# PERFORMANCE OF PROGENY FROM STEELHEAD AND RAINBOW TROUT CROSSES 

Final Report


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LOWER SNAKE RIVER
COMPENSATION PLAN

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Front cover shows the generalized life-cycle relationship between resident rainbow trout and anadromous steelhead. Fish photos courtesy of the U.S. Fish and Wildlife Service National Digital Library.

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## PREFACE

This report provides final summary information on a summer steelhead research experiment funded under the Lower Snake River Compensation Plan (LSRCP) Monitoring and Evaluation Program operated by the Oregon Department of Fish and Wildlife (ODFW) in the Grande Ronde and Imnaha river subbasins. Ongoing monitoring activities provide technical, logistical, and biological information to managers charged with maintaining viable steelhead populations and associated fisheries in Northeast Oregon. Reported herein are results of an experiment conducted from brood years 1997 to 2003 to further our understanding of cross-breeding relationships between anadromous and resident forms of Oncorhynchus mykiss in NE Oregon. Fish culture monitoring, survival, harvest, compensation program goals, and endangered species activities from these study years are reported elsewhere.

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## EXECUTIVE SUMMARY

Results from our breeding experiments suggest that resident $O$. mykiss can produce progeny that smolt and emigrate from their freshwater habitat. The production of the anadromous life history expression from progeny of resident parents in our experimental groups indicates that managers could produce anadromous individuals from resident parental stock. This suggests that if anadromous O. mykiss were lost from a system, artificial propagation of resident progeny could be a useful tool for restoring the anadromous run.

## STUDY AREA

This study was conducted in the Grande Ronde and Imnaha River basins located in northeast Oregon (Figure 1). The Grande Ronde and Imnaha rivers flow into the Snake River, which feeds the Columbia River. Breeding experiments were conducted at the Wallowa Fish Hatchery, located near the town of Enterprise, Oregon ( $45^{\circ} 41^{\prime} 77^{\prime \prime} \mathrm{N}, 117^{\circ} 29^{\prime} 25^{\prime \prime} \mathrm{W}$ ), using Wallowa River and Little Sheep Creek summer steelhead hatchery stocks, and wild rainbow trout collected from the Wallowa River and Joseph Creek drainages (Table 1). Wild O. mykiss in the Snake River basin are of the redband subspecies (O. mykiss gairdneri; Behnke 1992). Hatchery rearing occurred at Irrigon Fish Hatchery, located near the town of Irrigon, Oregon ( $45^{\circ} 90^{\prime} 07{ }^{\prime \prime N}, 119^{\circ} 49^{\prime} 511^{\prime W}$ ).

## INTRODUCTION

Many salmonids exhibit partial migration: the phenomenon of populations partitioned into migratory and non-migratory individuals (Jonsson and Jonsson 1993). Oncorhynchus mykiss exhibit a complex of life-history strategies ranging from residency in small headwater streams to anadromy involving migrations of hundreds of kilometers. In the Grande Ronde River basin of northeast Oregon, both resident and anadromous life-history forms coexist, and thus populations found there likely exhibit partial migration.

Partial migration may have important consequences for anadromous species listed under the Endangered Species Act (ESA). The recent decline of summer steelhead (Oncorhynchus mykiss) populations in the lower Snake River has prompted their listing under the ESA. Declines in steelhead are potentially due to elevated mortality rates associated with anadromous migrations. If resident and anadromous life-history characteristics result from a phenotypically plastic trait (i.e. a genetic trait that is highly variable due to influences from environmental factors), then elevated mortality associated with the anadromous type may be shifting the populations towards residency. Further, although the anadromous expression of the trait may be declining, the trait would not necessarily be lost. Identification of the plasticity of these traits would then be important for the management of these populations.

We investigated life history traits of $O$. mykiss with studies in both the hatchery and natural environment. We anticipated that these complimentary approaches would allow us to evaluate the relationship between the two life-history forms. They should further allow us to explore the feasibility of using hatcheries to produce anadromous progeny from resident parents if the number of anadromous life-history forms becomes severely depressed. The overall goal of this study was to determine the plasticity of life history forms, specifically the ability of resident adults to produce anadromous progeny.

In this report we:

1. Compare morphological (i.e., length, weight, and condition factor) and physiological attributes (i.e., a liver-somatic index and gill $\mathrm{Na}++\mathrm{K}+$ ATP-ase specific activity) of progeny from breeding crosses.
2. Use juvenile PIT tag detections at Columbia and Snake river dams to assess whether outmigration timing, the length of outmigrants, or the percent of detected outmigrants differs between the progeny of breeding crosses.
3. Use PIT tag detections at adult detection sites on Columbia and Snake river dams to assess whether the number of returning anadromous adults differs between the progeny of breeding crosses.


Figure 1. Map of the Grande Ronde River basin showing collection locations (dark circles) of resident rainbow trout adults used in breeding experiments. The dark square shows where progeny were released on lower Deer Creek; resident rainbow trout were also collected on upper sections of Deer Creek.

## METHODS

Beginning in 1998 and continuing through 2003, we collected wild resident adult O. mykiss from the Grande Ronde River basin and crossbred them with hatchery steelhead adults from the ODFW, Wallowa Hatchery stock (Table 1). Because maturation timing of resident adults was typically later than hatchery fish we were opportunistic as to the source of resident adults for the experiments. Ripe adults of both life histories were crossbred using the following combinations:
1.) Resident or rainbow ( Rb ) females ( F ) bred with Rb males ( M ); $\mathrm{RbF} \times \mathrm{RbM}$.
2.) RbF bred with anadromous (steelhead) males (StsM); RbF x StsM.
3.) Anadromous (steelhead) females (StsF) bred with RbM; StsF x RbM.
4.) StsF bred with StsM; StsF $\times$ StsM.

Table 1. Number of parental broodstock used to generate progeny for breeding experiments. Source stream codes for resident rainbow collections are as follows: $\mathrm{D}=$ Deer Creek, $\mathrm{P}=$ Prairie Creek, S = Sumac Creek, W = Wallowa River.

| Brood Year | Breeding Group | Females | Males | Resident Source |
| :---: | :---: | :---: | :---: | :---: |
| 1998 | RbF x StsM | 2 | 3 | D |
|  | StsF $\times$ RbM | 1 | 1 | D |
|  | StsF x StsM | 2 | 2 |  |
| 1999 | RbF $\times$ RbM | 2 | 9 | W, D |
|  | RbF x StsM | 2 | 4 | W, D |
|  | StsF x RbM | 2 | 5 | D |
|  | StsF x StsM | 2 | 2 |  |
|  | ResF x RbM | 2 | 5 | D |
|  | ResF x StsM | 2 | 2 | D |
| 2000 | RbF $\times$ RbM | 3 | 12 | S, D |
|  | RbF x StsM | 2 | 4 | S, D |
|  | StsF x RbM | 4 | 8 | D |
|  | StsF x StsM | 4 | 4 |  |
| 2001 | RbF $\times$ RbM | 3 | 4 | P |
|  | RbF x StsM | 3 | 2 | P |
|  | StsF x RbM | 2 | 2 | P |
|  | StsF x StsM | 2 | 2 |  |
| 2002 | RbF $\times$ RbM | 4 | 6 | P |
|  | RbF x StsM | 3 | 2 | P |
|  | StsF x RbM | 2 | 5 | P |
|  | StsF x StsM | 2 | 2 |  |
| 2003 | RbF $\times$ RbM | 3 | 3 | P |
|  | StsF x RbM | 1 | 2 | P |
|  | StsF x StsM | 1 | 1 |  |

During 1999, we also bred residualized females (ResF; progeny from hatchery-origin anadromous parents that exhibited a freshwater life history) with both RbM and StsM.

Eggs and progeny from these crosses were incubated and reared using our standard steelhead production methods. Eggs were stripped from each female, placed in small cups, and fertilized using milt from 1-4 males. Eggs resulting from crosses were held separately in divided trays and placed in incubators at the Wallowa Fish Hatchery. After eye-up, non-viable eggs were removed and viable eggs were counted. After approximately 450 daily temperature units (DTU) of incubation, eggs were transported to Irrigon Fish Hatchery for hatching and subsequent rearing. Each progeny type was reared separately, in circular tanks ( 188 cm diameter, 91 cm deep) at $11-14.5^{\circ} \mathrm{C}$, to smolt at an age of one year, and a target release size of 205 mm fork length (FL; 5 fish/lb). Water depth in each tank was 76 cm until fish grew large enough to jump out, then depth was reduced to 30.5 cm . After fish were reared to approximately 60 mm FL, we equalized densities in each tank by culling a random sample of individuals. All fish that were retained were PIT-tagged for subsequent detections.

During rearing, we evaluated smolt development of progeny from each breeding group. During all years smolt morphological development was evaluated using condition factor [(K) where: $\mathrm{K}=$ weight $\left.(\mathrm{g}) / \mathrm{FL}^{3}(\mathrm{~mm}) \times 10^{5}\right]$, and during 1998-1999 smolt physiological development was also evaluated using liver-somatic index [(LSI) where: LSI = liver mass / body mass • 100], and gill $\mathrm{Na}^{+}+\mathrm{K}^{+}$ATP-ase specific activity (moles $\mathrm{P} \cdot \mathrm{hr}^{-1} \cdot \mathrm{mg}$ protein ${ }^{-1}$ ). Beginning the January of each release year, randomly selected fish were sacrificed at approximately two-week intervals for smolt development evaluation. Prior to and after PIT-tagging, we periodically measured (FL) individuals from a sub-sample of each breeding group to track their growth history. All fish were also measured (FL) and subsamples were weighed just prior to release, at which time we noted if males were discharging milt, a signal of precocious maturation.

After approximately one year of growth, PIT-tagged fish were released directly into Deer Creek (a tributary of the Wallowa River that enters at river kilometer 18) at the Big Canyon Facility in early May. We monitored the detection of these PIT-tagged fish at Snake and Columbia River dam facilities, as indicators of smolt emigration from the Grande Ronde River system. This study was not designed to assess survival to adulthood of progeny from breeding crosses; such a study would require much larger numbers of PIT-tagged progeny than we released. However, we also monitored and report PIT tag detections in adult ladders at dam facilities one to three years following release as a possible indication of successful completion of an anadromous life cycle.

## RESULTS

Until 2000 we had difficulty finding sufficient numbers of resident females each year to produce adequate numbers of progeny from these parent crosses. During 1998 we collected and spawned five female and five male resident adults from Deer Cr . with three female and five anadromous adults from the Wallowa hatchery stock. These crosses resulted in the release of more than 200 progeny from each group except $\mathrm{RbF} \times \mathrm{RbM}$, which died during spawning (Table 2). During 1999 we collected and spawned two female and nine male resident adults from Deer Cr. with two female and four anadromous adults from the Wallowa hatchery stock and two residualized females that were captured at steelhead collection sites. These crosses resulted in the release of more than 350 progeny from each breeding group (Table 2). During 2000 we collected and spawned two female resident adults from Sumac Cr. (a tributary to Joseph Creek), one female resident from Deer Cr., and eight male resident adults from Deer Cr. with
four female and four anadromous adults from the Wallowa hatchery stock. These crosses resulted in the release of more than 1,000 total progeny from all breeding groups (Table 2). From 2001 onward we switched to Prairie Cr. (tributary to the Wallowa River) as a source of resident adults. In 2001 we spawned three resident females and six resident males with two female and four male Wallowa-stock adults. These crosses resulted in the release of more than 3,000 total progeny from all breeding groups (Table 2). In 2002 we spawned four resident females with six resident males, and released over 3,000 progeny from all crosses. Over 3,000 progeny from breeding crosses were again released in 2002, with three resident females spawned with three resident males.

Mean gill $\mathrm{Na}^{+}+\mathrm{K}^{+}$ATP-ase activity was more variable among 99-brood-year groups compared to those from the 1998 brood year. ATP-ase activity was generally similar and unchanged among the three groups of progeny (RbF x StsM, StsF x RbM, and StsF x StsM) during 1998 (Figure 2). However, just prior to release in May, ATP-ase activity of StsF x StsM progeny was significantly higher than ATP-ase activity of StsF x RbM progeny. ATP-ase activity of RbF x RbM progeny during 1999 initially declined during February and March but then increased through April and was significantly higher than all other groups just prior to release (Figure 3). In contrast, ATP-ase activity of RbF x StsM, StsF x RbM, and StsF x StsM progeny increased during February and March but then declined during April and early May. We did not measure ATP-ase activity for the 2000 and 2001 brood years.

Liver somatic index values for 1998 brood-year progeny generally increased before release but during 1999, these same groups were generally unchanged (Figure 4). The subset of 1998 brood-year progeny retained after the release date showed greater increases in their LSI values. Of these, StsF x StsM progeny showed the greatest increases and highest values compared to all other groups.

In general, progeny from $\mathrm{RbF} \times \mathrm{RbM}$ crosses were more variable in length just prior to release than those from other crosses, and they had lower median weights and higher median condition factors (Figure 5; Appendix Tables 1-6). Progeny groups from rainbow mothers had non-normal size-frequency histograms that were strongly skewed to the left in most brood years (Figures 6-11). In contrast, size-frequency histograms of progeny groups from steelhead mothers were more normally distributed. In addition, progeny groups from mixed parentage had distributions that were sometimes bimodal; including groups of both small and large individuals. When size-frequency distributions of released fish were skewed to the left, larger fish were generally detected at a higher rate at mainstem dam facilities than smaller individuals from the same group. Median fork length of fish detected at mainstem dam facilities was longer than at the time of release (Figures 6-11), except for StsF x RbM and StsF x StsM release groups in brood year 1998, the RbF x RbM release group in 2001, and the RbF x StsM release group in 2002. Percentage of precocious individuals was always greater for RbF $\times$ RbM progeny compared to all other groups from brood years 2000 through 2003.

Outmigrating progeny of StsF x StsM crosses arrived at Lower Granite Dam at an earlier median date than progeny from other crosses in five of six release years, and progeny from RbF x RbM crosses were last to arrive in four of five release years (Figure 12; Appendix Figures 13). Migration timing to Lower Granite Dam was significantly different among all breeding crosses (rank-based ANOVA, $P=0.050$ ), however only the pairwise comparison between RbF x RbM and StsF x StsM was statistically significant $(P=0.012)$. Across all release years, $6.1 \%$ of progeny from RbF x RbM releases were detected at juvenile observation sites on Columbia and Snake river dams, whereas $39.1 \%$ of StsF x StsM progeny were detected, and intermediate percentages were detected for crosses between resident and anadromous adults (Table 2;

Figure 13). Because the length of freshwater residency of juvenile steelhead may sometimes be two or more years (Randall et al. 1987), we investigated whether any of our progeny were observed at juvenile detection locations in the second year following release. Over the course of this experiment, less than $1.5 \%$ of released progeny were detected in the second year (Figure 14).

Table 2. Number of PIT-tagged progeny released, number detected at Snake and Columbia river mainstem dam facilities, and detection rate (percentage) from experimental release groups. Abbreviations for parental origin of release groups include rainbow ( Rb , resident origin), steelhead (Sts, anadromous origin), residualized (Res.; fish from anadromous parents that have switched to a freshwater life history), female (F), and male (M). Multiple entries in any release group during a single year indicate replicate groups.

|  | 1998 Brood Year |  |  | 1999 Brood Year |  |  | 2000 Brood Year |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Release Group | Number Released | Number Detected | $\begin{gathered} \text { Detection } \\ \text { Rate } \\ \hline \end{gathered}$ | Number Released | Number Detected | $\begin{gathered} \text { Detection } \\ \text { Rate } \\ \hline \end{gathered}$ | Number Released | Number Detected | $\begin{gathered} \text { Detection } \\ \text { Rate } \\ \hline \end{gathered}$ |
| RbF x <br> RbM | 0 | -- | -- | 365 | 24 | 6.6\% | 206 | 34 | 16.5\% |
| RbF x StsM | 209 | 79 | 37.8\% | 379 | 50 | 13.2\% | 87 | 22 | 25.3\% |
| StsF x RbM | 263 | 127 | 48.3\% | 390 | 132 | 33.8\% | $\begin{aligned} & 206 \\ & 174 \end{aligned}$ | $\begin{aligned} & 55 \\ & 49 \end{aligned}$ | $\begin{aligned} & 26.7 \% \\ & 28.2 \% \end{aligned}$ |
| $\begin{gathered} \text { StsF x } \\ \text { StsM } \end{gathered}$ | $\begin{aligned} & 290 \\ & 220 \end{aligned}$ | $\begin{aligned} & 152 \\ & 112 \end{aligned}$ | $\begin{aligned} & 52.4 \% \\ & 50.9 \% \end{aligned}$ | 411 | 148 | 36.0\% | $\begin{aligned} & 210 \\ & 241 \end{aligned}$ | $\begin{gathered} 88 \\ 108 \end{gathered}$ | $\begin{aligned} & 41.9 \% \\ & 44.8 \% \end{aligned}$ |
| ResF x RbM | -- | -- | -- | 405 | 75 | 18.5\% | -- | -- | -- |
| ResF x StsM | -- | -- | -- | 394 | 102 | 25.9\% | -- | -- | -- |


| Release Group | 2001 Brood Year |  |  | 2002 Brood Year |  |  | 2003 Brood Year |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Number Released | Number Detected | $\begin{gathered} \text { Detection } \\ \text { Rate } \\ \hline \end{gathered}$ | Number Released | Number Detected | $\begin{gathered} \text { Detection } \\ \text { Rate } \\ \hline \end{gathered}$ | Number Released | Number Detected | $\begin{gathered} \hline \text { Detection } \\ \text { Rate } \\ \hline \end{gathered}$ |
| RbF x | 348 | 0 | 0.0\% | 563 | 25 | 4.4\% | 412 | 5 | 1.2\% |
| RbM | 358 | 3 | 0.8\% | 434 | 22 | 5.1\% | 435 | 6 | 1.4\% |
|  | 413 | 2 | 0.5\% | 441 | 2 | 0.5\% | 418 | 9 | 2.2\% |
|  |  |  |  |  |  |  | 442 | 9 | 2.0\% |
|  |  |  |  |  |  |  | 444 | 3 | 0.7\% |
| RbF x | 493 | 49 | 9.9\% | 539 | 77 | 14.3\% | -- | -- | -- |
| StsM | 516 | 53 | 10.3\% | 516 | 79 | 15.3\% |  |  |  |
| StsF x | 480 | 51 | 10.6\% | 496 | 72 | 14.5\% | 311 | 53 | 17.0\% |
| RbM |  |  |  |  |  |  | 304 | 68 | 22.4\% |
| StsF x <br> StsM | 497 | 118 | 23.7\% | 480 | 87 | 18.1\% | 490 | 284 | 57.9\% |



Figure 2. Mean gill $\mathrm{Na}^{+}+\mathrm{K}^{+}$ATP-ase specific activity (moles $\mathrm{P} \cdot \mathrm{hr}^{-1} \cdot \mathrm{mg}^{\text {p }}$ protein ${ }^{-1} ; \pm 95 \% \mathrm{Cl}$ ) of progeny representing three experimental breeding groups from brood year 1998. A subset of the total progeny was held after the date when PIT-tagged fish were released for the detection evaluation.


Figure 3. Mean gill $\mathrm{Na}^{+}+\mathrm{K}^{+}$ATP-ase specific activity (moles $\mathrm{P} \cdot \mathrm{hr}^{-1} \cdot \mathrm{mg}^{\text {protein }}{ }^{-1} ; \pm 95 \% \mathrm{Cl}$ ) of progeny representing six experimental breeding groups from brood year 1999.


Figure 4. Mean liver somatic index [(g/g) • 1000] of progeny representing three and six experimental breeding groups from brood years 1998 and 1999, respectively. During 1998, a subset of the total progeny was held after the date when PIT-tagged fish were released for the detection evaluation.

During this study only eight PIT-tagged progeny from our breeding crosses were subsequently detected at adult observation sites on Columbia and Snake river dams (Table 3). Of these, it is likely that the two detections in 1998 at Lower Granite Dam were from fish that had outmigrated no farther than downstream of Lower Granite Dam, otherwise these fish would probably have been recorded at the Bonneville and/or McNary dam adult detection sites. Of the six remaining adults detected, each came from crosses using female steelhead.

## DISCUSSION

Results from our breeding experiments suggest that resident $O$. mykiss can produce progeny that smolt and emigrate from their freshwater habitat. Although at a reduced rate compared to StsF $\times$ StsM crosses, RbF $\times$ RbM, RbF $\times$ StsM, and StsF $\times$ RbM crosses all produced emigrating progeny that were detected at Snake and Columbia river facilities. The production of hatchery-reared emigrating progeny by $\mathrm{RbF} \times \mathrm{RbM}$ parents suggests that resident and anadromous life history traits are phenotypically plastic. This plasticity suggests that given suitable environments, resident fish have genetic traits allowing their progeny to exhibit the anadromous expression of this plastic life history trait. However, emigrating RbF $\times \mathrm{RbM}$ progeny do not necessarily indicate a successful life history transition. Returning adults that reproduced successfully would indicate successful transition to anadromy.


Figure 5. Boxplots of fork length (top panel; mm), weight (middle panel; g), and condition factor $(K)$ of progeny from breeding crosses, just prior to their stream release. Boxes represent the interquartile range containing $50 \%$ of the values; horizontal lines represent the median value. Vertical lines extending from each end of the box show the minimum and maximum values.


Figure 6. Length-frequency distributions of groups of PIT-tagged progeny released and detected from the 1998 brood year. Progeny groups resulted from three parental crossings: resident female (RbF) and anadromous male (StsM), anadromous female (StsF) and resident male (RbM), and StsF and StsM. Number of PIT-tagged progeny in each release group ( $n_{r}$ ), and number subsequently detected at mainstem dam facilities $\left(\mathrm{n}_{\mathrm{d}}\right)$ are also shown.

$60 \quad 80100120140160180200220240260280300320340$

## FORK LENGTH (mm)

Figure 7 Length-frequency distributions of groups of PIT-tagged progeny released and detected from the 1999 brood year. Progeny groups resulted from six parental crossings: resident female ( RbF ) with anadromous male (StsM), anadromous female (StsF) with resident male (RbM), StsF with StsM, RbF with RbM, residualized female (ResF) with RbM, and ResF with StsM. Number of PIT-tagged progeny in each release group ( $n_{r}$ ), and number subsequently detected at mainstem dam facilities $\left(\mathrm{n}_{\mathrm{d}}\right)$ are also shown.


Figure 8. Length-frequency distributions of groups of PIT-tagged progeny released and detected from the 2000 brood year. Progeny groups resulted from four parental crossings: resident female (RbF) with anadromous male (StsM), anadromous female (StsF) with resident male (RbM), StsF with StsM, and RbF with RbM. Number of PIT-tagged progeny in each release group ( $n_{r}$ ), and number subsequently detected at mainstem dam facilities ( $n_{d}$ ) are also shown.


Figure 9. Length-frequency distributions of groups of PIT-tagged progeny released and detected from the 2001 brood year. Progeny groups resulted from three parental crossings: resident female (RbF) with anadromous male (StsM), anadromous female (StsF) with resident male (RbM), and StsF with StsM. Number of PIT-tagged progeny in each release group ( $n_{r}$ ), and number subsequently detected at mainstem dam facilities $\left(\mathrm{n}_{\mathrm{d}}\right)$ are also shown.


Figure 10. Length-frequency distributions of groups of PIT-tagged progeny released and detected from the 2002 brood year. Progeny groups resulted from four parental crossings: resident female ( RbF ) with resident male ( RbM ), resident female (RbF) with anadromous male (StsM), anadromous female (StsF) with resident male (RbM), and StsF with StsM. Number of PIT-tagged progeny in each release group ( $\mathrm{n}_{\mathrm{r}}$ ) and number subsequently detected at mainstem dam facilities $\left(\mathrm{n}_{\mathrm{d}}\right)$ are also shown.


Figure 11. Length-frequency distributions of groups of PIT-tagged progeny released and detected from the 2003 brood year. Progeny groups resulted from three parental crossings: resident female (RbF) with resident male (RbM), anadromous female (StsF) with resident male (RbM), and StsF with StsM. Number of PIT-tagged progeny in each release group ( $n_{r}$ ) and number subsequently detected at mainstem dam facilities $\left(\mathrm{n}_{\mathrm{d}}\right)$ are also shown.

The production of the anadromous life history expression from progeny of resident parents in our experimental groups also indicates that managers could produce anadromous individuals from resident parental stock. This suggests that if anadromous O. mykiss were lost from a system, artificial propagation of resident progeny could be a useful tool for restoring the anadromous run. Factors responsible for extirpation of the original anadromous population would, of course, need to be addressed. However, this type of propagation has been accomplished for other salmonids (Kaeriyama et al. 1992) and rainbow trout transplanted to Argentina developed anadromous life histories after several generations as residents (Pascual 2001). Our resident fish came from riverine sources open to anadromy. Additional work would be needed to determine if the anadromous expression of the trait is lost in O. mykiss after extended isolation from anadromy, as has occurred after the construction of many dams that lack fish passage. In studies of salmon populations that have been landlocked for thousands of years, some populations maintained the ability to smolt (Foote et al. 1994; Kiiskinen et al. 2002) while others did not (Nilsen et al. 2003; Nilsen et al. 2007).

We did not perform an analysis to determine the parentage of our resident adults, therefore it is possible that some fish identified as resident-origin were actually first generation progeny of naturally-produced anadromous adults, that is, residualized steelhead. If this were the case it would represent a confounding factor in our results. First generation, -or even second or third generation - progeny of residualized steelhead may be more or less prone to maintain an entirely freshwater life-history than offspring whose recent lineage includes only freshwater residency. Given that residualized steelhead are more commonly male (Viola and Schuck 1995), the parentage question is most pertinent to $\mathrm{RbF} \times \mathrm{RbM}$ and StsF $\times \mathrm{RbM}$ pairings. We are unaware of studies which directly address the question of migratory behaviors of progeny from residualized steelhead or salmon, however our data from BY 1999 suggests that progeny from residual females migrate at intermediate rates relative to those of resident and anadromous females.

Progeny from Sts parents were apparently more physiologically prepared for smoltification at an earlier date than RbF $\times$ RbM progeny. ATP-ase activity of $\mathrm{RbF} \times \mathrm{RbM}$ progeny was still increasing when they were released in early May whereas it was declining for Sts progeny during the same period. For all groups, LSI remained relatively unchanged prior to release dates but increased in the 1998 brood-year group subsamples that were retained after the early-May release. Increasing LSI during this period may have been an indication that these fish were experiencing physiological changes in preparation to residualize. As expected, K was often lower for StsF x StsM progeny and often higher for RbF x RbM progeny when compared to other groups. Lower K values indicate that StsF x StsM progeny likely had more smolt-like or fusiform body characteristics.

Size frequency distributions of progeny just prior to release were different among groups; RbF x RbM progeny were highly variable in length and RbF x StsM, and StsF $\times$ RbM progeny showed bimodal distributions. These variable and bimodal distributions are indicative of dual life-history strategies in these groups, which was verified by their lower and intermediate detection rates at mainstem dams. Moreover, larger individuals from these groups were predominately detected at dam facilities suggesting that larger progeny were more likely to smolt than smaller progeny from the same parental groups. However, we also cannot exclude the possibility that size-dependent mortality was a greater factor during outmigration for resident by steelhead crosses than for steelhead x steelhead crosses.

Growth rate is known to influence whether salmonids smolt and become anadromous or fail to smolt and assume a freshwater residence (Thorpe 1987). In this study we reared the
progeny of all cross-breedings similarly, because we had no knowledge of the optimal growth rate that would induce smoltification for each progeny group. The Wallowa Hatchery stock steelhead used in this study is raised to smolt after one-year of freshwater rearing. However, given that naturally reproducing $O$. mykiss populations are known to produce smolts with freshwater residence times exceeding one year, it is plausible that the "one-year-to smoltification" growth trajectory employed in this study was not ideal for producing smolts from our wild resident trout matings. Future investigations into the feasibility of starting a steelhead stock with resident trout should also consider rearing experiments with a slower growth trajectory over a two-year period, which may initially produce more smolts and more returning adults.

In the most recent ten-year period for which data is available (1992 to 2001; Warren et al. 2009), smolt-to-adult (SAR) returns to Lower Granite Dam from programmatic Wallowa Hatchery steelhead releases averaged $0.55 \%$, and ranged widely from $0.21 \%$ to $1.33 \%$. By comparison, progeny from all StsF x StsM crosses in this study returned an estimated two adults for an SAR of $0.07 \%$. Therefore it appears that rearing or handling procedures during our experiments may have produced steelhead progeny that are predisposed to have lower survival to adulthood than conventionally reared smolts.

Although we were able to produce emigrating $\mathrm{RbF} \times \mathrm{RbM}$ progeny in hatchery conditions, it is still unclear whether wild resident adults produce such progeny in the Grande Ronde River system. Ruzycki et al. (2003) reported on a microchemistry methods study in which the strontium to calcium ratio of otoliths collected from juvenile O. mykiss in the Grande Ronde River basin were used successfully to determine maternal parentage (i.e., from a resident or anadromous female). The results suggest that resident adults do breed with anadromous adults in the Grande Ronde River. Some anecdotal evidence also suggests that they do interbreed. During spawning ground surveys we have observed small resident fish near redds of actively spawning anadromous females and each year we collect hundreds of residualized hatchery males at our steelhead collection facilities. In Prairie Creek, a tributary to the Wallowa River, resident adults spawn during the same time as anadromous adults. Temporal overlap in spawn timing could allow interactions among the life history traits although it is certainly not assured. Zimmerman and Reeves (2000) found reproductive segregation among resident and anadromous adults in the Deschutes River, OR but they also found low levels of both resident and anadromous progeny from alternate maternal origin in the Babine River, British Columbia. Although resident and anadromous adults do interbreed in the Grande Ronde River, we suspect these pairings are limited by temporal and spatial differences in spawning and from assortative mating of different-sized adults. Future microchemistry analysis will help in determining the extent of life history interactions in the basin. However, otolith microchemistry analysis will only allow us to determine maternal origin and thus cannot identify paternal contributions.


Figure 12. Median (dark bars) and range of arrival dates at Lower Granite (A) and Bonneville dams of juvenile progeny from breeding crosses that occurred in brood years 1998 through 2003.


Figure 13. Average percent of PIT-tagged progeny recorded at all juvenile observation sites on Columbia and Snake river dams. Vertical bars are 2 SE.


Figure 14. Average percent of PIT-tagged progeny recorded at all juvenile observation sites on Columbia and Snake river dams in the second migration year following release. Vertical bars are 2 SE.

Table 3. Detections of PIT-tagged progeny from breeding crosses recorded at adult observation sites on Columbia and Snake river dams. Codes for dams are as follows: BON = Bonneville, MCN = McNary, IHA = Ice Harbor, GRA = Lower Granite.

| Brood Year | Breeding Cross | Number of Adults | Dam Detections |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | BON | MCN | IHA | GRA |
| 1998 | RbF x StsM | 1 | -- | -- | -- | Sept. |
| 1998 | StsF x StsM | 1 | -- | -- | -- | Oct. |
| 1999 | StsF x RbM | 1 | July | Aug. | -- | Oct. |
| 2000 | StsF $\times$ RbM | 1 | Aug. | Sept. | Sept. | Oct. |
|  | StsF x RbM | 1 | July | Aug. | Aug. | Sept. |
|  | StsF x RbM | 1 | Oct. | -- | -- | -- |
| 2001 | StsF x StsM | 1 | Oct. | Oct. | Oct. | Oct. |
|  | StsF x StsM | 1 | Aug. | Sept. | Sept. | Sept. |

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APPENDICES

Appendix Table 1. Median fork length (mm), weight ( g ), and condition factor ( K ) from progeny from three breeding groups in brood year 1998. All metrics shown were measured on 5 May, 1999. See methods for definitions of abbreviations for parent types.

| Body measure | Breeding Group |  |  |
| :--- | :---: | :---: | :---: |
|  | RbF $\times$ StsM | StsF $\times$ RbM | StsF $\times$ StsM |
| Fork length $(\mathrm{mm})$ | 205 | 201 | 212 |
| Weight $(\mathrm{g})$ | 96.2 | 93.2 | 102.5 |
| Condition Factor | 1.08 | 1.14 | 1.07 |

Appendix Table 2. Median fork length (mm), weight (g), and condition factor (K) from progeny from six breeding groups in brood year 1999. All metrics shown were measured on 1 May, 2000. See methods for definitions of abbreviations for parent types.

| Body measure | Breeding Group |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | RbF x | RbF x | StsF $x$ | StsF $\times$ | Res. F x | Res. F x |
|  | RbM | StsM | RbM | StsM | RbM | StsM |
| Fork length (mm) | 166 | 200 | 205 | 201 | 208 | 204 |
| Weight $(\mathrm{g})$ | 35.8 | 75.8 | 95.7 | 86.8 | 100.7 | 92.8 |
| Condition Factor | 1.09 | 1.15 | 1.08 | 1.09 | 1.06 | 1.07 |

Appendix Table 3. Median fork length (mm), mass ( g ), and condition factor (K) from progeny from six breeding groups in brood year 2000. Two breeding groups, StsF x RbM and StsF x StsM, each had two replicate groups. All metrics shown were measured on 30 April, 2001. See methods for definitions of abbreviations for parent types.

|  | Breeding Group |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Body measure | RbF $x$ | RbF $x$ | StsF $x$ | StsF $x$ | StsF x | StsF x |
|  | RbM | StsM | RbM | RbM | StsM | StsM |
| Fork length $(\mathrm{mm})$ | 185 | 198 | 204.5 | 205 | 208 | 207 |
| Weight $(\mathrm{g})$ | 71.4 | 90.7 | 95.9 | 97.1 | 96.8 | 95.3 |
| Condition Factor | 1.10 | 1.12 | 1.12 | 1.11 | 1.07 | 1.07 |
| \% precocious | 15.5 | 11.5 | 8.2 | 7.7 | 7.2 | 4.3 |

Appendix Table 4. Median fork length (mm), mass ( g ), and condition factor ( K ) from progeny from six breeding groups in brood year 2001. Two breeding groups, RbF x RbM and RbF x StsM, had replicate groups. All metrics shown were measured on 29 April, 2002. See methods for definitions of abbreviations for parent types.

|  | Breeding Group |  |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Body measure | RbF x | RbF x | RbF x | RbF $x$ | RbF $x$ | StsF $\times$ | StsF x |
|  | RbM | RbM | RbM | StsM | StsM | RbM | StsM |
| Fork length (mm) | 170 | 172 | 168 | 193 | 191 | 194 | 202 |
| Weight $(g)$ | 59.4 | 63.9 | 54.5 | 78.9 | 81.5 | 84.3 | 87.5 |
| Condition Factor | 1.24 | 1.26 | 1.18 | 1.14 | 1.14 | 1.15 | 1.08 |
| \% precocious | 13.3 | 14.8 | 8.3 | 0.2 | 0.4 | 8.1 | 0.4 |

Appendix Table 5. Median fork length (mm), mass ( g ), and condition factor ( K ) from progeny from six breeding groups in brood year 2002. Two breeding groups, RbF x RbM and StsF x RbM, had replicate groups. All metrics shown were measured on 28 April, 2003. See methods for definitions of abbreviations for parent types.

|  | Body measure |  |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | RbF x | RbF x | RbF x | RbF $x$ | StsF x | StsF x | StsF x |
|  | RbM | RbM | RbM | StsM | RbM | RbM | StsM |
| Fork length (mm) | 183 | 182 | 171 | 192 | 191 | 189 | 193 |
| Weight $(\mathrm{g})$ | 75.2 | 93.3 | 64.7 | 89.7 | 76.1 | 61.4 | 79.1 |
| Condition Factor | 1.10 | 1.29 | 1.19 | 1.27 | 1.20 | 0.87 | 1.10 |
| \% precocious | 28.6 | 33.4 | 21.8 | 1.7 | 13.3 | 2.6 | 6.2 |

Appendix Table 6. Median fork length (mm), mass ( g ), and condition factor ( K ) from progeny from six breeding groups in brood year 2003. Two breeding groups, RbF x RbM and StsF x RbM, had replicate groups. All metrics shown were measured on 9 March, 2004. See methods for definitions of abbreviations for parent types.

|  | Breeding Group |  |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Body measure | RbF x | RbF x | RbF x | RbF $x$ | StsF $x$ | StsF $x$ | StsF x |
|  | RbM | RbM | RbM | RbM | RbM | RbM | StsM |
| Fork length (mm) | 168 | 161 | 161 | 149 | 172 | 168 | 171 |
| Weight $(\mathrm{g})$ | 60.9 | 59.0 | 54.4 | 47.3 | 62.7 | 58.8 | 55.2 |
| Condition Factor | 1.20 | 1.24 | 1.17 | 1.24 | 1.19 | 1.18 | 1.06 |
| \% precocious | 12.5 | 24.4 | 7.4 | 13.2 | 3.9 | 0.0 | 0.0 |



Appendix Figure 1. Percent of PIT-tagged progeny from brood year 1998 breeding crosses that were detected at Lower Granite Dam from May through August, following river release in early May, 1999. Progeny groups resulted from three parental crossings: resident female (RbF) and anadromous male (StsM), anadromous female (StsF) and resident male (RbM), and StsF and StsM.


Appendix Figure 2. Percent of PIT-tagged progeny from brood year 1999 breeding crosses that were detected at Lower Granite Dam from May through August, following river release in early May, 2000. Progeny groups resulted from six parental crossings: in (A) resident female (RbF) with anadromous male (StsM), anadromous female (StsF) with resident male (RbM), StsF with StsM, RbF with RbM, and in (B) residualized female (ResF) with RbM, and ResF with StsM.


Appendix Figure 3. Percent of PIT-tagged progeny from brood years 2000 (top panel) and 2001 breeding crosses that were detected at Lower Granite Dam from May through August, following river release in early May. Progeny groups resulted from four parental crossings: resident female (RbF) with resident male (RbM), RbF with anadromous male (StsM), anadromous female (StsF) with RbM, StsF with StsM.


Appendix Figure 4. Percent of PIT-tagged progeny from brood years 2002 (top panel) and 2003 breeding crosses that were detected at Lower Granite Dam from May through August, following river release in early May. Progeny groups resulted from four parental crossings: resident female (RbF) with resident male (RbM), RbF with anadromous male (StsM), anadromous female (StsF) with RbM, StsF with StsM.

