Walla River, which ranged from 0.051 to 0.232 between 1999 and 2003 (P. Howell, U.S. Forest Service, unpublished data).

Longer-term data sets from SFWW River and Mill Creek suggest that annual survival rates for juvenile bull trout may vary substantially between years and among populations. Based on our data, model selection provided little support for significant variation in annual survival among the three years of this study, and the most parsimonious model was time-invariant. Although we were able to estimate the mean survival rate across years, additional years of data would be necessary to clearly determine differences in annual survival. Consequently, we recognize that the estimates of standard error from any of the models described here may be negatively biased with regards to true process variance. With additional years of data, we would ideally have used a random-effects model to parse out process variance associated with our estimates (White et al. 2002). However, such analyses require numerous years of data and improve with high recapture rates, both conditions that are often not logistically feasible in fisheries studies. Despite intense effort and our use of multiple sampling techniques, the combination of low survival rates, low recapture probabilities, and high emigration rates for juvenile bull trout limited our ability to utilize more complex models.

Conservation and management implications.—Our research suggests that in some systems juvenile bull trout emigrate from spawning and rearing habitat continually throughout the year, and across a range of sizes. In our study system, a high proportion of juvenile bull trout emigrated from natal habitat at lengths as small as 80-120 mm TL. After leaving their natal stream, juvenile bull trout migrated downstream at various rates, and thereafter utilized more

than 50 km of downstream habitat within the larger river system. As bull trout are typically not considered sexually mature until they exceed approximately 300 mm TL, our findings indicate that subadult bull trout will use a wide range of rearing habitat throughout the Walla Walla River system for several years before returning to spawn. In addition to documenting juvenile migratory behavior, our research demonstrates the importance of incorporating emigration rates into survival analyses for species that demonstrate variable migration patterns.

We provide some of the first field-based estimates of juvenile bull trout annual survival based on marked individuals. These estimates can provide a baseline against which to compare future studies of juvenile bull trout survival in more impacted systems. Further, our estimates of age-1 and age-2 bull trout survival can be used to help improve the accuracy and predictive ability of bull trout population viability models. Given the sensitivity of bull trout population growth to variations in survival at early life stages, stage-specific estimates of vital rates are imperative for the development and use of reliable stage-structured population models. In turn, such models can be used to evaluate bull trout population viability under different management scenarios, and to develop sound recovery plans for this imperiled species.

REFERENCES

- 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* 137:1709-1722.
- Anglin, D.R., D. Gallion, M. Barrows, C. Newlon, and R. Koch. 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, 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. 1992. Effect of heterogeneous survival on bird-banding model confidence interval coverage rates. *The Journal of Wildlife Management* 56:111-116.
- 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. White. 2004. Encounter history modeling of joint mark-recapture, tag-resighting and tag-recovery data under temporary emigration. *Statistica Sinica* 13:1037-1055.
- Barker, R. J., and G. White. 2001. Joint analysis of live and dead encounters of marked animals Pages 361-367 in *Wildlife and people: Priorities for the 21st Century.*, R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, *editors*. Proceedings of the Second International Wildlife Management Congress, Bethesda, Maryland.
- Bradford, M. 1995. Comparative review of Pacific salmon survival rates. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1327-1338.
- Brakensiek, K.E., and D.G. Hankin. 2007. Estimating Overwinter Survival of Juvenile Coho Salmon in a Northern California Stream: Accounting for Effects of Passive Integrated Transponder Tagging Mortality and Size-Dependent Survival. *Transactions of the American Fisheries Society* 136:1423-1437.
- Burnham, K.P. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199-213 in J. D. Lebreton, and P. M. North, *editors*. *Marked individuals in the study of bird population*. Birkhauser Verlag, Basel, Switzerland.
- Burnham, K.P., and D.R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York, New York.

- Buzby, K., and L. Deegan. 1999. Retention of anchor and passive integrated transponder tags by Arctic grayling. *North American Journal of Fisheries Management* 19:1147-1150.
- 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*). *The Auk* 119:778-789.
- Collins, C.T., and P.F. Doherty. 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.A. Keeler, and R.A. Cunjak. 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.
- Doherty, P.F., and coauthors. 2002. Sources of variation in breeding-ground fidelity of mallards (*Anas platyrhynchos*). *Behavioral Ecology* 13:543-550.
- 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. Willamette National Forest, Eugene, Oregon.
- Goetz, F.A. 1997. Diel behavior of juvenile bull trout and its influence on selection of appropriate sampling techniques. *Friends of the Bull Trout Conference Proceedings*:387-402.
- 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.
- Hillborn, R., T.P. Quinn, D.E. Schindler, and B.E. Thompson. 2007. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences of the United States of America* 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.

- Hornel, K., and P. Budy. 2008. Temporal and spatial variability in the migration patterns of juvenile and subadult bull trout (*Salvelinus confluentus*) in Northeast Oregon. Transactions of the American Fisheries Society 137:869-880.
- Hornel, 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.
- Houde, E.D. 1994. Differences in marine and freshwater fish larvae: implications for recruitment. Journal of Marine Science 51:91-97.
- 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., and coauthors. 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 of 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., and coauthors. 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., and G. Gries. 2002. Survival of stream-dwelling Atlantic salmon: Effects of life history variation, season, and age. Transactions of the American Fisheries Society 131:838-854.
- 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. Fisheries Management Report No. 104.

- 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, USA.
- 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.
- Nichols, J.D., S.L. Stokes, J.E. Hines, and M.J. Conroy. 1982. Additional comments on the assumption of homogeneous survival rates in modern bird banding estimation models. *The Journal of Wildlife Management* 46:953-962.
- 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.
- Peterson, D.P., and K.D. Fausch. 2003. Upstream movement by nonnative brook trout (*Salvelinus fontinalis*) promotes invasion of native cutthroat trout (*Oncorhynchus clarki*) habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1502-1516.
- Pollock, K.H. 1991. Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present, and future. *Journal of the American Statistical Association* 86:225-238.
- Prentice, E., T. Flagg, and C. McCutcheon. 1990. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. Pages 317-322 in N. C. Parker, and coeditors, *editors*. *Fish-marking techniques*. American Fisheries Society, Symposium 7, Bethesda, Maryland.
- Quinn, T. P. 2005. *The behavior and ecology of Pacific salmon and trout*. University of Washington Press, Seattle, Washington.
- Rieman, B.E., and J.D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. USDA General Technical Report, INT-302.

- Rodriguez, 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 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.
- Seber, G. A. 1965. A note on the multiple-recapture census. *Biometrika* 52:249-259.
- 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. Bull Trout Task Force, Calgary, Alberta.
- Spangler, R. E., and D. L. Scarnecchia. 2001. Summer and fall microhabitat utilization of juvenile bull trout and cutthroat trout in a wilderness stream, Idaho. *Hydrobiologia* 452:145-154.
- 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.
- 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., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120-139.
- White, G., A. B. Franklin, and T. M. Shenk. 2002. Estimating parameters of PVA models from data on marked animals. Pages 169-190 in S. R. Beissinger, and D. R. McCullough, *editors*. Population Viability Analysis. University of Chicago Press, Chicago.
- 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., and coauthors. 2006. Remote monitoring of fish in small streams. *Fisheries* 31:492-502.

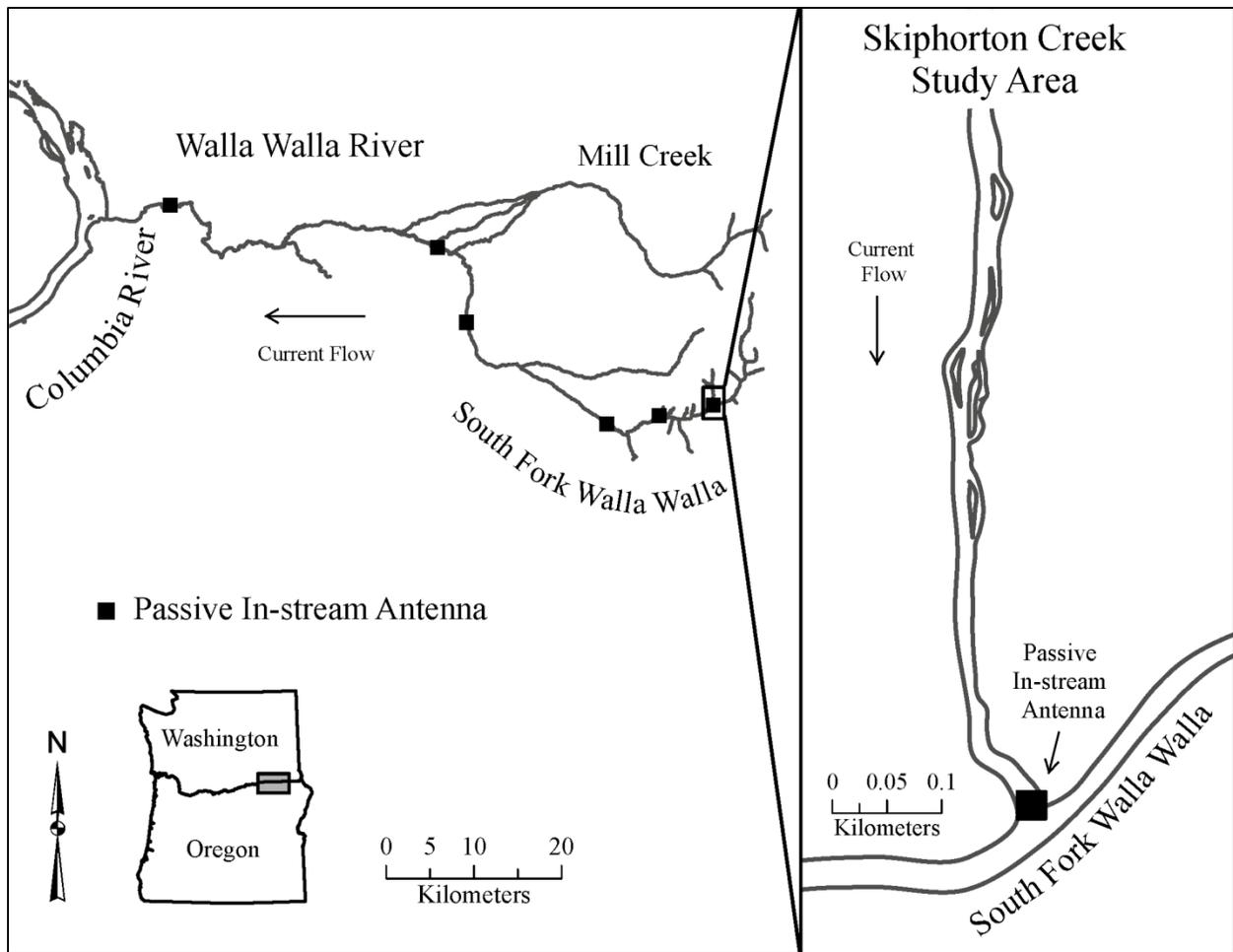


Figure 1. Map of the study area, Skiphorton Creek, Oregon, where juvenile bull trout were initially captured and marked. Marked fish could be resighted throughout the South Fork Walla Walla and Walla Walla River system, including at any of the six passive in-stream antennae located downstream of the study area.

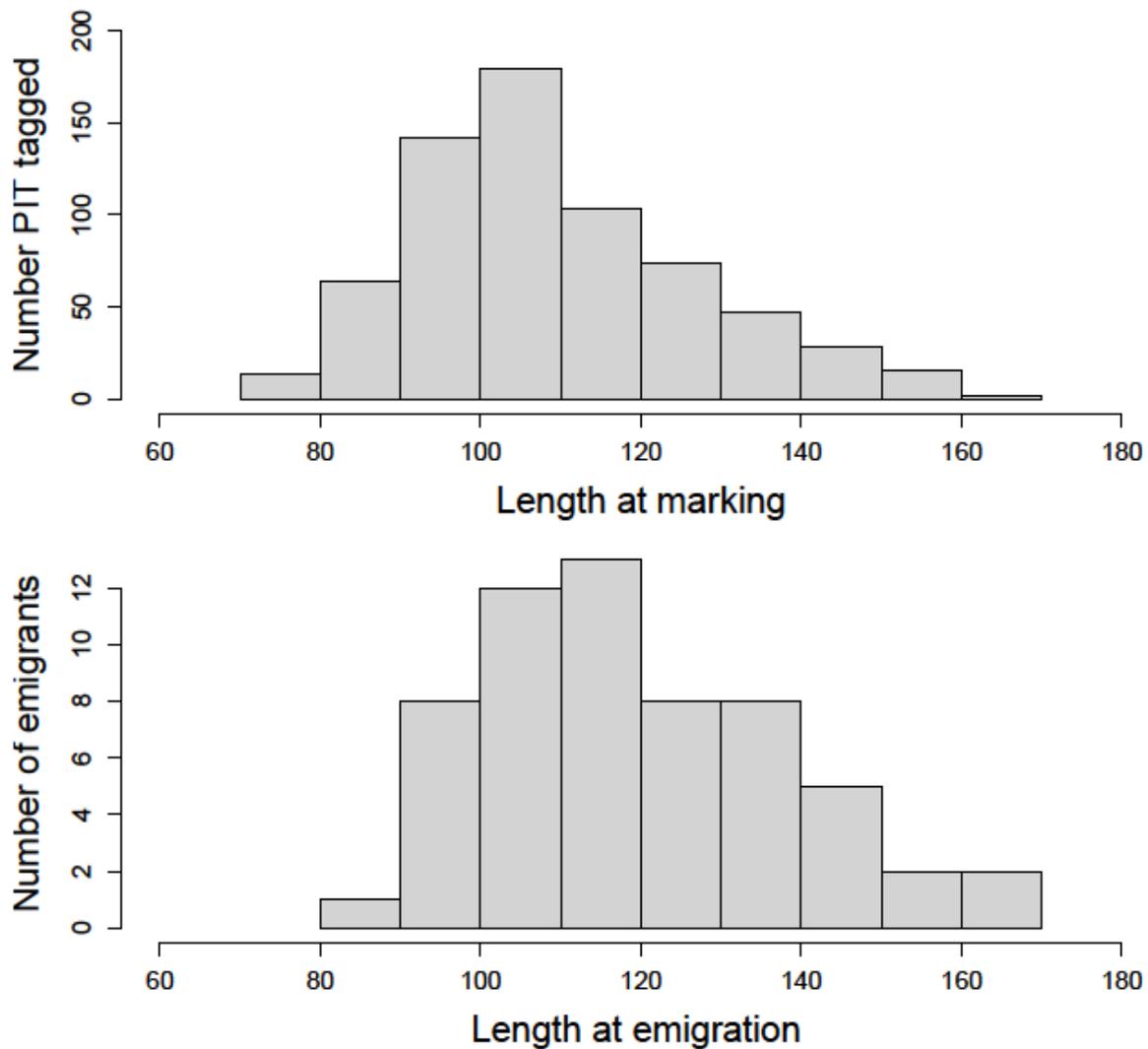


Figure 2. (Top panel) Length at capture of juvenile bull trout captured in Skiphorton Creek, Oregon and marked with PIT tags. (Bottom panel) Estimated length at emigration from the Skiphorton Creek study area. Emigration was determined by when PIT-tagged fish were detected at a passive in-stream antenna 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.

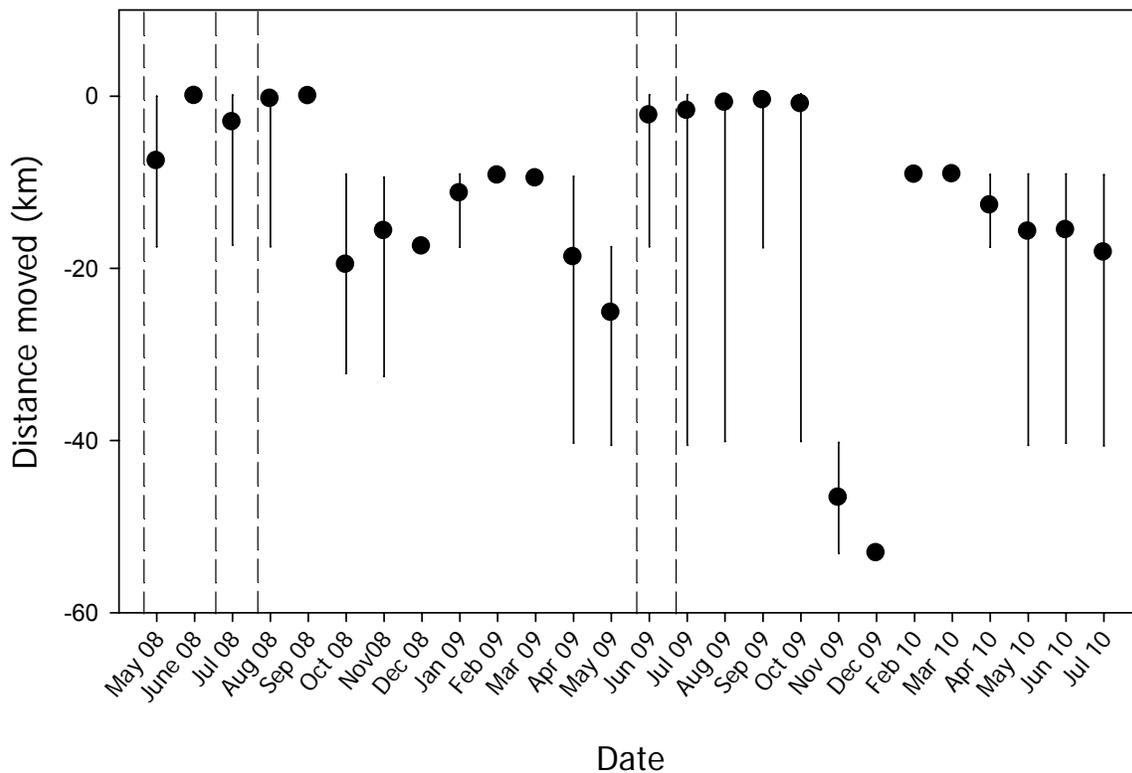


Figure 3. Direction of juvenile bull trout movements per month inferred from combined resight data from passive in-stream antennae, surveys with a mobile antenna, and active recaptures. Positive values represent distance (km) moved upstream, and negative values represent distance moved downstream. Closed circles represent mean distance moved and bars represent the maximum and minimum distance traveled for a given month. Vertical dashed lines represent discrete mark-recapture events.

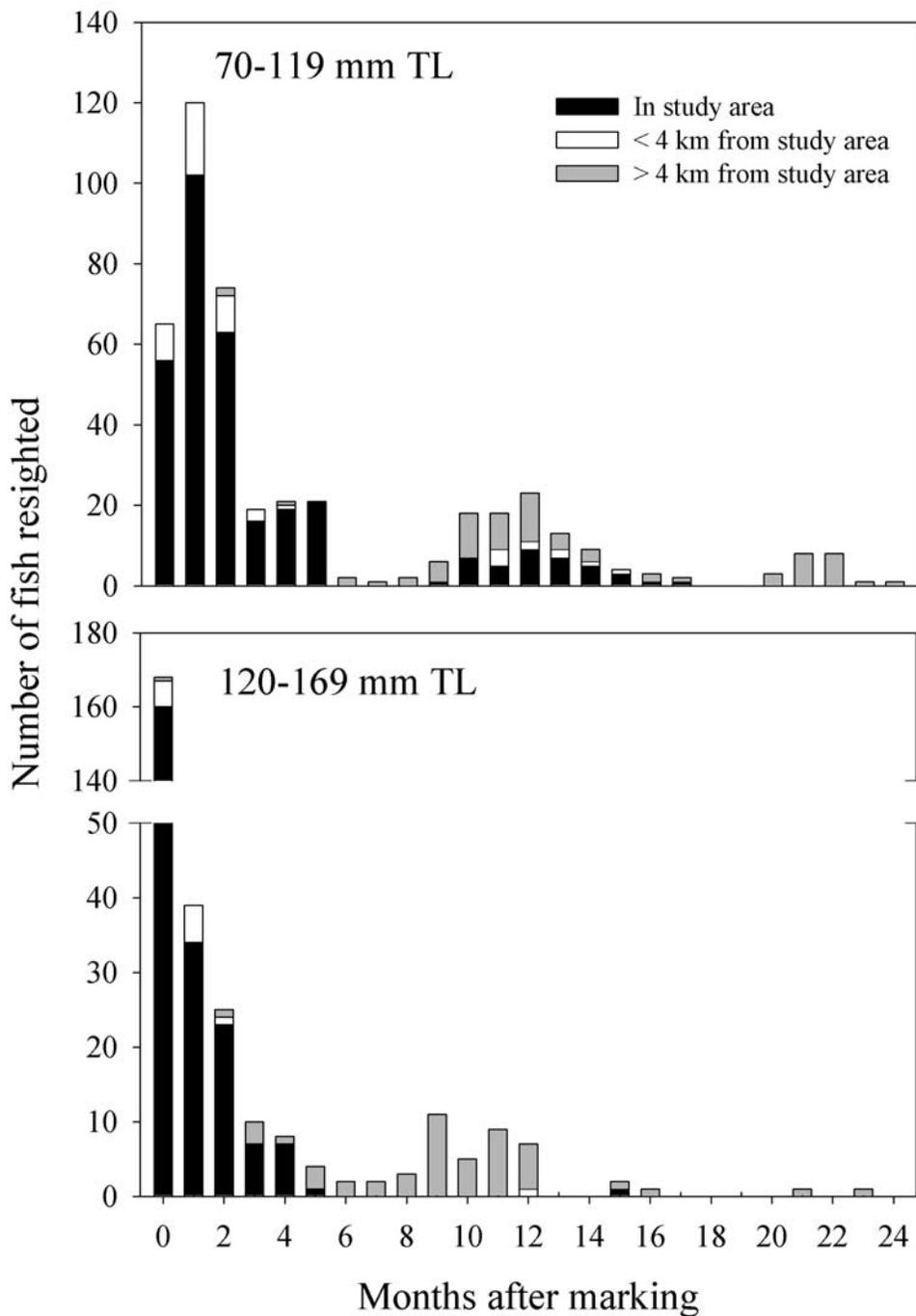


Figure 4. Number of fish resighted per month after initial capture and marking. Juvenile bull trout were resighted in the Skiphorton Creek study area (black bars), between 1-4 km from study area (white bars), and > 4 km away from the study area (grey bars).

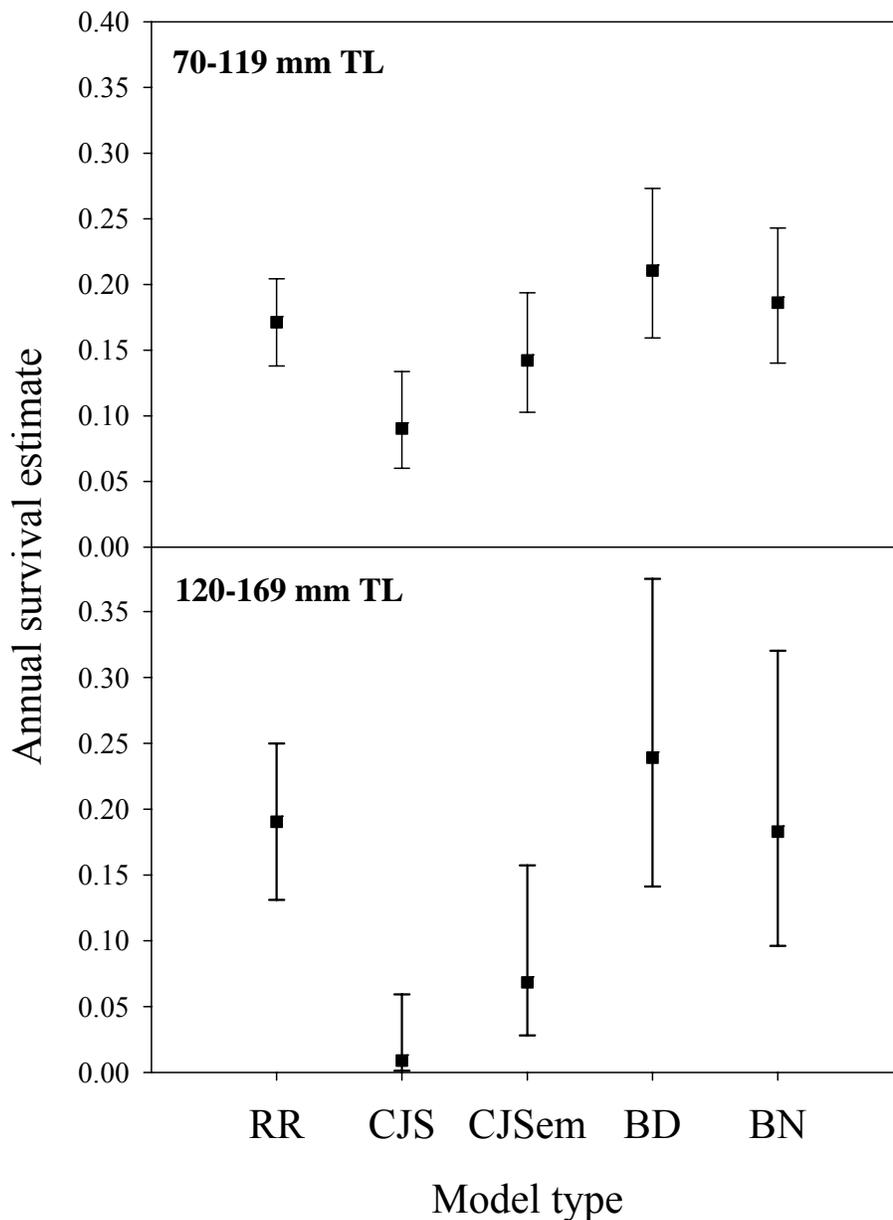


Figure 5. Estimates of survival probability for juvenile bull trout marked in Skiphorton Creek, Oregon, calculated using different methods (RR = return rate, CJS = naïve Cormack-Jolly-Seber, CJS EM = CJS with ad hoc emigration, BD = Barker model with dead recoveries, BN = Barker model without dead recoveries). Error bars represent 95% confidence intervals.