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ARTICLE

Smoltification in an Impounded, Adfluvial Redband Trout Population Upstream from an Impassable Dam: Does It Persist?

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Abstract

This study evaluated whether a population of adfluvial redband trout *Oncorhynchus mykiss gairdnerii* (a subspecies of rainbow trout) in Mann Creek and Reservoir, southwestern Idaho, continues to undergo smoltification. This population had an anadromous component before the construction of main-stem and tributary dams in 1958 and 1967, respectively. Smoltification was assessed by quantifying the proportion of juvenile migrants that displayed high skin reflectance, comparing mean gill Na^+,K^+-ATPase activity among migrants, and examining migration timing compared with that of neighboring steelhead (anadromous rainbow trout) populations. Approximately one-quarter of the 1,502 juvenile migrants trapped and examined displayed the intermediate or high skin reflectance (nonbanded silvery coloration) characteristic of smolts; the other fish maintained a banded coloration more typical of resident fish. For 78 samples of gill filaments over the course of the migration season (18 March to 3 June), Na^+,K^+-ATPase activity varied considerably among fish (0.95–5.81 μmol Pi $\cdot$ h^{-1} $\cdot$ mg $protein^{-1}$) and doubled in nonbanded fish over the course of the migration period. ATPase activity was significantly higher for nonbanded fish than for banded fish at the end of the migration period (21 May – 4 June). Juvenile adfluvial redband trout migrated from Mann Creek in approximate synchrony with neighboring steelhead populations. These results suggest the possibility that in areas in the Snake River drainage where steelhead have been extirpated as a result of artificial barriers, remnant populations retain the potential for anadromy.

In the Columbia River basin east of the Cascade Mountains and to barrier falls on the Kootenai, Pend Oreille, Snake, and Spokane rivers, all native rainbow trout *Oncorhynchus mykiss* including anadromous forms, or steelhead, are designated Columbia River redband trout *O. mykiss gairdnerii* (Behnke 1992). Redband trout can be found in diverse habitats that include small montane headwater streams, large rivers, desert streams, reservoirs and lakes, and marine waters (Behnke 1992; Muhlfeld 2002; Quinn 2005; Walters et al. 2005). In the upper Snake River basin, Idaho, dams and other barriers have commonly restricted populations of the species that formerly had anadromous components to potadromous (river-rearing) or adfluvial (lake- or reservoir-rearing) life histories. Before 1958, fish could migrate in the Snake River above and below the present day Hells Canyon Dam complex (Brownlee, Oxbow, and Hells Canyon dams) and complete an anadromous life history (steelhead). One such population is found in the Mann Creek drainage in southwestern Idaho, where steelhead that historically had access to Mann Creek were blocked after the completion of the Hells Canyon complex. The closure of Mann Creek Dam and completion of the irrigation reservoir in 1967 (capacity, 13,563,000 m^3; drainage area, 138.6 km^2; full pool surface area, 114.5 ha; mean depth, 10.0 m, normal pool elevation, 880.1 m; Young et al. 1977; Dillon 1991; Kozfkay et al. 2009) further restricted fish movement, isolating them to the reservoir and the inflowing stream (Figure 1).

Results of several studies suggest the possibility that redband trout populations that were historically sympatric with steelhead will retain the capability of completing an anadromous life history if migratory paths were reconnected (Pascual et al. 2001;

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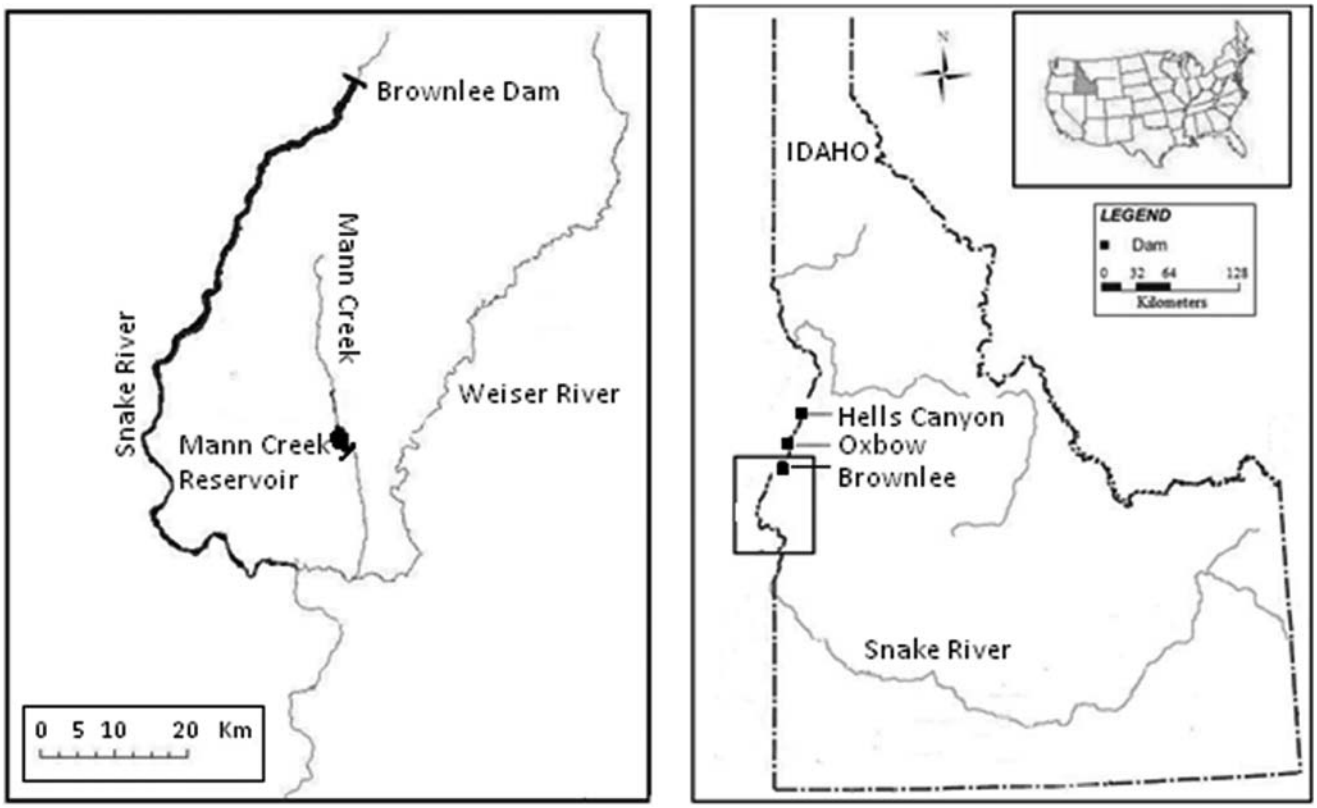

FIGURE 1. Study area indicating location of Mann Creek, Weiser River drainage, southwestern Idaho, relative to Brownlee Dam (left panel), and Hells Canyon, Oxbow, and Brownlee dams on the Snake River (right panel).

Thrower and Joyce 2004; Thrower et al. 2008). Examples exist of residual *O. mykiss* populations that produce anadromous offspring. Thrower and Joyce (2004) documented an Alaskan rainbow trout population that produced anadromous offspring after 70 years of isolation in freshwater. Pascual et al. (2001) documented anadromy in a stock of rainbow trout that was thought to originate from a resident freshwater population. Genetic analyses also suggest that gene flow between sympatric resident and anadromous forms of rainbow trout is more common than previously suspected (Olsen et al. 2006; McPhee et al. 2007; Pearsons et al. 2007).

Numerous factors can determine whether a salmonid can complete an anadromous life cycle. One important life history factor is the ability of juveniles to undergo smoltification, the physiological and morphological adaptation to seawater in preparation for ocean life. Smoltification and migration in individual fish can be influenced by growth, size, water temperature, and photoperiod (Zaugg and Wagner 1973; Pereira and Adelman 1985; Hirata et al. 1988). Additionally, genetics (Nichols et al. 2008) and landscape features (Narum et al. 2008) may influence life history expression and whether fish undergo smoltification. Numerous physical and biological indicators of the complex process of smoltification have been reported, including decreased condition factor (Zaugg and McLain 1972; Beeman et al. 1995), a silver body coloring or high skin reflectance (Haner et al. 1995), and increased Na^+,K^+-ATPase activity levels in the gill filaments (Zaugg and McLain 1972). The enzyme assay that detects Na^+,K^+-ATPase activity in gill filaments is one of the more quantitative measures of smoltification progress (Schrock et al. 1994).

In this study we evaluated whether the redband trout population inhabiting Mann Creek and the reservoir that once had an anadromous component (before 1958) continues to undergo smoltification. Presence or absence of smoltification was assessed by (1) comparing the proportion of migrants displaying a silver, smolt-like body coloration (putative smolts) with those migrants not displaying such coloration (putative nonsmolts), (2) comparing mean Na^+,K^+-ATPase activity in the gill filaments of putative smolts and putative nonsmolts, and (3) comparing the migration timing of the study population with the migration of neighboring anadromous steelhead populations in the Snake River basin.

METHODS

Sampling.—Juvenile redband trout migrants were captured with a rotary screw trap (Thedinga et al. 1994; Roper and Scarnecchia 2000) positioned 2 km above the reservoir from 18 March to 3 June 2009. Water temperature was recorded hourly at the screw trap location with a Hobo Pro version 2 water

temperature data logger. Stream discharge was measured periodically throughout the trapping season with a flowmeter to establish a relationship between discharge and staff-gauge readings from a gauge located near the trap.

Fork length (FL) for each fish captured was recorded to the nearest millimeter and weight (W) to the nearest 0.1 g. Condition factor (K) was calculated for each fish by means of the formula $K = W/\mathrm{FL}^3$ (Westers 2001). Scale samples were collected from each fish and independently aged by two readers. An age was assigned to each fish by using a double-blind protocol described by Scarnecchia et al. (2006). Fish age was determined from each scale sample independently by two readers and when discrepancies occurred, samples were re-aged independently by the same two readers. If there were any remaining discrepancies, the two readers consulted with each other and identified a single age for the sample.

Juveniles were assigned one of three body coloration patterns described by Negus (2003): banded, intermediate, or silver (Figure 2). Banded fish retained all parr marks, and the body was dark, colorful, or both. Intermediate fish had no parr marks near the head, but marks remained visible near the caudal fin. Silver fish no longer had any parr marks present and body coloration was silvery. We attempted to collect a minimum of 10 gill tissue samples from each body coloration designation (banded, intermediate, and silver) per month during the entire migration period (March through June). However, there were no silver migrants in March and very few in April. Therefore, we grouped intermediate and silver fish together as nonbanded fish for comparisons of ATPase activity.

Fish were euthanized with a lethal dose (150 mg/L) of tricaine methanesulfonate (MS-222) before collecting gill tissue samples. A sample was collected from the first gill arch of each fish by cutting off a 1-cm^2 piece of gill tissue and placing it in a 1.7-mL microcentrifuge tube containing 1.0 mL of SEI buffer (300 mM sucrose, 20 mM EDTA, 100 mM imidazole, pH 7.4). Each gill tissue sample was held on dry ice until it was transferred to an -80°C freezer after the sampling interval. Gill Na^+,K^+-ATPase activity (μmol Pi $\cdot$ h^{-1} $\cdot$ mg protein^{-1}) was measured by means of a whole homogenate enzyme assay method (Johnson et al. 1977).

Comparisons of migration timing between Mann Creek redband trout and Snake River steelhead populations were made by comparing 50% passage dates (i.e., the date when 50% of total captures passed a trap or geographic point). For reference, we used 50% passage dates for steelhead smolts captured at Lower Granite Dam (LGR), the first dam encountered by steelhead smolts out-migrating to the ocean from the Snake River basin. Passage dates for LGR were retrieved from the Columbia River Data Access in Real Time (DART) site (www.cbr.washington.edu/dart/pass_hrt.html),

FIGURE 2. Banded (top; 186 mm FL), intermediate-colored (middle; 162 mm FL), and silver-colored (bottom; 191 mm FL) juvenile redband trout migrants captured in Mann Creek, Idaho, during the 2009 emigration period. [Figure available online in color.]

hereafter referred to as DART. The theoretical 50% passage date for Mann Creek redband trout at LGR was calculated by adding the number of days estimated to travel from the Mann Creek trap to LGR to the 50% passage date at the trap in Mann Creek. Redband trout would have to travel approximately 424 km downstream to reach LGR. We used published travel rates for steelhead smolts (Giorgi et al. 1997; Moore et al. 2010) and mean travel times reported by DART from populations in the Snake River basin that travel approximately 400 km to estimate travel time from Mann Creek to LGR.

Analyses.—Analysis of variance (ANOVA) (significant at $P \leq 0.05$) was used to compare mean ATPase activities between banded and nonbanded fish for three migration periods: early (19 March–10 April), middle (28 April–5 May), and late (21 May–4 June). If a significant difference was found, the Tukey's Honestly Significant Difference (HSD) procedure identified which sample means were statistically different (Zar 1984). Correlation analysis was used to determine whether any relationship existed between Na^+,K^+-ATPase activity and FL, *K*, or age. We used ANOVA to determine whether mean FL was significantly different among color designations (banded, intermediate, and silver). If a significant difference was found, Tukey's HSD procedure identified which color designations differed in mean FL (Zar 1984). All statistical analyses were conducted with SAS version 9.2.

RESULTS

We trapped and examined 1,502 juvenile redband trout for coloration differences. Of that number, 397 fish (26.4%) were observed to have intermediate or silver body coloration (nonbanded), which suggested that these individuals may have been undergoing smoltification. There were two noticeable peaks in the proportion of intermediate and silver-colored fish captured at the trap (Figure 3). The abundance of intermediate fish first peaked during the week of 15 April and peaked a second time 3 weeks later during the week of 6 May. This bimodal pattern was also seen in silver fish with the first peak occurring the week of 6 May and the second peak 2 weeks later on 20 May.

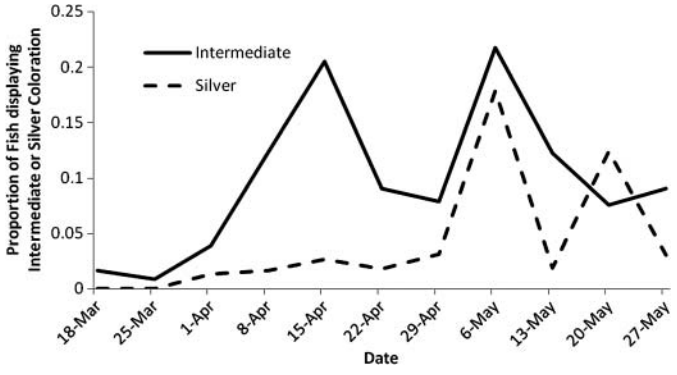

FIGURE 3. Weekly proportion of redband trout displaying intermediate or silver body coloration captured from a rotary screw trap in Mann Creek, Idaho, in 2009.

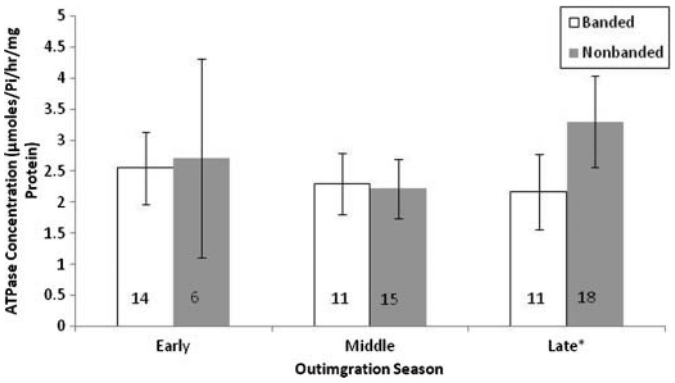

FIGURE 4. Mean gill Na^+,K^+-ATPase concentration (error bars represent 95% confidence intervals) for banded and nonbanded fish grouped into three periods of the migration season: early (19 March–10 April), middle (28 April–5 May), and late (21 May–4 June), in 2009. Numbers on bars indicate sample size. An asterisk (*) indicates a statistically significant difference between banded and nonbanded fish.

Gill tissue was collected from 78 fish over the course of the migration season. The Na^+,K^+-ATPase activity varied considerably among fish (0.95–5.81 µmol Pi · h^{-1} · mg $protein^{-1}$). Banded fish had a mean gill ATPase activity of 2.38 µmol Pi · h^{-1} · mg $protein^{-1}$, while nonbanded fish (including those with intermediate and silver body coloration) had a mean gill ATPase activity of 2.89 µmol Pi · h^{-1} · mg $protein^{-1}$. Mean gill Na^+,K^+-ATPase activity was significantly different ($F = 3.17$, $P = 0.012$) between banded and nonbanded fish for the late migration period (Figure 4) but was not significant for the early or middle periods. The mean gill ATPase activities for nonbanded fish observed in this study ranged from 1.71 µmol Pi · h^{-1} · mg $protein^{-1}$ in late April to 3.40 µmol Pi · h^{-1} · mg $protein^{-1}$ in the third week of May, a 98% increase over that time period.

There were no significant correlations between gill Na^+,K^+-ATPase activity and age, FL, or *K*. Individual ATPase activities and FLs grouped by body coloration displayed no clear patterns (Figure 5). However, mean FL was significantly different for

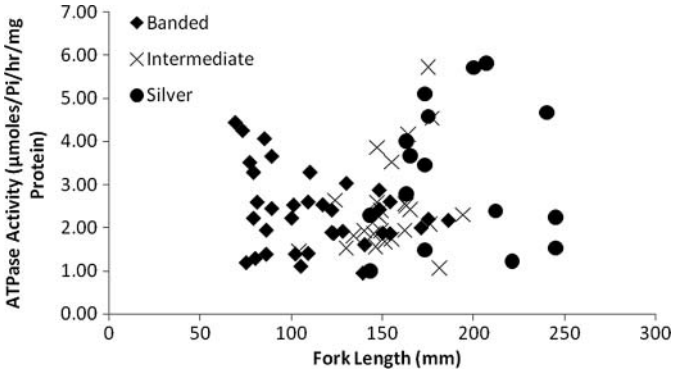

FIGURE 5. Fork length and gill Na^+,K^+-ATPase activity for individual fish grouped by body color.

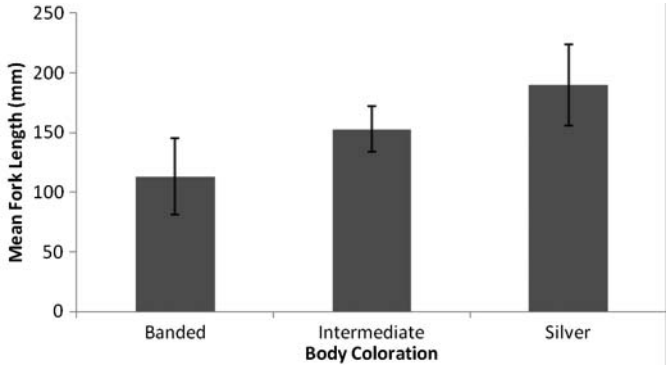

FIGURE 6. Mean FL by body color designation for redband trout migrants captured in Mann Creek, Idaho. All color types were significantly different from one another ($P < 0.001$). Error bars represent 95% confidence intervals.

each body coloration pattern ($P < 0.001$; Figure 6). Banded fish (mean FL = 114 mm) were smaller than fish of intermediate coloration (mean FL = 153 mm) or fish of silver coloration (mean FL = 190 mm). Migrants captured and analyzed for gill ATPase activity ranged from 1 to 4 years old. Nonbanded fish (intermediate and silver combined) made up a greater proportion of the older ages, and all age-1 fish were banded (Figure 7).

Peak migration occurred on 9 April with a total catch of 111 fish for that date. In 2009, the 50% passage date of steelhead smolts at Lower Granite Dam was 3 May (data from DART). Fifty percent of the total redband trout migrants had passed our Mann Creek screw trap by 13 April (Figure 8). Travel rates reported from several sites in the Columbia River basin ranged from 8 to 30 km/d, and the mean of those rates was 23.2 km/d (Table 1). The estimated travel time from Mann Creek to LGR was 18 d (range, 14–53 d), which was determined using the mean travel rate of 23.2 km/d and the range of 8–30 km/d. By using those travel rate estimates, the 50% passage date at LGR for redband trout migrating from Mann Creek was determined to have been 1 May (range, 23 April–6 June).

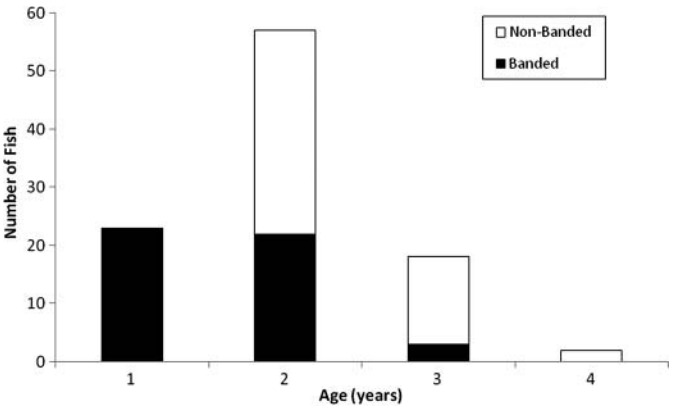

FIGURE 7. Age distribution and body color proportion by age-class for redband trout sampled ($n = 100$) for gill Na^+,K^+-ATPase activity in Mann Creek, Idaho.

TABLE 1. Reported travel rates for steelhead smolts in the U.S. Pacific Northwest. DART data (www.cbr.washington.edu/dart) were derived as arithmetic mean travel times from the trap site to Lower Granite Dam divided by the travel distance.

Location	Travel rate (km/d)	Source
Mid-Columbia River	30.4	Giorgi et al. (1997)
Puget Sound, Washington	26–28	Moore et al. (2010)
Hood Canal, Washington	8–10	Moore et al. (2010)
South Fork Salmon River, Idaho	26.3	DART (2009)

DISCUSSION

Results from this study suggest that an adfluvial redband trout population isolated in this reservoir system for over 40 years has retained physiological, morphological, and behavioral characteristics associated with smoltification. The evidence consists of (1) elevated gill Na^+,K^+-ATPase activities observed in nonbanded migrants, (2) a prevalence of migrating fish with high skin reflectance (i.e., intermediate or silver body coloration), and (3) migration timing that appears to be synchronous with neighboring steelhead populations. Moreover, nonbanded fish demonstrated an increase in gill ATPase activity as the sample period progressed. This increase in ATPase activity during active migration is consistent with results of other studies of migratory juvenile salmonids (Zaugg and McLain 1972; Ewing et al. 1979; Negus 2003).

The relative seasonal increase in gill Na^+,K^+-ATPase activity for nonbanded fish observed in this study (1.71–3.40 μmol Pi · h^{-1} · mg $protein^{-1}$) is commonly observed in anadromous smolts. Kerstetter and Keeler (1976) reported a mean ATPase activity of 0.25 μmol Pi · h^{-1} · mg $protein^{-1}$ for wild steelhead captured in the Trinity River in the Klamath River drainage in early March, and a peak of 3.1 μmol Pi · h^{-1} · mg $protein^{-1}$ occurring the week of 11 May. Zaugg et al. (1985) reported a mean gill ATPase activity of 35 μmol Pi · h^{-1} · mg $protein^{-1}$ for wild steelhead captured at Lower Granite Dam on 27 April and a peak of 55 μmol Pi · h^{-1} · mg $protein^{-1}$ during the week of 10 May, a 57% increase. Atlantic salmon smolts *Salmo salar* in the Rock River, Vermont, had a mean gill ATPase activity of approximately 4 μmol Pi · h^{-1} · mg $protein^{-1}$ on 21 April; mean activity increased by 87% to a peak of approximately 7.5 μmol Pi · h^{-1} · mg $protein^{-1}$ on 21 May (Whalen et al. 1999). Most of these studies reported similar changes in magnitude from low to peak mean gill ATPase activities for smolts, which supports the idea that some fish in Mann Creek were undergoing a similar parr–smolt transformation.

The maximum mean level of gill Na^+,K^+-ATPase activity observed (3.40 μmol Pi · h^{-1} · mg $protein^{-1}$) in the putative smolts (i.e., intermediate and silver fish) was lower than what has been reported for some other steelhead populations. Mean

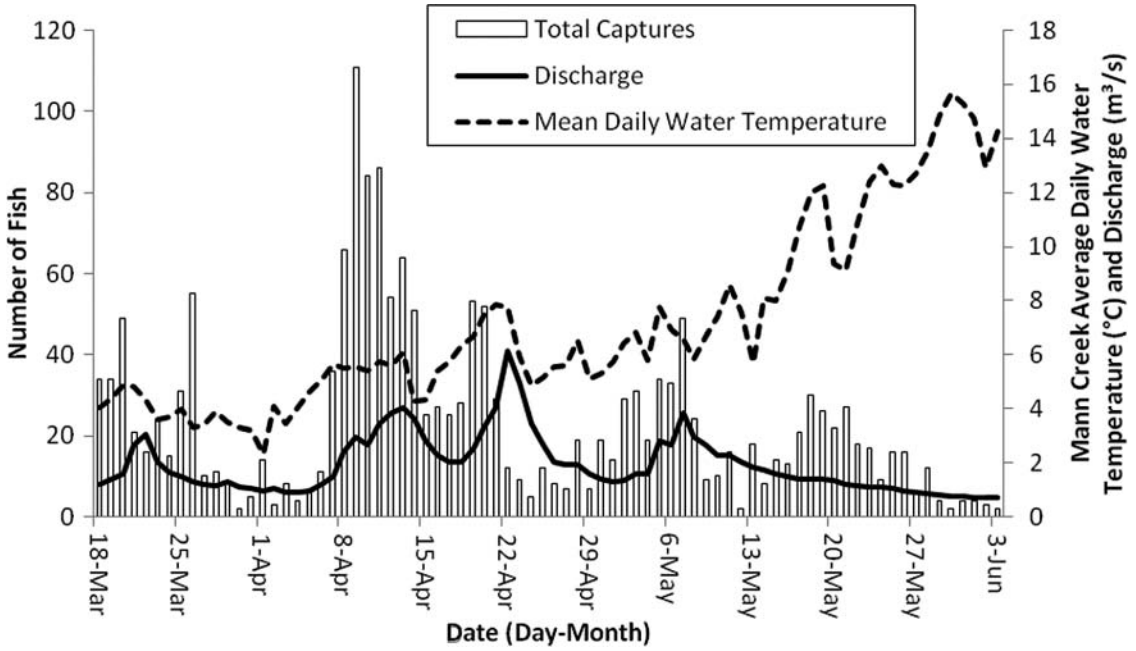

FIGURE 8. Mean daily discharge and water temperature, and numbers of juvenile redband trout captured daily from a screw trap in Mann Creek, Idaho.

ATPase activities of 35–55 μmol Pi · h^{-1} · mg $protein^{-1}$ (Zaugg et al. 1985) and 10–40 μmol Pi · h^{-1} · mg $protein^{-1}$ (Beeman et al. 1995) were reported for wild steelhead smolts in the Snake and Columbia river drainage. However, other studies have reported gill ATPase activities similar to those observed in our study (Kerstetter and Keeler 1976; Whalen et al. 1999; Ewing et al. 2001). The most plausible explanation for differences among observed ATPase activities is the methodology used in the assay. Some studies used detergents that purify enzymes (e.g., Zaugg et al. 1985; Beeman et al. 1995), whereas others used fish homogenates that do not purify enzymes (e.g., Ewing et al. 2001). Jorgensen (1975) concluded that using homogenates was the most appropriate method for evaluating enzyme concentrations over a time series, such as Na^+,K^+-ATPase concentrations over the course of a migration season.

Although no apparent relationship between gill Na^+,K^+-ATPase activity and FL, age, or *K* was found in this study, banded, intermediate, and silver fish differed significantly in mean FL. Banded fish were the smallest and silver fish were the largest. The FL differences observed in this study were consistent with other studies that noted larger salmonids tend to undergo smoltification while smaller fish within the population do not (Thorpe et al. 1982; Hirata et al. 1988; Negus 2003). Although some studies have documented a relationship between *K* and smoltification of juvenile salmonids (e.g., Beeman et al. 1995), other studies found no such association (Beckman et al. 1999; Negus 2003).

Some small (<110 mm FL) banded fish that did not have increased gill ATPase activity nevertheless appeared to be actively migrating from Mann Creek to the reservoir. Ewing et al. (1980) observed seaward-migrating juvenile Chinook salmon *O. tshawytscha* that did not show elevated gill ATPase activity. It may also be possible that a component of migrants were not responding to a genetic or physiological trigger to undertake an anadromous form but were simply responding to short-term changes in environmental factors such as stream discharge, in-stream competition, or food availability. Olsen et al. (2006) concluded that brown trout *S. trutta* had great plasticity in their decision to migrate; fish that had good growth opportunity remained and fish that had poor growth opportunity migrated. In a laboratory study of brown trout, Wysujack et al. (2009) also concluded that food availability influenced migratory decisions and low food availability led to higher numbers of migratory fish. Both studies provide a rationale for why we did not see an association between gill ATPase activity and size, *K*, or age of migrants. The migratory decision may not be strictly driven by a predetermined size, condition, or age, but rather by individual growth opportunities coupled with genetic factors.

Genetic studies have identified genome regions associated with smoltification traits (e.g., Nichols et al. 2008); however, the studies did not provide clear evidence that smoltification or anadromy is genetically controlled. Thrower and Joyce (2004) found that an isolated rainbow trout population in Alaska continued to produce smolts even though a barrier that had blocked their return migration for 70 years imposed strong selection against emigration from the lake. Thrower and Joyce (2004) nevertheless found that anadromous parents produced more anadromous offspring than did resident parents in laboratory

studies. Furthermore, Thrower and Hard (2009) found that migrant progeny of resident *O. mykiss* had much lower marine survival rates than migrant progeny of anadromous parents, and Pearse et al. (2009) found that relatively few resident *O. mykiss* successfully completed an anadromous life cycle. Although smoltification is a necessary process for salmonids to complete an anadromous life cycle, it is only one of many factors that determine whether a fish can successfully migrate to and from a marine environment.

In our study area, coastal-origin hatchery rainbow trout *O. mykiss irideus* have been stocked extensively since 1967 (Kozfkay et al. 2009). These stockings may have led to introgression of native and hatchery fish. Genetic analyses indicated that fish sampled from Mann Creek Reservoir were introgressed (Matt Campbell, Idaho Department of Fish and Game, unpublished data), while fish sampled in the headwaters of Mann Creek did not show signs of introgression (Kozfkay et al. 2011). There is evidently a barrier that prevented hatchery fish from introgressing with the headwater populations. However, it is unknown whether the putative smolts in our study are derived from the introgressed population, the pure population, or both populations. Future studies should examine genetic differences between the banded and nonbanded fish in this study as they could provide important information regarding smoltification traits and capabilities in *O. mykiss*.

Our results suggest the possibility that in portions of the Snake River drainage where steelhead have been extirpated as a result of artificial barriers, remnant populations may retain the potential for anadromy if migratory paths were reconnected. To fully interpret the evidence presented here that an isolated redband trout population continues to undergo morphological, physiological, and behavioral changes associated with smoltification, future research should examine other *O. mykiss* populations, especially those in more interior regions, that have been blocked from migration for much longer periods of time. Examining populations with a longer history of isolation from marine environments could be useful for understanding the persistence of smoltification capabilities as well as other co-occurring aspects of redband trout life history.

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