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ARTICLE

Comparison of Two Life History Strategies after Impoundment of a Historically Anadromous Stock of Columbia River Redband Trout

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Abstract

In this study we collected information on abundance, age structure, migration, and exploitation to characterize the population demographics and reproductive characteristics of a historically anadromous Columbia River Redband Trout *Oncorhynchus mykiss gairdneri* population now isolated in a southwestern Idaho reservoir and limited to resident and adfluvial life histories. We estimated there were 3,905 adfluvial individuals in Mann Creek Reservoir in October 2008 based on a mark–recapture population estimate. The adfluvial population sex ratio of 2.78 females per male captured at a weir, peak spawn timing near the peak of the hydrograph (late April), age at spawning (4–6 years), and growth patterns (slow growth in the stream followed by rapid growth in the reservoir) were all characteristic of an anadromous population. Resident fish abundance was not estimated, but the fish were characterized by relatively slow growth, earlier sexual maturity, and a reverse sex ratio (0.23 females per male) compared with the adfluvial fish. The two life histories (resident and adfluvial) and their differential use by the sexes are consistent with life history theory, which suggests female salmonids maximize fitness by increasing body size and fecundity while males attempt to maximize survival at the expense of growth. The migratory fish in this drainage that could have historically exercised an anadromous life history appear to be exercising the next-best option, an adfluvial life history, which has relatively similar costs and benefits to the anadromous form as distinct from the stream-resident form. Future studies should evaluate other similar native populations isolated in reservoir systems because these populations could play a role in recovery of endangered steelhead (anadromous Rainbow Trout) populations in the western USA.

The ecological and evolutionary relationships between sympatric resident Rainbow Trout *Oncorhynchus mykiss* and steelhead (anadromous Rainbow Trout) have been studied in several localities (Zimmerman and Reeves 2000; Narum et al. 2004; Heath et al. 2008). The focus of most of the research has been related to gene flow between the two forms, resident and anadromous, and whether or not resident fish can produce anadromous offspring and vice versa (Zimmerman and Reeves 2000). Reproductive isolation has been documented for some sympatric populations (Zimmerman and Reeves 2000) but not for others (Narum et al. 2004; Heath et al. 2008).

Heath et al. (2008) concluded that no broad generalizations can be made concerning reproductive isolation of sympatric resident and anadromous forms. Thrower and Joyce (2004) documented resident Rainbow Trout producing anadromous offspring and Pascual et al. (2001) reported an introduced resident Rainbow Trout population in Argentina potentially giving rise to an anadromous form. However, others have been less optimistic that resident trout could contribute to steelhead recovery in specific sympatric populations (Zimmerman and Reeves 2000; Independent Scientific Advisory Board 2005).

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In contrast to the numerous studies of sympatric resident and anadromous Rainbow Trout, there has been relatively little research regarding interior populations of Columbia River Redband Trout *O. mykiss gairdneri* derived from an anadromous component, such as those that occur above barrier dams (Holecek et al. 2012). In the Snake River basin above Hells Canyon Dam exist many isolated Columbia River Redband Trout populations that were formerly anadromous, but because of barriers are now restricted to freshwater and are no longer able to complete an anadromous life history. These formerly anadromous fish may remain sympatric with resident forms and express an adfluvial life history (i.e., spawning in streams and rearing in reservoirs or lakes). Understanding the life history characteristics of one such adfluvial population of Columbia River Redband Trout in Idaho existing above barrier dams may provide valuable ecological and management information about how impoundments influence key life history characteristics. Rainbow Trout exhibit substantial plasticity in expressing an array of life history strategies, which precludes generalizations about important life history characteristics such as growth, abundance, or reproduction. Each population must be managed with regard to its distinct life history (or histories) and whether or not these life histories are altered by impoundment.

The objective of this study was to characterize population size, growth, exploitation, and reproductive characteristics of the Columbia River Redband Trout inhabiting Mann Creek Reservoir and Mann Creek upstream of the reservoir to understand key life history attributes now that the population can no longer

express an anadromous life history. The stock shows evidence of the retention of potential anadromy (Holecek et al. 2012), so understanding the past role and future potential of anadromy is necessary in interpreting the observed life history of this stock. We evaluated several specific life history aspects of the adfluvial form, including abundance, exploitation rates, growth, reproductive characteristics, and recruitment. For the resident form we evaluated age, growth, and reproductive characteristics to compare the two current life history strategies.

METHODS

Study area.—The study area includes Mann Creek Reservoir and Mann Creek upstream of the reservoir in southwestern Idaho in the Snake River drainage above the Hells Canyon Complex Dams (Figure 1). Mann Creek Reservoir was completed in 1967 following the construction of Mann Creek Dam, a U. S. Bureau of Reclamation project. The reservoir has an active capacity of 13,563,000 m³, a drainage area of approximately 138.6 km², a full pool surface area of 114.5 ha, a mean depth of 10.0 m, and a normal pool elevation of 880.1 m (Young et al. 1977; Dillon 1991; Kozfkay et al. 2009). Mann Creek, the only direct tributary to the reservoir, flows approximately 25 km south into the reservoir from the headwaters, which originate at an elevation of approximately 2,100 m. The land surrounding Mann Creek Reservoir is high-desert sagebrush-steppe habitat.

Mann Creek Reservoir was built as an irrigation reservoir and as a result there are large annual fluctuations in water

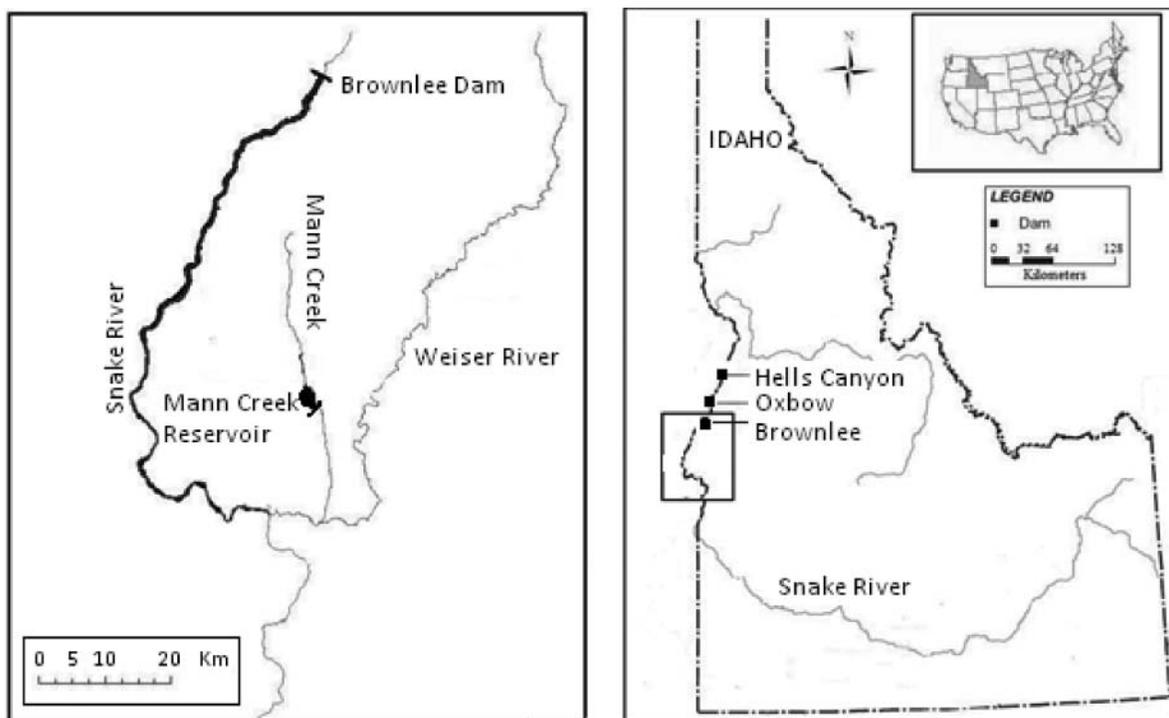


FIGURE 1. Study area map of Snake River Hells Canyon Dams and the Mann Creek, Weiser River drainage, southwestern Idaho.

volume and limnological conditions. During our 2008–2009 study the reservoir was reduced an average of approximately 85% in volume from 13,563,000 m³ to 2,220,303 m³. Water level drawdowns for the past 16 years have ranged from 12.8 to 19.5 m in elevation, the lowest water levels occurring in late summer and early fall (Kozfkay et al. 2009). However, the reservoir does have a minimum conservation pool (861 m) that prevents complete drawdowns from occurring (Kozfkay et al. 2009).

The Columbia River Redband Trout we investigated inhabit both Mann Creek Reservoir and Mann Creek upstream of the reservoir. Steelhead had access to Mann Creek prior to construction of the Hells Canyon Complex in the Snake River; they were reported in many tributaries to Mann Creek during surveys in the early 1940s (McIntosh et al. 1995). After construction of Hells Canyon dams the anadromous form of Columbia River Redband Trout was extirpated from the Snake River drainage above those dams, and the resulting population from Mann Creek was probably a fluvial form that had access to the Snake and Weiser rivers. However, shortly after the completion of the Hells Canyon Complex, Mann Creek Dam further restricted movement of Columbia River Redband Trout, isolating them to the small reservoir and the inflowing river and resulting in the current resident and adfluvial population we investigated. Adfluvial fish use both Mann Creek and Mann Creek Reservoir to complete their life cycle. Adults spawn in Mann Creek and juveniles rear there before migrating to the reservoir where they grow and sexually mature prior to returning to Mann Creek to spawn. Resident fish remain in Mann Creek, where they become sexually mature and complete their life cycle.

Numerous other sport fish species inhabit the reservoir, including stocked Rainbow Trout, Largemouth Bass *Micropterus salmoides*, Smallmouth Bass *Micropterus dolomieu*, and Black Crappie *Pomoxis nigromaculatus* (Kozfkay et al. 2009). Since 1967, the Idaho Department of Fish and Game has stocked the reservoir with Rainbow Trout from several sources. There have also been sporadic stockings of Mann Creek with catchable Rainbow Trout. Current stocking rates for Mann Creek Reservoir call for 8,000 catchable size triploid Rainbow Trout to be stocked annually (3,000 in April, 2,000 in May, and 3,000 in September; Kozfkay et al. 2009). Mann Creek and Mann Creek Reservoir are open to fishing year-round. The fishery is managed under general harvest regulations; daily bag limit for trout is 6 fish of any size.

Juvenile recruitment.—Annual recruitment of juvenile Columbia River Redband Trout from Mann Creek to the reservoir was estimated using a rotary screw trap (Thedinga et al. 1994; Roper and Scarnecchia 2000) placed approximately 2 km above the confluence of the creek and the reservoir. Juvenile fish captured were anesthetized, enumerated, and measured for total length (TL; mm). Out-migrants were marked with a unique fin clip and released 100 m upstream of the screw trap to estimate daily trap efficiency (Roper and Scarnecchia 2000). In 2008 the screw trap was operated from 12 April to 13 June, except for 14 nonconsecutive days when high water prevented operation. In

2009, stream flows were lower, and the screw trap was operated continuously every day from 18 March to 3 June.

The trapping season was stratified into periods of varying length but similar trap efficiency. Trap efficiency was calculated as

$$u_j = \frac{\sum_{i=1}^n R_{ji}}{M_j},$$

where u_j is the trap efficiency for the day n when most fish are recaptured, R_{ji} is the number of recaptured juveniles from the j th release and the i th day, and M_j is the number of marked juveniles released (Roper and Scarnecchia 2000). Total juvenile recruitment from Mann Creek was calculated with program GAUSS using a Bailey (1951) modified maximum likelihood method developed by Steinhorst et al. (2004).

Resident fish sampling.—Resident fish were sampled in Mann Creek above the reservoir by backpack electrofishing 15 reaches (each 100 m) from April to August 2008 and via operation of the rotary screw trap (described above) in 2008 and 2009. Slight pressure was applied to the abdomen of captured fish to check for presence of eggs or milt. Resident fish were distinguished from adfluvial fish based on size and maturity. Fish less than 250 mm TL and sexually mature (presence of milt or fully developed eggs) were classified as residents while fish greater than 250 mm and sexually mature were classified as adfluvial. Immature fish were not assigned as either adfluvial or resident fish because it was possible they could express either life history type.

Population estimate of adfluvial fish.—We estimated the population size of wild adfluvial Columbia River Redband Trout in the reservoir in October 2008 using mark–recapture methods (Seber 1982). Fish for marking were captured using three gears: a purse seine (165 m long, 10-mm mesh), a boat-mounted electrofisher (Smith-Root 5,000 W, pulsed DC, 120 pulses/s), and four trap nets (1-m × 2-m frames, 10-m lead, 19-mm bar mesh). The purse seine sampled pelagic areas of the reservoir that provided sufficient depth (approximately 8 m or greater). Electrofishing of all shoreline habitats was initiated just after sunset for 3–5 h. Trap nets were deployed to randomly sample bays with gradual bottom slopes. All fish captured were measured (TL; mm), identified as either a hatchery fish (absence of an adipose fin and dorsal fin erosion; Bosakowski and Wagner 1994) or wild fish, marked with a caudal fin punch, and released.

One week after marking had been completed, recapture efforts were made using three gears: the purse seine, electrofishing, and gill nets. Eight experimental gill nets (four sinking and four floating) 46 m long and 2 m wide with 6 equal panels of different mesh sizes (1.9, 2.5, 3.2, 3.8, 5.2, and 6.4 cm) were deployed overnight. Gill nets were deployed in a stratified random sampling pattern with four nets set in the north half of the reservoir and four in the south half. Sampling with purse seines and electrofishing were as described for the marking effort. All

fish captured were examined for a caudal fin punch, identified as hatchery or wild origin, measured (TL; mm), and released.

Population size was calculated using Chapman's (1951) modification of the Peterson estimate

$$\hat{N} = \frac{(M + 1)(C + 1)}{(R + 1)} - 1,$$

where \hat{N} = the population estimate, M = the number of marked fish, C = total number of fish in the recapture event, and R = the number of marked fish caught during the recapture event. The assumptions of this estimate were that (1) the population was closed, (2) all fish had equal capture probability, (3) capture and marking did not affect catchability, (4) fish did not lose their marks between sampling, and (5) all marks were reported. The 95% confidence intervals (CIs) for the population estimate were calculated using a Poisson distribution of R (Seber 1982).

Exploitation rates of adfluvial fish.—Annual exploitation rate was estimated using a tag-derived estimate that was initiated in October 2008 by anchor-tagging 245 adfluvial trout during the mark–recapture estimate. For a second tag based estimate, 675 anchor-tagged wild trout were released downstream of a weir between 2 March and 14 June 2009. For both tag return estimates, the number of tags reported by anglers to an Idaho Fish and Game hotline as being caught in the subsequent year after marking was used to calculate exploitation (μ'):

$$\mu' = \mu/\lambda(1 - \text{Tag}_1)(1 - \text{Tag}_m),$$

where μ is the unadjusted exploitation (number of tags recovered/number of tags released), λ is the tag reporting rate, Tag_1 is the estimated tag loss and Tag_m is the estimated tagging mortality (Meyer et al. 2008). We estimated tag loss (5.7%) from results of this study and used the mean angler reporting rate (53%) reported by Meyer et al. (2009) as part of a statewide angler exploitation investigation in Idaho. Meyer et al. (2009) reported short-term (7 d) tagging mortality of trout as 0% to 1.8%. Meyer et al. (2008) assumed long-term tagging mortality for trout was 15%; their estimate was based primarily on literature values reported for centrarchids (Hayes et al. 1997; Miranda et al. 2002). We have no tagging mortality estimates to compare so we used two values, 2% and 15%, for long-term tagging associated mortality and assumed that the true value is within those bounds.

Run timing, sex ratios, and abundance of adfluvial fish.—To assess the run timing, sex ratios, and spawner abundance for the migratory portion of the spawning population ascending from the reservoir, we operated a picket weir located 1 km upstream from the confluence of Mann Creek and the reservoir from February through June, to bracket the suspected spawning season (February–June; Busby et al. 1996). Migratory adults were sampled over the period 25 February to 15 June 2009. There were 8 d during this interval, however, when

the trap was breached as a result of high water and fish were not sampled.

Upstream migrants were captured, enumerated, measured (TL; mm), weighed (g), marked with a T-bar anchor tag, and released upstream of the weir. Anchor tags were placed approximately 10 mm below the anterior half of the dorsal fin at a 45° angle to the long axis of the fish and then gently tugged to ensure they were locked behind the pterygiophores of the dorsal fin (Mourning et al. 1994). We assigned sex to each fish captured at the weir based on secondary sexual characteristics (presence of kype or milt for males and presence of ovipositor or eggs for females). Mortalities observed at the weir and from 90 harvested fish observed during creel surveys confirmed that secondary sexual characteristics were an accurate predictor of sex for mature fish (100% accuracy). Sex was assigned to each fish prior to a necropsy where gonads were removed to confirm true sex of each fish. Observed sex ratios were compared to an expected 1:1 ratio using a chi-square goodness of fit test ($\alpha = 0.05$; Zar 1984). To estimate anchor tag loss a subsample of fish were marked with both an anchor tag and an opercle punch; a standard hole punch was used to remove a 1-cm diameter hole of tissue from the left operculum of the fish. Fifty upstream migrants were opercle-punched and anchor-tagged, and all downstream migrants were examined for both marks.

The run timing was characterized in three ways: the distribution of time of ascent, the distribution of time of descent, and the amount of time an individual fish remained in the creek above the trap (i.e., number of days between upstream capture and downstream recapture). A t -test was used to determine if the number of days spent in the creek above the trap differed between males and females. Spawner abundance into Mann Creek was estimated using the same Chapman-modified Peterson equation previously described. The mark group was fish migrating upstream, and the recaptures were the downstream migrants (postspawn) that were captured and examined for marks before being released below the weir. The 95% CIs were estimated using normal approximation methods because R was greater than 50 (Seber 1982).

Age and growth.—To obtain age-specific information on growth for resident and adfluvial fish we collected scales from above the lateral line and between the posterior edge of the dorsal fin and the anterior edge of the adipose fin (Scarnecchia 1979). Scale samples were sealed in an envelope until they were pressed between glass slides for imaging. Digital images (25 × and 40 × magnification) of each prepared structure were captured using a Leica DC 500 camera attached to a Leica DM4000B compound microscope. Ages were assigned to fish using a double-blind protocol described by Scarnecchia et al. (2006). Each sample was aged independently by two readers and any discrepancies were re-aged independently by the same two readers. If there were any remaining discrepancies the two readers consulted and identified a single age for the sample. Scale annuli were identified by tightly banded and discontinuous or broken circuli (Lux 1971).

Growth rates were characterized with the von Bertalanffy growth model expressed as

$$(TL)_t = L_\infty (1 - e^{-K(t-t_0)}),$$

where $(TL)_t$ is total length at time t , L_∞ is the maximum theoretical length, K is the growth coefficient, and t_0 is an initial condition time coefficient where length is theoretically 0 (von Bertalanffy 1957).

Fecundity and age at maturity.—Fecundity data were collected from trout of different ages to provide information regarding migratory decisions and any potential differences observed in sex ratios of migratory fish. Fecundity (F) was determined by removing and enumerating eggs from a subsample of females collected at the weir trap. The gonadosomatic index (GSI; DeVlaming et al. 1982), gonad weight/total weight $\times 100$, for 24 females was also reported and compared with fecundity, age, and total length. Age at maturity data were collected from fish sampled at the weir and a rotary screw trap.

Stream discharge and temperature.—A staff gauge and thermograph (Hobo v2) were placed at the weir site to monitor daily average stream discharge and temperature. Discharge was measured periodically throughout the season to establish a relationship to staff gauge readings through regression analysis (Holecek and Walters 2007). Discharge (Q) was measured over a wide range of staff gauge readings (h) and a power function based on a log-log regression equation was fitted to the data ($Q = 0.713 \cdot e^{2.5891 \text{ hours}}$; $r^2 = 0.98$). The regression equation was then used to estimate discharge for each day that a staff gauge reading was recorded.

RESULTS

Juvenile Recruitment

Annual recruitment of juvenile Columbia River Redband Trout to the reservoir was 4,854 in 2008 and 8,127 in 2009 (95% CI: 7,366–9,752). Mean TL for juveniles captured in 2009 (107 mm) was larger than 2008 (97 mm). Peak capture of fish occurred in late May in 2008 and mid-April in 2009. For both years, peak captures at the trap occurred on an ascending limb of the hydrograph.

Resident Fish Sampling

We collected 22 resident Columbia River Redband Trout in Mann Creek above the reservoir. Ten were captured during backpack electrofishing and 12 were captured in the rotary screw trap. We examined 405 fish during backpack electrofishing and 2,381 at the rotary screw trap. Sex ratio of mature resident trout was 0.23 females per male.

Population Estimate in the Reservoir

We captured and marked 253 wild Columbia River Redband Trout in the October 2008 marking event and captured 424 wild fish 5 d later, of which 27 were identified by the caudal

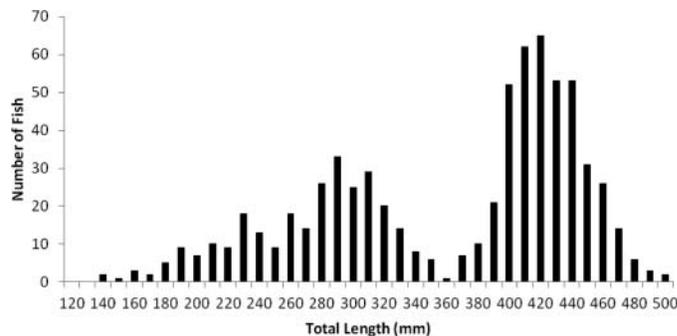


FIGURE 2. Length-frequency distribution of Columbia River Redband Trout captures from the mark-recapture estimate in Mann Creek Reservoir, Idaho.

punch as recaptures. The population estimate in the reservoir was 3,905 (95% CI: 3,750–5,871). Total lengths of fish in the sample ranged from 140 to 500 mm TL (Figure 2).

Exploitation

Tag-derived exploitation rates from the fish tagged and released in 2008 adjusted for tag loss, tagging mortality, and angler reporting rates were 20.0% using a long-term tagging mortality rate of 2% versus 23.1% using a 15% mortality rate. Estimated exploitation rates from fish tagged and released in 2009 were 30.5% using a long-term tagging mortality rate of 2% versus 35.2% using a 15% rate.

Run Timing, Sex Ratios, and Spawner Abundance

Adfluvial Columbia River Redband Trout were captured at the Mann Creek weir from 2 March to 14 June during the 2009 spawning season (Figure 3). We captured 445 upstream migrants, of which 420 were released upstream (25 were sacrificed for fecundity measurements). The first upstream fish was captured on 2 March and the last on 2 June. We captured 658 postspawn downstream migrants, the first on 21 March and the last on 14 June. Of the 658 downstream captures, 269 were recaptures tagged as upstream migrants. Of the 35 fish previously marked with an opercle punch that were recovered, 2 were missing anchor tags, for an estimated tag loss of 5.7%. Correcting for tag loss, we estimated that 284 tagged downstream migrants were captured at the weir.

The spawning abundance (i.e., upstream run size of migrants) from Mann Creek Reservoir into Mann Creek was estimated at 973 fish (95% CI: 925–1,022). Mean length of fish captured was 427 mm TL (range 265–561 mm; Figure 4). The mean weight of fish captured was 739 g (range 187–1,540 g). Of 823 adfluvial fish captured and identified at the weir, 218 (26%) were males and 605 (74%) were females or a sex ratio of 2.78 females per male ($P < 0.0001$). Migratory females spent significantly fewer days above the weir (mean: 34 d, 95% CI: 32–34) than males (mean: 47 d, 95% CI: 42–53 d; $P < 0.001$).

There were no significant correlations between stream discharge or temperature and daily catch of upstream or downstream migrants. However, some patterns were observed

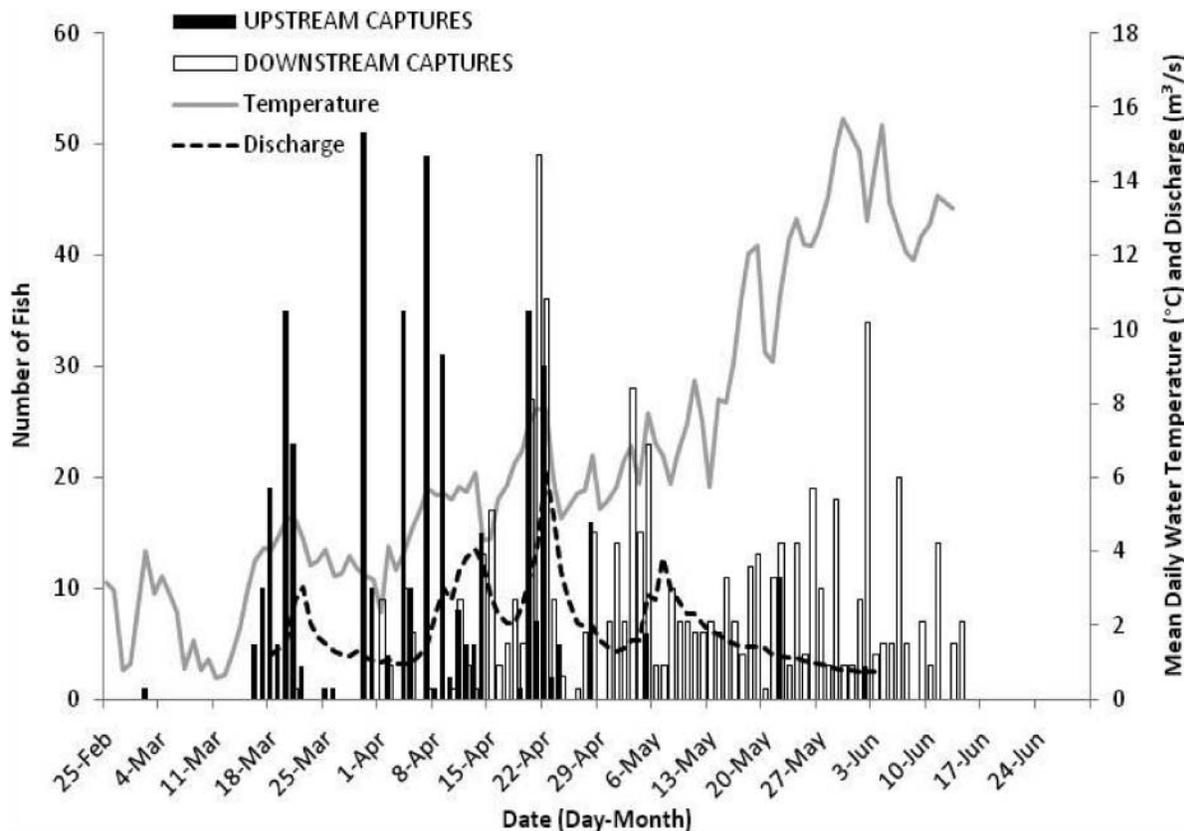


FIGURE 3. Number of Columbia River Redband Trout captured during 2009 spawning season at the weir site on Mann Creek, Idaho, and mean daily water temperature and discharge.

related to stream discharge and fish capture at the weir. Peak fish captures for upstream migrants occurred during an ascending limb of the hydrograph. Capture of upstream migrants usually dropped significantly, however, at periods of peak discharge (Figure 4). Capture of downstream migrants was highest during peak discharge, including the second highest single daily capture of downstream migrants (36), which occurred on the same

day as the highest daily discharge ($6.12 \text{ m}^3/\text{s}$). No clear patterns of capture could be identified in relation to stream temperature.

Age and Growth

Adfluvial fish ranged from ages 1 to 9, while resident fish were ages 1 to 4. Estimated growth of migratory adults captured in the reservoir was higher than estimated rates for resident fish captured in Mann Creek, based on scale length-at-age data fitted to von Bertalanffy growth curves (Figure 5).

Fecundity and Age at Maturity

Mean fecundity for 24 adfluvial females (TL range, 309–476 mm) was 2,345 eggs (range, 1,204–4,063 eggs). The GSI averaged 16.4 (range, 12.6–22.6), but there were no significant correlations between GSI and age, length, or fecundity. The earliest maturity observed for adfluvial fish was age 2 for males and age 3 for females. The largest proportion of the spawning run consisted of age-4 and age-5 fish, and younger fish (ages 2–3) were typically males (Figure 6). The sex ratio of mature adfluvial age-2 and 3-fish ($n = 25$) was significantly skewed towards males (3.2 males per female; $P = 0.0167$). Sexually mature stream-resident trout ranged from 113 to 219 mm TL. The earliest observed maturity for stream residents was age-1

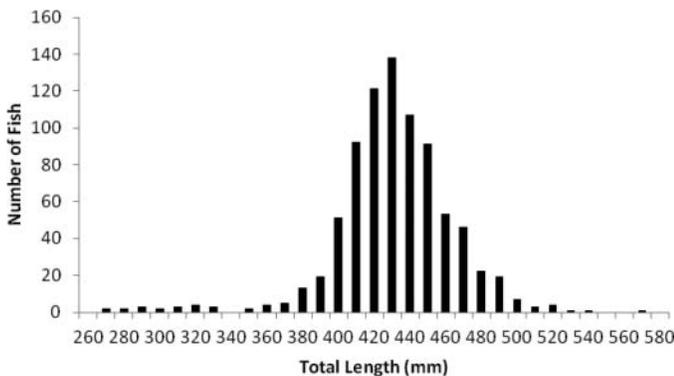


FIGURE 4. Length-frequency distribution of Columbia River Redband Trout captured at the weir on Mann Creek, Idaho.

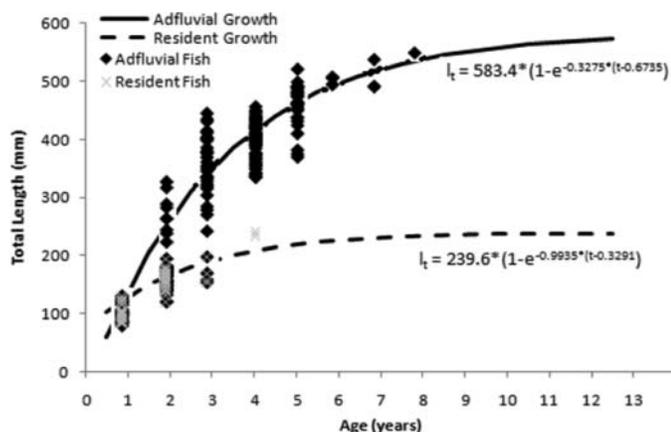


FIGURE 5. Growth comparison between resident and adfluvial Columbia River Redband Trout from Mann Creek drainage, Idaho. Data points represent individual fish used to develop growth curves.

for males and age-2 for females. There were three mature males (113–124 mm TL) assigned age 1.

DISCUSSION

Life Histories

Results of this study and a related study on the same stock (Holecek et al. 2012) present a clearer picture of the life history of the Mann Creek population of Columbia River Redband Trout than heretofore available. Holecek et al. (2012) found evidence that the ability of this stock to undergo smoltification has been retained, even though the fish has not been able to migrate to the sea since 1967. Knowledge of the past potential for anadromy is needed to fully understand the current life history patterns observed in this stock. The population now consists of resident and adfluvial fish. Resident fish grew slowly, reached a maximum estimated length of 239 mm TL (Figure 3), matured earlier

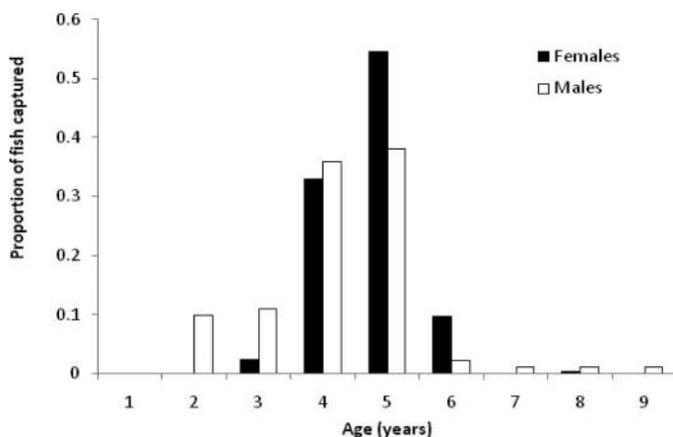


FIGURE 6. Age-class distribution of mature Columbia River Redband Trout captured at a weir in Mann Creek, Idaho, during the 2009 spawning season. Females ($n = 258$) and males ($n = 92$) were aged using scale samples.

than adfluvial fish, and had an estimated lower fecundity than adfluvial fish. Most fish that remained as residents were males (0.23 females per male). For adfluvial fish, naturally produced juveniles reared in the stream for 1–4 years, with most juveniles migrating to the reservoir at age 1 or 2. Based on 2 years of incomplete sampling, approximately 5,000–8,000 juveniles ages 1–4 emigrated from the stream to the reservoir annually. Juveniles grew more rapidly in the reservoir than in the stream, and they returned upstream to Mann Creek to spawn 1–3 years after entering the reservoir. Mature individuals began migrating upstream from the reservoir into Mann Creek in the spring as early as February, spawned in late April and early May near the peak of the hydrograph, and then returned to the reservoir after spawning. Adfluvial spawners captured at the weir were predominately females (2.78 females per male), consistent with the idea that juvenile adfluvial migrants were also predominantly females (i.e., more males remained as residents). Mature males spent more time in the spawning stream above the trap than did mature females; females evidently left shortly after spawning, while males were present 2 weeks longer overall. Spawning is probably not an annual event for all fish of reproductive age; approximately 1,000 fish spawned in Mann Creek in 2009, only 25% of the total population size estimated for the reservoir. Of the fish captured from the reservoir population, 45% exceeded 400 mm TL, the size at which length most or all fish would be sexually mature. Most fish (93%) captured at the weir exceeded 400 mm TL.

Life History Strategies

The two life histories (resident in Mann Creek, adfluvial in the reservoir) and the differential male–female manifestations in Columbia River Redband Trout can best be understood in the contexts of the evolution of migratory life histories (i.e., anadromous and its current abbreviated form, adfluvial) and in terms of the differential approaches for maximizing fitness in male and female salmonids (Jonsson 1985; Gross 1987). Gross (1987) argued that migratory anadromous and adfluvial life histories have evolved as fish undertake migrations to maximize growth and fecundity, typically at the expense of delayed maturation and higher mortality. Resident fish that volitionally residualize may have less growth opportunity but earlier maturation and higher survival (Quinn 2005). In accordance with life history theory (Gross 1987), several investigators concluded that the benefit to fitness from being large is often greater for females than for males (Jonsson 1985; Stearns 1992; Fleming 1998; Hendry et al. 2004; Quinn 2005). Even small male salmonids may have millions of sperm (Munkittrick and Moccia 1987), whereas the effective fecundity of females (egg number) increases greatly with fish size. Except for the benefits that large size in males may confer in competing for females, males may benefit from residualization in streams, especially when they can mature sooner (albeit at a smaller size) and when predation and other potential causes of mortality are greater for migrants (Gross 1987; Fleming 1998). Females, in contrast, may gain more of a fitness advantage from becoming migratory and reaching a larger size,

even at the expense of delayed maturation and higher mortality rates. The resident, adfluvial, and anadromous life histories can thus be viewed along a continuum (Rounsefell 1958), progressively greater potential growth and fecundity occurring for females adopting the most migratory form (anadromy). The anadromous form is especially likely to evolve where growth potential of the resident (or adfluvial) life histories is very low compared with the anadromous life history. Females are more likely than males to see the benefits of an anadromous life history. For males, in contrast, several different life histories may typically be alternatively adaptive, including resident, adfluvial, and anadromous forms.

This framework for the evolution of migratory behavior is supported by several specific results from Mann Creek, including fecundity, ages at migration and maturation, sex ratios of migrants and residents, presence of predators and other mortality factors, and time spent on the spawning grounds. The Mann Creek findings are in turn supported by results from other studies. For example, the length–fecundity relationship strongly supported the idea that fecundity gains accrued to those fish with an adfluvial life history. The mean fecundity for 24 adfluvial females in Mann Creek (2,345 eggs) averaged more than 10 times the fecundity of a 200-mm TL (191 eggs) resident female Columbia River Redband Trout inhabiting a desert stream in southwest Idaho (Schill 2009). Fecundity gains for females able to have an anadromous life history would have in turn been greater than for the adfluvial life history. Quinn (2005) reported that female steelhead average 721 mm and have a fecundity of 4,923; these values were derived from population-specific average values but the origin of the populations was unclear.

Similarly, for age at migration and maturation, younger mature fish (age 2–3) that migrated were predominately males, suggesting that age at maturity was younger for males than females. Younger maturation in males than females was also observed for the resident fish. Schill (2009) also observed that male Columbia River Redband Trout matured younger than females by 1 or 2 years, and Fleming (1998) concluded that young age at maturity was a common tactic for male salmonids. Male rainbow and Columbia River Redband Trout have been observed maturing as young as age 1 (Scott and Crossman 1973) but no evidence indicates that females mature that young.

The preponderance of females among the migratory fish (i.e., those rearing in the reservoir and ascending Mann Creek through the weir to spawn) and the preponderance of males among the resident fish of Mann Creek is also consistent with life history theory for salmonids and has been observed in numerous other studies (Jonsson 1985; Fleming 1998; Quinn and Myers 2004). Campbell et al. (2012) reported that 65.1% of Snake River steelhead sampled at Lower Granite Dam were females. Biette et al. (1981) reported a median sex ratio of 1.56:1 females to males for 21 stocks of adfluvial Rainbow Trout in the Great Lakes; all but four of the stocks had a sex ratio skewed towards females. In some cases sex ratios in a given year may be affected by differential year-class strengths that may lead to more (perhaps

younger) male migrants in a given year. Overall, however, the predominant pattern is for more female migrants.

The bimodal size distribution of fish captured in the reservoir in the fall was different than the size distribution of fish captured at the weir the following spring. These results were expected and are indicative of a broader range of age-classes present in the reservoir than for those that spawn the following spring. Very few fish less than 400 mm TL were observed at the weir, whereas a large number of fish between 200 and 300 mm TL were observed in the reservoir in the fall. Because juvenile out-migration to the reservoir peaks in the spring (April and May), we suspect many of the smaller fish (200–300 mm TL) observed in the reservoir during the fall (October) population estimate were juvenile migrants from April and May of the same year. The size distribution of fish captured at the weir also supported our designation of resident trout as those that were sexually mature and less than 250 mm TL. The smallest adfluvial upstream migrant caught at the weir trap was 265 mm TL.

We also observed a broader range of age-classes in adfluvial fish relative to resident fish, and it is unclear why this was observed. The most plausible explanation is the annuli on scales of smaller resident fish are difficult to identify. Several studies of resident Rainbow Trout in small streams have reported difficulty in accurately aging fish, particularly older age-classes, with the use of scales (Hining et al. 2000; Cooper 2003; Schill et al. 2010). If we underestimated ages of resident fish, this suggests growth could be slower than we estimated; however, the relative life history comparisons between adfluvial and resident fish would not change.

Although we did not study predation on Columbia River Redband Trout in the reservoir and stream, the presence of both Smallmouth and Largemouth Bass in the reservoir (Kozfkay et al. 2009) in sufficient abundance to support fishing indicates that potential predators exist. Both species have been shown to consume young Rainbow Trout (Shrader and Moody 1997; Zimmerman 1999). In contrast, the stream fish community consists of Bridgelip Suckers *Catostomus columbianus*, Shorthead Sculpin *Cottus confusus*, and Longnose Dace *Rhynchichthys cataractae*, all of which are native species. None of these fish are reported to be significant predators of Rainbow Trout. Bridgelip Suckers feed primarily on periphyton and aquatic insects (Dauble 1980), while Shorthead Sculpin (Johnson et al. 1983) and Longnose Dace (Thompson et al. 2001) feed primarily on benthic macroinvertebrates, although Shorthead Sculpin do occasionally consume salmonid eggs (Johnson et al. 1983). Similarly, humans were also a more significant predator of Rainbow Trout in the reservoir relative to the stream. Overall, the available evidence strongly suggests that predation on Columbia River Redband Trout is much higher in the reservoir than in the stream. Such predation and harvest would be part of the cost of the adfluvial life history resulting in substantial benefits to male residualization.

The longer period of time spent above the weir by mature males than females is also consistent with other studies on

iteroparous salmonids, where females leave shortly after spawning and males remain to seek additional spawning opportunities (Quinn and Myers 2004). Migratory males spending more time in the stream during spawning season may also contribute to skewed sex ratios observed from fish examined during creel surveys in Mann Creek Reservoir by Holecek (2010), who reported a sex ratio of 2.88 females per male for 66 harvested wild fish. Holecek (2010) reported that the months of May and June accounted for 52% of wild trout harvest and 30% of annual angler effort in the reservoir, suggesting females that return to the reservoir quickly are more likely to be harvested than males that remain in the stream where there is less fishing pressure (Holecek 2010). Schill et al. (2007) reported very low exploitation rates and angler effort for resident Columbia River Redband Trout in southwest Idaho streams. This observed pattern again illustrates the different life history strategies between males and females: females return to the reservoir where growth opportunity is higher but harvest is also higher, while males maximize spawning opportunity at the expense of growth opportunity.

We conclude that the migratory fish in the Mann Creek drainage that historically exercised an anadromous life history appear to be exercising the next best option, an adfluvial life history, which is probably similar in relative costs and benefits to the anadromous form. This pattern of life history modification to adfluvial may be occurring in other locations in the region where anadromy has been eliminated. The creation of reservoirs in the western USA has resulted in great habitat alteration and fragmentation for Rainbow Trout populations (Thurow et al. 2007). Results of our study area suggest that this wild Columbia River Redband Trout population has adapted relatively well to this altered habitat and now provides a recreational fishery. The ability of the species to adapt readily to altered habitats is well supported by their wide geographic distribution (MacCrimmon 1971) and diverse life histories (Behnke 1992). Future studies should evaluate other similar native populations isolated in reservoir systems because there is evidence that such populations could potentially serve a role in recovery of extinct or critically endangered steelhead populations (Thrower et al. 2008).

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