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ARTICLE

Life History Diversity in Klamath River Steelhead

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Abstract

Oncorhynchus mykiss exhibits a vast array of life histories, which increases its likelihood of persistence by spreading risk of extirpation among different pathways. The Klamath River basin (California–Oregon) provides a particularly interesting backdrop for the study of life history diversity in *O. mykiss*, in part because the river is slated for a historic and potentially influential dam removal and habitat recolonization project. We used scale and otolith strontium isotope (⁸⁷Sr/⁸⁶Sr) analyses to characterize life history diversity in wild *O. mykiss* from the lower Klamath River basin. We also determined maternal origin (anadromous or nonanadromous) and migratory history (anadromous or nonanadromous) of *O. mykiss* and compared length and fecundity at age between anadromous (steelhead) and nonanadromous (Rainbow Trout) phenotypes of *O. mykiss*. We identified a total of 38 life history categories at maturity, which differed in duration of freshwater and ocean rearing, age at maturation, and incidence of repeat spawning. Approximately 10% of adult fish sampled were nonanadromous. Rainbow Trout generally grew faster in freshwater than juvenile steelhead; however, ocean growth afforded adult steelhead greater length and fecundity than adult Rainbow Trout. Although 75% of individuals followed the migratory path of their mother, steelhead produced nonanadromous progeny and Rainbow Trout produced anadromous progeny. Overall, we observed a highly diverse array of life histories among Klamath River *O. mykiss*. While this diversity should increase population resilience, recent declines in the abundance of Klamath River steelhead suggest that life history diversity alone is not sufficient to stabilize a population. Our finding that steelhead and Rainbow Trout give rise to progeny of the alternate form (1) suggests that dam removal might lead to a facultatively anadromous *O. mykiss* population in the upper basin and (2) raises the question of whether both forms of *O. mykiss* in the Klamath River should be managed under the same strategy.

Oncorhynchus mykiss displays a vast array of life histories. The species exhibits anadromous (steelhead) and nonanadromous (Rainbow Trout) forms, both of which are capable of spawning

repeatedly in a lifetime (Shapovalov and Taft 1954; Behnke 1992; Busby et al. 1996; Willson 1997). Steelhead and Rainbow Trout can occur in sympatry, with (Seamons et al. 2004; Kuzishchin

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et al. 2007; McPhee et al. 2007; Pearsons et al. 2007) or without (Zimmerman and Reeves 2000; Narum et al. 2004) interbreeding, and can give rise to progeny of the alternate form (Viola and Schuck 1995; Riva-Rossi et al. 2007; Courter et al. 2013). Rainbow Trout reside in freshwater for the duration of their lives, display varying degrees of movement (e.g., residency, potadromy), and reach sexual maturity at an age of 1–10 (typically 2–3) years (Willson 1997; Moyle 2002). Steelhead spend 1–7 (typically 2–3) years in freshwater, from several months to 6 (typically 2) years at sea, and then return to freshwater to spawn (Busby et al. 1996; Willson 1997; Savvaitova et al. 2000; Hodge et al. 2014). In total, *O. mykiss* displays at least 36 different life histories (Moore et al. 2014).

Life history diversity increases the likelihood of population persistence by spreading the risk of extirpation among life histories (Stearns 1992; Watters et al. 2003; Fox 2005). Research suggests, for example, that the stability of Pacific salmon *Oncorhynchus* spp. and steelhead abundance is positively related to life history diversity (e.g., Greene et al. 2010; Shindler et al. 2010; Moore et al. 2014). Accordingly, the conservation and enhancement of diversity are important components of Pacific salmonid recovery (McElhany et al. 2000; Ruckelshaus et al. 2003; Beechie et al. 2006). Facilitating the recolonization of historical habitat above dams may be a particularly effective strategy for increasing life history diversity and thus population resilience (Beechie et al. 2006).

The Klamath River basin (California–Oregon) provides an interesting backdrop for the study of life history diversity in *O. mykiss* for several reasons. First, a dam removal and habitat recolonization project of unprecedented scale is slated to occur on the main stem. The Klamath River has been divided by one or more impassable dams since 1918, and today four dams near the California–Oregon border block anadromous fishes from accessing more than 650 km of historical habitat in the upper basin (Hamilton et al. 2005; Hamilton et al. 2011). Under the proposed action, all four dams would be removed (USDOI and CDFG 2012). Second, the basin below the dams (hereafter, the lower Klamath River basin) supports California's most productive steelhead fishery (Hopelain 1998). Last, little is known about the current life history diversity in the lower basin. The last basin-specific and comprehensive evaluation of *O. mykiss* life histories (Hopelain 1998), which was conducted more than 30 years ago, suggested that steelhead in the lower Klamath River basin exhibit substantial life history diversity. However, since that study was conducted, wild Klamath River stocks have declined (NRC 2008; Quiñones et al. 2014) and at least one significant change in life history has occurred (incidence of the half-pounder life history declined from 80% to 11% in the Trinity River subbasin; Hodge et al. 2014). Dam removal is predicted to favor increased life history diversity in Klamath River *O. mykiss* (USDOI and CDFG 2012).

Otolith strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) analysis provides a valuable tool for the retrospective determination of life history

in fishes. In particular, otolith $^{87}\text{Sr}/^{86}\text{Sr}$ ratios can be used to determine both maternal origin (anadromous or nonanadromous; Courter et al. 2013) and migratory history (Kennedy et al. 2002) in polymorphic species. The utility of such analyses is based on several assumptions: (1) that the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of surface water reflects the underlying geology of the watershed and remains constant through time (Kennedy et al. 2000; Bacon et al. 2004), (2) that $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in otoliths record the chronological environmental history of individual fish (Kennedy et al. 2000; Kennedy et al. 2002; Bacon et al. 2004), and (3) that the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of ocean water is globally uniform (= 0.70918; Hodell et al. 1991; Kennedy et al. 2002; Miller and Kent 2009) and differs significantly from that of freshwater. The analysis of maternal origin is founded on the additional assumptions that otolith core chemistry reflects the environment in which yolk precursors develop and that yolk formation is mostly complete when anadromous females are still at sea (Kalish 1990; Volk et al. 2000; Zimmerman and Reeves 2002). Assuming these conditions are met, otolith strontium isotope analysis should be a viable technique for determining both maternal origin (anadromous or nonanadromous) and migratory history (anadromous or nonanadromous) of Klamath River *O. mykiss*.

In this study we used scale analysis and otolith strontium isotope analysis to quantify life history diversity in wild *O. mykiss* from the lower Klamath River basin (California). Specifically, we examined variability in the duration of freshwater and ocean rearing, age at maturation, and incidence of repeat spawning. We also examined the relationship between maternal origin and migratory history of *O. mykiss* and compared length and fecundity at age between steelhead and Rainbow Trout.

METHODS

Study site.—The 423-km-long Klamath River drains into the Pacific Ocean in northwestern California (Figure 1). The basin historically produced as many as several million adult steelhead per year. However, abundance declined to an estimated 400,000 adults by 1960 and declined further through the 1990s (NRC 2008). Fish migration in the main stem is currently blocked by a series of four major dams: Iron Gate (river kilometer [rkm] 306 [measured from the river mouth]), Copco 2 (rkm 319), Copco 1 (rkm 320), and J. C. Boyle (rkm 362). Main-stem dams at rkm 375 (Keno) and rkm 409 (Link River) allow for fish passage. Major tributaries to the Klamath River below Iron Gate are the Trinity, Salmon, Scott, and Shasta rivers. Dams on the Trinity River (Lewiston, rkm 180 [measured from the confluence with the Klamath River]; Trinity, rkm 191) and Shasta River (Dwinell, rkm 65 [measured from the confluence with the Klamath River]) prevent fishes from accessing historical habitat. Anadromous fishes of the lower Klamath River basin include (in addition to steelhead) Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, Coastal Cutthroat Trout *O. clarkii clarkii*, Green Sturgeon

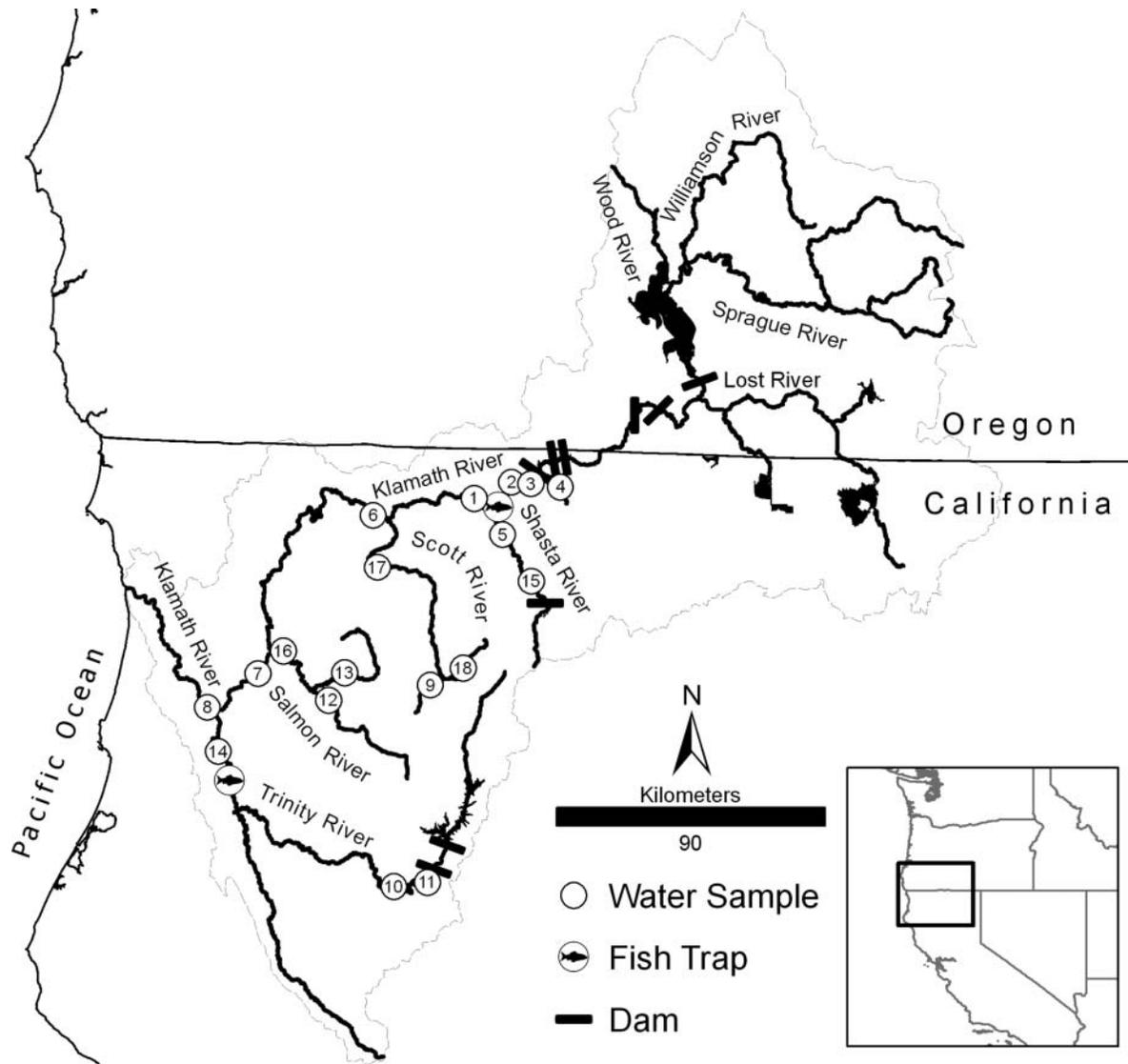


FIGURE 1. Map of the Klamath River basin, including the locations of dams, fish traps, and water sampling sites.

Acipenser medirostris, Pacific Lamprey *Entosphenus tridentatus*, and Eulachon *Thaleichthys pacificus*.

Fish capture and handling.—Fish capture and handling procedures were approved under Humboldt State University Institutional Animal Care and Use Committee Protocol 06/07-F 175A. Wild *O. mykiss* ($n = 655$) were captured from August 2007 through April 2009 at fish trapping facilities on the Trinity (rkm 35; August–November 2007–2008) and Shasta (rkm 1; October–December 2008) rivers and using hook and line on the main stem and major tributaries (Figure 1). Fish were assumed to be representative of fall- and winter-run steelhead and Rainbow Trout. The fork length (mm; but to the nearest centimeter at trapping facilities), sex, and time and location of capture were recorded for each fish.

Scale collection and analysis.—Scales were collected from *O. mykiss* and visually analyzed following the methods of

Davis and Light (1985). Life history landmarks (e.g., seawater entry, spawning events) were identified in scale patterns and used to reconstruct individual life histories. Distances between landmarks and the scale focus were measured using image analysis software (Image Pro Plus; Media Cybernetics, Bethesda, Maryland). Lengths at landmarks were back-calculated using the Fraser–Lee equation (Fraser 1916; Lee 1920; Carlander 1982) and an intercept (30.0 mm) derived from the body length–scale radius relationship for Klamath River steelhead ($n = 566$, FL range = 380–830 mm; Hopelain 1998). An individual was classified as nonanadromous if evidence of saltwater growth was absent from its scale pattern and as anadromous if evidence of saltwater growth was present in its scale pattern. Nonanadromous individuals were classified as Rainbow Trout if fork length at capture was >298 mm (the 95th percentile for length at ocean entry) or age at capture was

TABLE 1. Examples of the notation system used to describe *O. mykiss* life histories (adapted from Hopelain 1998). Freshwater years are located to the left of the forward slash (/), and saltwater years are located to the right. A lowercase h signifies a nonspawning half-pounder migration, and a lowercase s signifies a spawning migration.

Description	Freshwater age (years)	Saltwater age (years)			Total age (years)	Notation
		Half-pounder	Growth	Spawn		
Rainbow Trout	4				4	4/
Half-pounder	2	1			3	2/h
Half-pounder	2			1	3	2/1s
Adult steelhead	1	1		1	3	1/h.1s
Adult steelhead	3		1	2	6	3/1.2s

>3 years (the maximum observed age at ocean entry). Nonanadromous individuals that were <298 mm and ≤3 years at capture (1.4% of the sample set) were excluded from further analyses because we could not predict their future pathway. Sea age at capture was used to distinguish between adult steelhead (sea age at capture >1 year) and half-pounders, which are steelhead that return to freshwater in the year of initial ocean entry (sea age at capture ≤1 year) on an amphidromous, and less often, anadromous, migration (Hodge et al. 2014). A fish was omitted from further analyses if all of its scales were regenerated and lacked a complete pattern of circuli (concentric rings). Because a small proportion of Klamath River steelhead spawn in the year of initial ocean entry (Hodge et al. 2014), length-at-age data from half-pounders were entered into the probability-of-maturation model developed by Hodge et al. (2014) to retrospectively identify breeding events. We assumed that steelhead spawned in the year of initial ocean entry if the probability of maturation as a half-pounder, as predicted by length in freshwater (Hodge et al. 2014), was >0.5. Life histories were reported using the formatting style of Hopelain (1998) (Table 1).

Water sample collection and analysis.—We collected and analyzed water samples from throughout the lower Klamath River basin to map strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) signatures in the watershed and to validate that the isotopic signatures of lower basin streams differed from that of the ocean. In June of 2003, water samples ($n = 18$) were collected from the mainstem Klamath River and the four major tributary subbasins using 50-mL polypropylene tubes (Figure 1). Approximately 3 mL of 1% nitric acid was added to each water sample upon collection to stop biological activity. Samples were kept cool between the time of collection and analysis.

Water samples were prepared and analyzed in 2007 at the University of California at Davis Interdisciplinary Center for Plasma Mass Spectrometry following the methods of Courter et al. (2013). Water samples were prepared into representative Sr solutions, and Sr isotope ratios were measured using a multicollector inductively coupled plasma mass spectrometer (MC-ICP-MS; Nu Instruments Limited, Wrexham, United Kingdom). To determine whether the Sr isotope ratios of lower

Klamath River basin streams differed from that of the ocean, we used *t*-tests with a Bonferroni correction ($= \alpha/18$). All analyses were performed in R (R Core Team 2010) at $\alpha = 0.05$ unless specified otherwise.

Otolith collection and analysis.—Otoliths were collected from a random subsample ($n = 65$) of fish that were captured with hook and line and sacrificed for evaluations of sexual maturity and fecundity (Hodge et al. 2014). Sagittal otoliths were extracted with forceps, rinsed, and dried. Left sagittae were mounted to glass slides with Crystalbond thermoplastic resin. Right sagittae were used and assumed to provide a comparable result (Campana et al. 2000; Outridge et al. 2002) if the left was damaged or showed signs of vaterite, a crystalline form of calcium carbonate that confounds chemical analysis (Tzeng et al. 2007). Otoliths were sectioned around the core along the dorsoventral axis. Core sections were remounted to slides, ground with 1,200-grit sandpaper, and polished with a 0.05- μm alumina paste. Sections were flipped and the process was repeated. Otolith sections were then washed in 1% nitric acid, rinsed in an ultrasonic bath, and dried under a class-100 laminar flow hood.

Otolith Sr isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) were measured using laser ablation inductively coupled plasma mass spectrometry, as described by Courter et al. (2013). The single difference between our procedures and those of Courter et al. (2013) was that in our study, core-to-edge (or edge-to-edge) otolith transects were ablated at a rate of 10 $\mu\text{m}/\text{s}$ by a 40- μm -diameter laser beam pulsing at a rate of 20 Hz. An in-house marine carbonate standard was measured by laser ablation inductively coupled plasma mass spectrometry prior to each analytic session, and the mean $^{87}\text{Sr}/^{86}\text{Sr}$ ratio (0.70920 [SD = 0.00004]) was consistent with established values of marine carbonate (e.g., Outridge et al. 2002; Miller and Kent 2009; Courter et al. 2013). Before Sr isotope data were analyzed, visual (digital photographs) and chemical ($^{87}\text{Sr}/^{86}\text{Sr}$) cues were used to locate the core, freshwater growth, and saltwater growth regions of individual otoliths (Miller and Kent 2009).

Maternal origin was determined by comparing Sr isotope ratios from the core and first-summer-growth regions of otoliths. Because water sample analysis suggested that Sr isotope ratios in the lower Klamath River basin were significantly lower

TABLE 2. Incidence of nonanadromy (Rainbow Trout), the half-pounder life history, and repeat spawning among adult *O. mykiss* sampled in the lower Klamath River basin in 2007–2009.

River (sample size)	Nonanadromous incidence (%)	Half-pounder incidence (%) ^b	Anadromous			
			Spawning trip (%)			
			1st	2nd	3rd	4th
Klamath (81) ^a	22.2	96.8	82.5	12.7	4.8	0.0
Trinity (295)	1.4	11.0	84.2	13.1	2.4	0.3
Salmon (19)	42.1	58.3	63.6	9.1	18.2	9.1
Scott (16)	75.0	75.0	100.0	0.0	0.0	0.0
Shasta (9)	11.1	100.0	87.5	12.5	0.0	0.0
All (423)	10.2	29.2	83.6	12.7	3.2	0.5

^aFor the Klamath River, 97% of the samples were collected from upstream of the Trinity River confluence.

^bSource: Hodge et al. (2014).

approximately 7% of all the *O. mykiss* sampled and 10% of all the adults sampled (FL: mean = 284 mm, SE = 9, range = 268–508 mm). Nonanadromous life histories were displayed by fish from throughout the basin, though rates of nonanadromy varied widely among subbasins (Table 2). Overall, the age of Rainbow Trout at sampling ranged from 2 to 6 years (mean = 3.60 years; SE = 0.13). Approximately 57% of Rainbow Trout were female.

Steelhead composed 93% of all the *O. mykiss* sampled (FL: mean = 512 mm, SE = 5, range = 256–810 mm) and 90% of all the adults sampled. Anadromous life histories varied both in time spent in freshwater and in time spent at sea. Among steelhead, smolt age ranged from 1 to 3 years (mean = 1.92 years; SE = 0.02) and smolt length ranged from 112 to 394 mm (mean = 216 mm; SE = 2). Smolt age and smolt length varied among subbasins (Table 3). The time at sea for maiden spawners varied from 2 to 4 months (e.g., 3/1s) to 4 years (e.g., 1/h.2.1s). Across subbasins, from 0% to 36% of adult steelhead were repeat spawners (Table 2). Of the 488 steelhead for which sex could be determined, 223 (46%) were male and 265 (54%) were female; 35 of 62 repeat spawners were female.

Isotopic Signatures in Streams

Strontium isotope ratios (⁸⁷Sr/⁸⁶Sr) in waters of the lower Klamath River basin ranged from 0.703737 to 0.708283

(Table 4; Figure 1). The ⁸⁷Sr/⁸⁶Sr ratio of the main stem generally increased with distance downstream and the number of major confluences. Isotope ratios were significantly lower in freshwater than in the ocean (≤ 0.70828 versus 0.70918, respectively; $t \leq -523.14$, $P < 0.001$), suggesting that otolith ⁸⁷Sr/⁸⁶Sr ratios can be used to determine the maternal origin and migratory history of Klamath River *O. mykiss*.

Maternal Origin and Migratory History

Otolith microchemistry revealed variable relationships between the maternal origin and migratory history of *O. mykiss* (Figure 3). Five fish that were identified as Rainbow Trout and 58 that were identified as steelhead. Fifty-four of the steelhead were determined to be half-pounders, two of which migrated only to the estuary before returning to freshwater. Two fish were excluded from the analysis upon discovery that their otoliths contained vaterite. One of the five Rainbow Trout was identified as progeny of nonanadromous maternal origin, two were identified as progeny of anadromous maternal origin, and two were identified as progeny of unknown maternal origin. Of the 58 steelhead, 38 were identified as progeny of anadromous females, 11 were identified as progeny of nonanadromous females, and 9 were identified as progeny of unknown maternal origin (because the maternal signature could not be reliably determined).

TABLE 3. Comparison of fork length at ocean entry (mean \pm SE) and age composition (the percent of the subbasin sample is given in parentheses) of steelhead from the lower Klamath River basin ($n = 561$).

Smolt age	Fork length (mm)				
	Klamath River ^a	Trinity River	Salmon River	Scott River	Shasta River
1	186 \pm 5 (21)	194 \pm 5 (16)	199 \pm 8 (18)	214 (15)	190 (6)
2	234 \pm 4 (65)	205 \pm 2 (77)	224 \pm 5 (75)	272 \pm 25 (85)	261 \pm 14 (75)
3	254 \pm 12 (13)	215 \pm 9 (7)	259 \pm 4 (7)		329 \pm 16 (19)
All ages	226 \pm 4	203 \pm 2	222 \pm 5	263 \pm 23	269 \pm 14

^aFor the Klamath River, 97% of the samples were collected from upstream of the Trinity River confluence.

TABLE 4. Strontium isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) in the lower Klamath River basin (SDs = 0.000021). The numbers correspond with the water sampling locations designated in Figure 1.

Number	Location	$^{87}\text{Sr}/^{86}\text{Sr}$
1	Klamath River below Shasta River	0.703737
2	Klamath River below Iron Gate	0.703779
3	Iron Gate Hatchery	0.703813
4	Bogus Creek	0.703940
5	Lower Shasta River	0.704182
6	Klamath River below Scott River	0.704650
7	Klamath River below Salmon River	0.705214
8	Klamath River below Trinity River	0.705673
9	South Fork Scott River	0.705715
10	Upper Trinity River	0.706132
11	Trinity River Hatchery	0.706185
12	South Fork Salmon River	0.706448
13	North Fork Salmon River	0.706563
14	Lower Trinity River	0.706601
15	Middle Shasta River	0.706737
16	Salmon River	0.707166
17	Scott River	0.707519
18	East Fork Scott River	0.708283

Potential Influences and Consequences of Maternal Origin and Migratory History

On average, an individual was more likely to follow the migratory path (anadromous or nonanadromous) of its mother

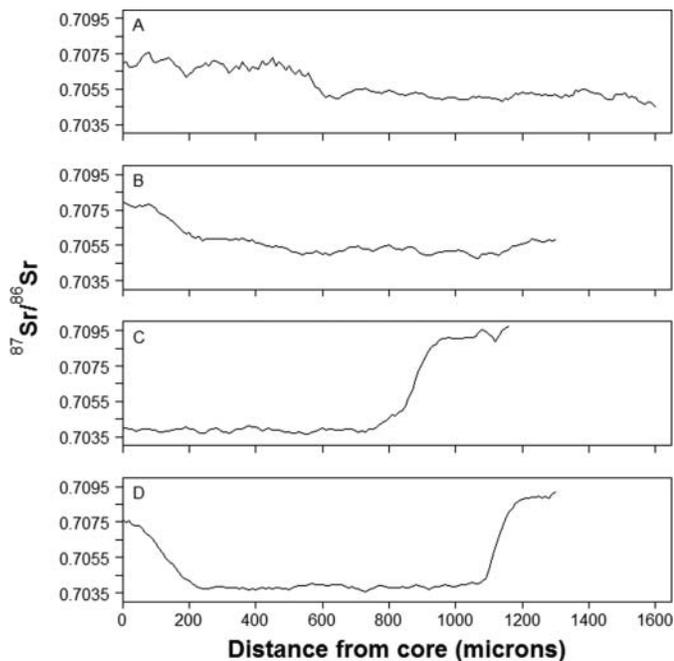


FIGURE 3. Representative otolith $^{87}\text{Sr}/^{86}\text{Sr}$ transects from Rainbow Trout of (A) nonanadromous and (B) anadromous mothers and steelhead of (C) nonanadromous and (D) anadromous mothers.

than to display the alternate life history ($\chi^2 = 68.77$, $df = 3$, $P < 0.001$; $n = 52$). Among juvenile steelhead, neither length at age 1 ($F_{1,45} = 0.06$, $P = 0.810$) nor length at ocean entry ($F_{1,43} = 0.30$, $P = 0.586$) was related to maternal origin. However, length at age 2 was greater among juvenile steelhead of anadromous maternal origin than among those of nonanadromous maternal origin (163 ± 6 mm [mean \pm SE] versus 135 ± 8 mm, respectively; $F_{1,36} = 5.35$, $P = 0.027$). A small sample size precluded a similar analysis of Rainbow Trout.

In general, freshwater growth was more rapid among Rainbow Trout than among juvenile steelhead (Table 5; Figure 4). Based on scale analyses, the mean annual growth of Rainbow Trout was 103 mm/year (SE = 3; range = 27–225 mm/year), whereas mean annual growth of juvenile steelhead was 86 mm/year (SE = 1; range = 23–229 mm/year). Consequently, juvenile Rainbow Trout were significantly larger than juvenile steelhead of equal age. One exception was that length at age 1 did not differ between Rainbow Trout and smolt age-1 steelhead.

Steelhead at sea generally grew faster and reached greater lengths at age than their nonanadromous counterparts in freshwater (Table 5; Figure 4). The exception was again steelhead that smolted at age 1, which grew at a similar or slower rate than Rainbow Trout once they reached age 3. As a consequence of their small relative size, Rainbow Trout were significantly less fecund than steelhead at breeding ages (≥ 3 years). For example, the estimated mean fecundity of an age-4 Rainbow Trout was 1,421 eggs (SE = 161), whereas the estimated mean fecundity of an age-4 steelhead was 4,170 eggs (SE = 65).

DISCUSSION

Our study contributes to the existing evidence of life history diversity in *O. mykiss*. Thorpe (1998) suggested that *O. mykiss* display up to 32 distinct life history categories at maturity. Shapovalov and Taft (1954) observed 34 life history categories at maturity among Waddell Creek (California) steelhead, Hopelain (1998) observed 28 among Klamath River steelhead, and Moore et al. (2014) observed 36 between Nass River (32) and Skeena River (31) steelhead (British Columbia). We identified 38 distinct life history categories at maturity in Klamath River *O. mykiss*.

That we identified more life history diversity in Klamath River *O. mykiss* than did Hopelain (1998) could potentially be explained by two or more factors. First, we included nonanadromous life histories in our study, whereas Hopelain (1998) did not. Second, life history patterns may have differed in some way between 1981–1983 and 2007–2009. We observed 10 life history categories at maturity that Hopelain (1998) did not, only four of which were nonanadromous pathways.

Although we identified about the same number of pathways as Moore et al. (2014), the maximum observed age of Klamath River *O. mykiss* (7 years) was approximately half that of

Table 5. Comparison of length (mean \pm SE) at age between Rainbow Trout and steelhead from the lower Klamath River basin. Significant differences are highlighted in bold italics (ANOVA with Bonferroni-corrected $\alpha = 0.0167$).

Total age	Fork length (mm)			
	Rainbow Trout	Smolt age 1	Steelhead Smolt age 2	Smolt age 3
1	106 \pm 3	112 \pm 2	90 \pm 1	86 \pm 2
2	209 \pm 9	386 \pm 9	170 \pm 2	149 \pm 5
3	312 \pm 10	559 \pm 8	462 \pm 4	216 \pm 8
4	368 \pm 18	637 \pm 15	582 \pm 4	458 \pm 15
5	434 \pm 17	669	642 \pm 9	551 \pm 28

Skeena River (13 years) and Nass River (14 years) steelhead. Klamath River steelhead exhibited less diversity in, and shorter durations of, freshwater rearing than did Skeena River and Nass River steelhead (1–3 years versus 1–6 years) but displayed unmatched diversity in association with the half-pounder life history. The between-basin differences in the duration of freshwater rearing and life span are consistent with observations that smolt age and longevity increase with increasing latitude (e.g., Withler 1966; l'Abée-Lund et al. 1989; Jonsson and l'Abée-Lund 1993).

While Klamath River *O. mykiss* arrived at the spawning grounds by numerous pathways, it appears that all fish displayed one of three basic trajectories: nonanadromy, anadromy with a half-pounder migration, or anadromy without a half-pounder migration. Interestingly, three different trajectories emerged when we distinguished *O. mykiss* from across the basin by growth. A fast-growing group smolted at age 1, an intermediate-growing group remained in freshwater for life, and a slow-growing group smolted at age 2 or 3.

Our findings regarding nonanadromy both supported and differed from other studies. Because the tendency for anadromy may decrease with increasing migratory difficulty (distance or elevation; Kristoffersen 1994; Wood 1995; McPhee et al. 2014; but see Ohms et al. 2014), we were not surprised to find Rainbow Trout in tributaries like the Scott and Shasta rivers, the mouths of which are located 230 and 284 km upstream of the ocean, respectively. On the other hand, because nonanadromy is typically more common among males than females in salmonids that display facultative anadromy (Krogus 1982; Jonsson and Jonsson 1993; Ohms et al. 2014), we were surprised that the majority of Rainbow Trout sampled were female. The high rates of nonanadromy we observed in female *O. mykiss* might suggest that the fitness benefits of time at sea (increased size and fecundity), which are typically more pronounced in females than males, are relatively small for Klamath River *O. mykiss* (Hendry et al. 2004). This notion is supported by the existence of half-pounders, which in the year of initial ocean entry trade growth opportunities at sea for a higher probability of survival in freshwater (Hodge et al. 2014). That we captured more female Rainbow Trout than male Rainbow Trout might also reflect sampling bias, though it is difficult to identify why susceptibility to, or efficacy of, capture would be greater for the former than the latter.

The results of otolith microchemistry provided additional evidence that Klamath River steelhead displayed facultative anadromy. Namely, we observed sympatric occurrence of anadromous and nonanadromous *O. mykiss* and observed that, although maternal origin and migratory history typically aligned, both steelhead and Rainbow Trout produced progeny of the alternate form. This finding suggests that steelhead and

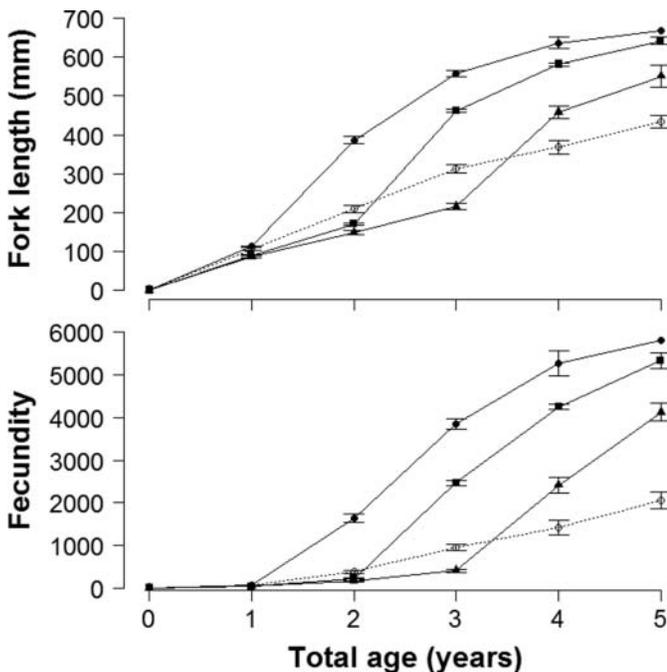


FIGURE 4. Comparison of length (top panel) and fecundity (bottom panel) at age between anadromous (solid lines, closed symbols [smolt age: 1 = circles, 2 = squares, 3 = triangles]) and nonanadromous (dotted line, open circles) *O. mykiss* from the lower Klamath River basin (error bars = SEs; $n = 591$). Fecundity was estimated using the basin-specific relationship developed by Hodge et al. (2014): fecundity = $\alpha \cdot FL^\beta$, where $\alpha = 0.2128$ (95% confidence limits = 0.0615, 0.7359), FL = fork length at the time of breeding, and $\beta = 2.4301$ (SE = 0.3003).

Rainbow Trout may interbreed (Zimmerman and Reeves 2000) and coincides with findings by others (e.g., Seamons et al. 2004; McMillan et al. 2007; McPhee et al. 2007). For example, Zimmerman and Reeves (2000) found using otolith microchemistry that while most Babine River (British Columbia) *O. mykiss* displayed the same life history as their mother, Rainbow Trout gave rise to anadromous progeny and steelhead gave rise to nonanadromous progeny. Seamons et al. (2004) found genetic evidence that nonanadromous males contributed to the steelhead population in Snow Creek, Washington, and McPhee et al. (2007) confirmed with DNA analysis that gene flow occurred between alternate life history forms of *O. mykiss* in streams of Kamchatka, Russia. Our results might be corroborated (or contradicted) with genetic tests of reproductive exchange between steelhead and Rainbow Trout in the lower Klamath River basin.

Our microchemistry-based determinations of maternal origin should be interpreted conservatively for two reasons. First, fish of anadromous maternal origin could have been misidentified as progeny of nonanadromous maternal origin. Prior research shows that in progeny of steelhead that make difficult spawning migrations and (or) enter rivers six or more months before spawning, otolith core chemistry may reflect the freshwater environment rather than the marine environment (Volk et al. 2000; Donohoe et al. 2008). Accordingly, freshwater residence prior to spawning could have potentially diluted the maternal marine influence in the progeny of wild Klamath River steelhead. Second, fish of nonanadromous maternal origin could have been misidentified as progeny of anadromous maternal origin. Our water chemistry analyses showed that isotopic signatures differed significantly between certain neighboring watersheds (e.g., the East Fork Scott and South Fork Scott rivers), and subsequent analyses revealed that the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio in a small tributary to the Klamath River exceeded the global marine value (Quiñones and Hobbs, unpublished data). Also, $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in the freshwater growth regions of six otoliths exceeded the global marine value. It is therefore conceivable that a nonanadromous mother that reared in a stream with a relatively high $^{87}\text{Sr}/^{86}\text{Sr}$ ratio and spawned in a stream with a relatively low $^{87}\text{Sr}/^{86}\text{Sr}$ ratio passed a “false indicator” of anadromous maternal origin to her progeny. We believe it is unlikely that all steelhead of nonanadromous maternal origin and Rainbow Trout of anadromous maternal origin were falsely classified as such because (1) some Klamath River steelhead (winter-run fish in particular) spend less than 6 months in freshwater prior to spawning (Barnhart 1994; NRC 2004) and (2) relatively few Rainbow Trout rearing–spawning scenarios would lead to false indicators of anadromous maternal origin. Thus, while the proportions of steelhead with Rainbow Trout mothers, and Rainbow Trout with steelhead mothers, should be interpreted conservatively, we are relatively confident in our finding that *O. mykiss* gave rise to progeny of the alternate form.

The costs and benefits of anadromy were more evident in the context of migratory history than in the context of maternal origin. We were unable to identify any clear effect of maternal origin on length at age. However, on average, anadromy conferred a benefit with respect to the length and fecundity of adults. The smaller and less fecund (nonanadromous) phenotype might persist in a population with access to the ocean because it benefits from enhanced lifetime survival relative to the larger and more fecund (anadromous) phenotype (Hendry et al. 2004; Hodge et al. 2014). Alternatively, the smaller phenotype might persist because it benefits (relative to its counterpart) from a higher incidence of repeat spawning and (or) the ability to exploit streams that are too small for the larger, anadromous phenotype (Kendall et al. 2015, and sources therein). Overall, the expression of both anadromous and nonanadromous forms should increase the likelihood of population persistence by spreading the risk of extirpation between forms (Sloat et al. 2014).

While the high degree of life history diversity observed in Klamath River *O. mykiss* should increase population resilience, comparison of findings from the Klamath River basin with findings from another basin suggests that the relationship between diversity and population stability is complex. If diversity alone was a reliable predictor of stability, the lower Klamath River aggregate might be among the most resilient *O. mykiss* populations on the West Coast, as our study documents an extraordinary level of variability in a single watershed. We observed a greater number of life histories than Moore et al. (2014) observed in the Nass River watershed. Nevertheless, the Nass River steelhead population was relatively stable from 2000 to 2011 (Moore et al. 2014), whereas the Klamath River steelhead population declined through the 1980s and 1990s (NRC 2004, 2008), and between which times Hopelain (1998) observed 28 life history categories at maturity and we observed 38. That an uncommonly diverse population declined in abundance suggests that diversity alone is not sufficient to stabilize a population. Nevertheless, if the Klamath River dam removals increase life history diversity among *O. mykiss* as predicted (USDOI and CDFG 2013), we would expect a resulting increase in population stability (Greene et al. 2010; Shindler et al. 2010; Moore et al. 2014).

The results of this study have two additional implications with respect to species conservation and recovery. First, our finding that steelhead and Rainbow Trout give rise to progeny of the alternate form and thus potentially interbreed suggests that dam removal might lead both to a facultatively anadromous *O. mykiss* population in the upper basin and to the co-occurrence of, and reproductive exchange between, coastal steelhead–Rainbow Trout *O. mykiss irideus* and inland Redband Trout *O. mykiss newberri*. Meanwhile, results from other studies of *O. mykiss* (e.g., Thrower et al. 2008; Holecek et al. 2012; Wilzbach et al. 2012) further support the notion that Redband Trout could display anadromy in the absence of

dams. Collectively, it appears that dam removal could result in two mechanisms of *O. mykiss* recovery, whereby fish from the lower basin recolonize historical habitat in the upper basin (Brenkman et al. 2008; Pess et al. 2008; Anderson et al. 2014) and inland Redband Trout refresh and contribute to the steelhead–Rainbow Trout population in the lower basin. Second, our results have relevance with respect to the scope of the evolutionarily significant unit. To date, the Klamath Mountains Province Steelhead evolutionarily significant unit has excluded Rainbow Trout because of the lack of evidence of genetic exchange between the anadromous and nonanadromous phenotypes (Busby et al. 1994). Although our results do not provide genetic evidence of reproductive exchange, they suggest that steelhead and Rainbow Trout might interbreed in the lower Klamath River basin. Moreover, our findings raise the question of whether both forms of *O. mykiss* should be managed under a joint strategy.

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