ARTICLE

Resident rainbow trout produce anadromous offspring in a large interior watershed

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Abstract: Rainbow trout (*Oncorhynchus mykiss*) have diverse life histories, including both freshwater-resident and anadromous "steelhead" life-history forms. Here, we demonstrate that female resident rainbow trout produce anadromous offspring that survive and return to spawn as adult steelhead. This study represents the first successful attempt to quantify steelhead production rates from female resident rainbow trout across a large watershed. Otolith microchemistry ($^{87}Sr/^{86}Sr$) techniques were used to determine the maternal life history (resident or anadromous) of 498 emigrating steelhead kelts in the Yakima Basin, Washington. Five geochemically distinct freshwater rearing regions were identified within the basin. All five regions were predicted to produce steelhead with resident maternal life histories. Basin-wide, 20% and 7% of steelhead collected in 2010 and 2011, respectively, had resident maternal life histories. Cross-life-history form production may be critical to persistence of anadromous life histories within partially anadromous salmonid populations, particularly in areas where anadromous fish abundance is low due to natural or anthropogenic influences.

Résumé : Les truites arc-en-ciel (*Oncorhynchus mykiss*) présentent divers types de cycle biologique; elles comptent notamment une forme résidant en eau douce et une forme anadrome. Nous démontrons que des truites arc-en-ciel femelles résidentes peuvent produire des rejetons anadromes qui survivent en mer et retournent en eau douce pour frayer. L'étude constitue la première tentative fructueuse de quantifier les taux de production de truites arc-en-ciel anadromes issues de femelles résidentes à l'échelle d'un grand bassin versant. Des techniques de microchimie ($^{87}Sr/^{86}Sr$) des otolithes ont été utilisées pour déterminer le cycle biologique (résident ou anadrome) maternel de 498 bécards de cette espèce émigrant du bassin de la rivière Yakima, dans l'état de Washington. Cinq régions d'alevinage en eau douce distinctes sur le plan géochimique ont été cernées dans ce bassin. Il avait été prédit que ces cinq régions produiraient des individus anadromes associés à des cycles biologiques maternels résidents. À l'échelle du bassin, 20 % et 7 % des truites anadromes prélevées en 2010 et 2011, respectivement, étaient associées à des cycles biologiques maternels résidents. La production de formes caractérisées par des cycles biologiques distincts d'une génération à l'autre pourrait être essentielle à la persistance des cycles biologiques anadromes dans les populations de salmonidés partiellement anadromes, en particulier dans les régions où l'abondance de poissons anadromes est faible en raison d'influences naturelles ou anthropiques. [Traduit par la Rédaction]

Introduction

Partial migration, when one portion of an animal population migrates while the other portion remains sedentary (Lundberg 1988), has been well documented in a variety of fish species, including salmonids (Jonsson and Jonsson 1993; Table 1). A related term, "partial anadromy", refers more specifically to a behavioral strategy whereby fish of the same population adopt divergent anadromous and resident freshwater life-history strategies (Hendry et al. 2004). Evolutionarily stable migration plasticity is thought to be a response to environmental stochasticity and density-dependent survival (Lundberg 1987; Kaitala et al. 1993). Life-history diversity, represented by these mechanisms, is believed to buffer against extinction (Hilborn et al. 2003; Greene et al. 2010). Such diversity may be particularly important to the perpetuation of salmonids facing a variety of natural and anthropogenic causes of mortality.

The term "steelhead", which has been conventionally used to identify anadromous rainbow trout, represents one of several potential life-history forms within *Oncorhynchus mykiss* populations (Pavlov et al. 2001). Stream residency is also common for this species, with resident individuals remaining in fresh water throughout their life cycle, often moving between suitable habitats (Gowan et al. 1994), but never venturing to the ocean. In watersheds with ocean access, researchers have found that in addition to interbreeding (McMillan et al. 2007), resident rainbow trout and steelhead can produce progeny of the alternate life-history form (Pascual et al. 2001; Thrower and Joyce 2004; Korman et al. 2010). These findings indicate that life-history trajectories of partially anadromous salmonid populations are driven by a combination of genetic predispositions and environmental cues (Jonsson and Jonsson 1993; Hendry et al. 2004).

The extent to which resident and anadromous *O. mykiss* life-history forms are reproductively mixed remains somewhat equivocal. In some cases, researchers have found evidence for reproductive isolation between the two forms (e.g., Zimmerman and Reeves 2000), while others have found evidence for substantial reproductive exchange (e.g., Pascual et al. 2001). There is need for resolution concerning the question of whether resident rainbow trout and steelhead are reproductively isolated in the majority cases (Behnke 2002) to inform whether population assessments should be expected to quantify the impact of resident rainbow trout on the persistence of steelhead.

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Table 1. Salmonid species known to exhibit both freshwater-resident and anadromous life-history forms within the same watershed.

Common name	Scientific name	Reference
Atlantic salmon	*Salmo salar*	Fleming 1998
Brown trout	*Salmo trutta*	Jonsson 1985
Sockeye salmon	*Oncorhynchus nerka*	Wood 1995
Masu salmon	*Oncorhynchus masou*	Arai and Tsukamoto 1998
Cutthroat trout	*Oncorhynchus clarkii*	Zimmerman et al. 1997
Rainbow trout	*Oncorhynchus mykiss*	Pavlov et al. 2008
Dolly Varden	*Salvelinus malma*	Koizumi et al. 2006
Bull trout	*Salvelinus confluentus*	Brenkman and Corbett 2005
Brook char	*Salvelinus fontinalis*	Curry et al. 2010
Arctic char	*Salvelinus alpinus*	Nordeng 1983

Observational studies (McMillan et al. 2007), breeding experiments (Thrower and Joyce 2004), genetic analyses (Olsen et al. 2006; McPhee et al. 2007; Christie et al. 2011), and otolith microchemistry (Zimmerman and Reeves 2002) are used to examine partial anadromy in rainbow trout populations. Otolith primordial chemistry, specifically the strontium to calcium (Sr/Ca) ratio, is a well-established method of determining maternal life history of partially anadromous salmonids (Kalish 1990; Rieman et al. 1994; Volk et al. 2000). Bony material in the otolith is laid down in a concentric circular pattern throughout the fish's life. Each ring has a chemical makeup that can reflect the habitat occupied when the ring was formed because chemicals in the environment, such as Sr, are readily incorporated into the otolith mineral lattice (Campana 1999). Maternal life-history form is identifiable within the otolith primordia, which develops during early life stages (McKern et al. 1974) when nutrition is provided by the egg yolk and, therefore, retains a diagnostic chemical signal indicating whether the female parent occupied freshwater or marine habitats during oogenesis (Kalish 1990; Volk et al. 2000). In recent years, these techniques have been expanded to include measurement of precise chemical and isotopic data at fine spatial resolution across the entire otolith (Kennedy et al. 2000; Barnett-Johnson et al. 2005; Woodhead et al. 2005). Natal origins of fish have been identified by pairing otolith chemistry with water chemistry data (Kennedy et al. 2000; Barnett-Johnson et al. 2008; Muhlfeld et al. 2012). Thus, analysis of otolith chemistry data provides information about maternal life history and habitat areas occupied during freshwater rearing.

Applying a combination of maternal life history and natal origin identification techniques to rainbow trout populations is useful because fish population assessments typically focus on genetically distinct groupings, which can inhabit relatively small geographic regions within watersheds. This combined approach can be used to quantify reproductive contributions within and between life-history forms to identify whether rates of cross-life-history form production of steelhead vary spatially. For example, anadromous life-history forms existing at higher elevations or further from the ocean may be more dependent on the resident life-history form for reproductive output. Conversely, juveniles may be less likely to exhibit anadromy in habitats favorable to a nonmigratory life history, such as areas with low migration success (Narum et al. 2008) or stream flow conditions suited for residency (Mills et al. 2012).

Available genetic and observational data collected on rainbow trout populations throughout the Pacific Rim (Pascual et al. 2001; Thrower and Joyce 2004; McPhee et al. 2007) suggest that in habitats with ocean access, resident rainbow trout produce some anadromous offspring that survive and return as adult steelhead. To test this hypothesis, we quantified the proportion of steelhead produced by native female resident rainbow trout in the Yakima Basin, Washington, using otolith primordial Sr isotope ratios. We also examined whether the proportion of steelhead derived from resident female spawners differed spatially by comparing Sr isotope ratios from freshwater growth portions of the otolith with ratios from water samples collected throughout the basin.

Methods

Study site

The Yakima Basin is a 16 000 km² interior Columbia Basin watershed that drains the eastern slopes of the Cascade Mountain Range and discharges into the Columbia River (river kilometre (rkm) 539; Fig. 1). The Yakima Basin hosts a variety of habitat types ranging from high elevation mountain streams to large, seasonally stable rivers and arid, low elevation ephemeral streams. Like many other major Columbia River tributaries, the Yakima River contains resident rainbow trout and steelhead. Hatchery steelhead supplementation has not occurred in the Yakima Basin since the early 1990s, and hatchery stray rates from other Columbia Basin populations remain low, typically <5% (Conley et al. 2008). Trout stocking does occur in lakes and ponds adjacent to the Yakima River; however, trout plantings in the river itself have not occurred since 1984, and tributary stocking has not occurred since the mid-1990s. Genetic analysis indicated that resident trout are similar to native steelhead and are quite distinct from the hatchery stocks (Busack et al. 2005). Thus, the lack of present-day *O. mykiss* hatchery influence makes the Yakima Basin an ideal place to study steelhead production by native resident rainbow trout across a variety of riverine habitat types over a large geographic area.

Otolith sample collections

While *O. mykiss* are iteroparous, repeat spawning by steelhead in the middle Columbia River region is low. For example, only ~3%–4% of adults returning to the Yakima River are known to spawn multiple times (Branstetter et al. 2010). In an effort to bolster steelhead returns, the Yakama Nation Fisheries Program developed a practice of reconditioning emigrating kelts in hopes of increasing the proportion of fish that survive their first spawning event to return and reproduce a second time (Branstetter et al. 2010). Downstream adult steelhead migrants are collected during late spring and summer in the lower Yakima River at the Yakama Nation's Chandler Juvenile Evaluation Facility (Fig. 1), near Prosser Dam where they are held and fed at Prosser Hatchery until release during the late fall. Roughly one-third die before the release date. Three hundred native adult steelhead carcasses were collected at Prosser Hatchery during the summer and fall of 2010. An additional 209 carcasses were collected in the spring, summer, and fall of 2011. All steelhead collected exceeded 480 mm. This was thought to be a reasonable size cutoff for partitioning steelhead from resident rainbow trout because resident rainbow trout ≥480 mm are rare in the Yakima Basin (Temple et al. 2012), and resident rainbow trout >350 mm have not been observed in the lower Yakima River (Karp et al. 2007; J. Hubble, US Bureau of Reclamation, unpublished data; A.L. Fritts, Washington Department of Fisheries and Wildlife, unpublished data).

The mechanism for elevated Sr concentrations (Sr/Ca) in the otolith primordia of steelhead and other anadromous salmonids is known and provides the basis for expecting that a maternal-derived Sr isotope ratio ($^{87}Sr/^{86}Sr$) would occur via the same mechanism. However, for the purpose of quantifying the maternal life-history identification error rate (i.e., determining that a steelhead was derived from resident mother when in fact it was derived from an anadromous mother), 20 hatchery steelhead carcasses were collected from throughout the mid-Columbia Basin in 2011, including the Klickitat River and mainstem Columbia River (rkm 570). Presumably, all hatchery fish should have anadromous origins because they were selectively bred using anadromous fish. Otoliths from Columbia Basin hatchery steelhead were mixed with Yakima Basin steelhead otoliths prior to lab analysis. This

Fig. 1. Map of the Yakima Basin showing the location of the seven water sampling regions, water sample sites (black dots), and steelhead kelt collection facilities near Prosser Dam (fish icon).
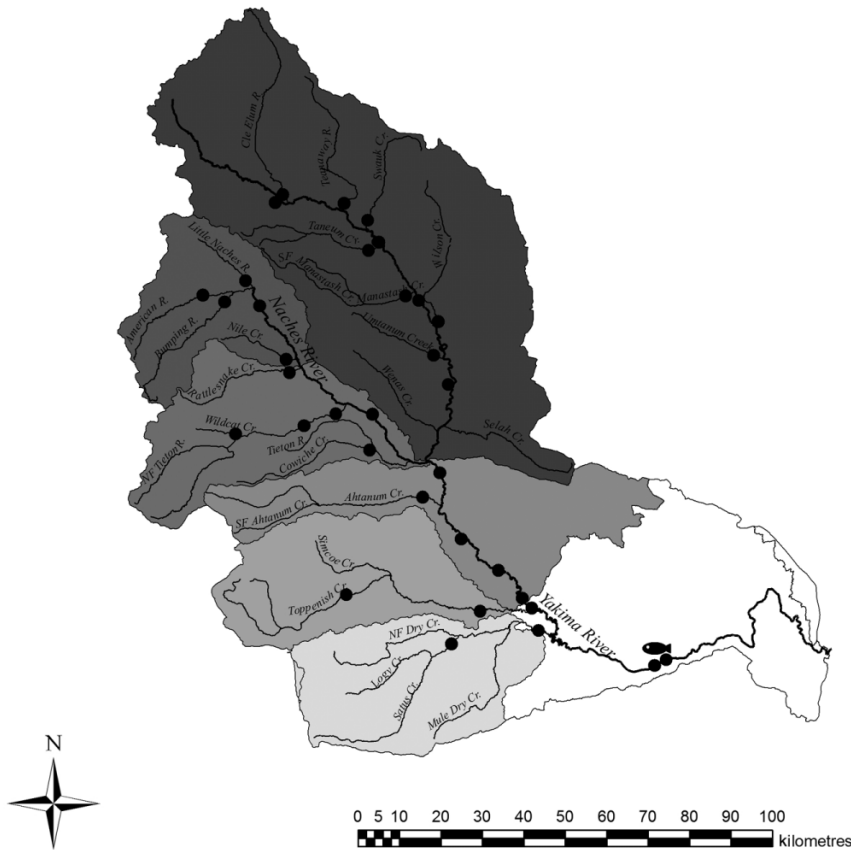
provided a blind test of the analytical techniques to ensure that anadromous mothers were not being misidentified as resident maternal parents because of depuration of the marine Sr signature or variability in laboratory results.

Sagittal otoliths were extracted from each fish, cleaned, and dried. Otoliths were then mounted in the sagittal plane on glass microscope slides with Crystal Bond thermoplastic resin (Crystalbond 509, Ted Pella Inc. Redding, California), sanded to the primordial core on both sides with 1200 grit wet–dry sandpaper, and polished with 0.3 μm alumina and a polishing cloth. Polished otoliths were washed with 1 mol·L^{-1} chemical grade nitric acid for 5 to 10 s, rinsed in an ultrasonic water bath for 5 min, and dried under a class 100 laminar flow hood. For laser ablation, otoliths were remounted on petrographic glass slides, with 20 individual otoliths per slide. Digital images of otoliths were taken at ×10 magnification on a CH30 Olympus compound microscope before and after laser ablation assays. To ensure the surface of the

primordial core was exposed for laser assay, we examined the focal plane of the primordial rings with a microscope. If the leading edge of the primordial rings was clearly visible, we could be sure that the primordial core was at the surface of the sample. Otolith cores were also examined after laser ablation to be sure the core material was completely ablated.

Water sample collections

A water chemistry profile was generated for the Yakima Basin by collecting water samples from 34 candidate stream reaches, including the Yakima River main stem and 17 major tributaries, to characterize water ^{87}Sr/^{86}Sr values in seven regions within the Yakima Basin (Fig. 1). Sample locations were chosen to cover the full range of habitats used by steelhead during their life cycle. Water samples were collected at base flow conditions during the fall of 2010 and 2011, in the direct flow of water using 50 ml polypropylene tubes, acidified with 1 mol·L^{-1} nitric acid and fil-

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Fig. 2. Examples of $^{87}Sr/^{86}Sr$ values derived from steelhead sagittal otoliths collected in the lower Yakima River with (*a*) anadromous and (*b*) resident maternal life histories using laser ablation coupled with plasma mass spectrometry. The elevated primordial core $^{87}Sr/^{86}Sr$ value was used to distinguish anadromous from resident maternal life histories. (*c*) Photograph of polished steelhead sagittal otolith with dotted line indicating the approximate location of laser ablation transects.
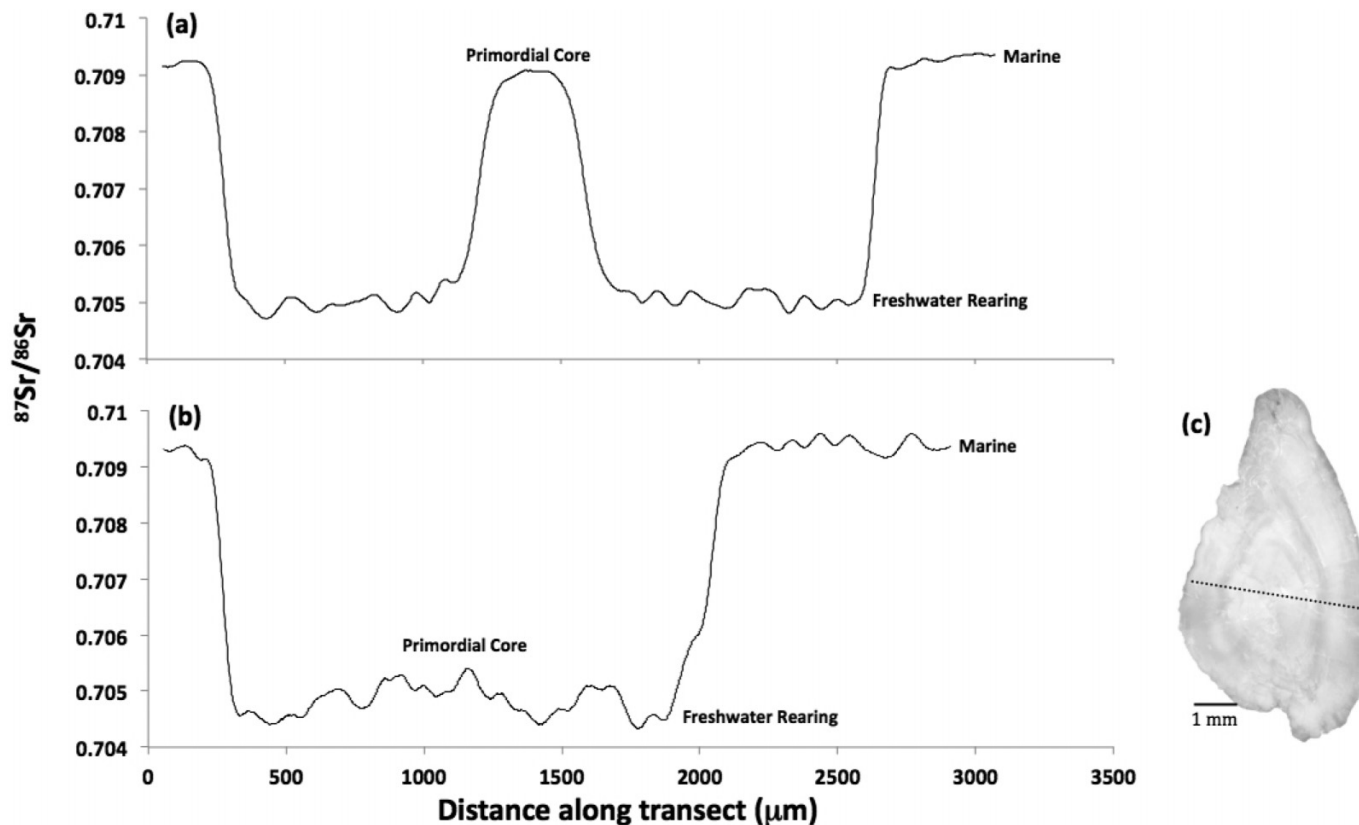
tered with a 0.45 μm filter. Samples were kept cool prior to microchemical analysis.

Geochemical analysis

Otolith and river water $^{87}Sr/^{86}Sr$ values were measured at the University of California Davis Interdisciplinary Center for Plasma Mass Spectrometry. For otolith analysis, a multicollector inductively coupled plasma mass spectrometer (Nu Plasma HR (Nu032) from Nu Instruments Ltd.) was interfaced with a Nd:YAG 213 nm laser (New Wave Research UP213) for Sr isotope measurement by laser ablation (LA-MC-ICP-MS technique). A laser beam of 55 μm diameter traversed across the otolith from the core to the edge at 10 μm·s^{-1}. All data were normalized for instrumental mass discrimination by monitoring $^{86}Sr/^{88}Sr$ ratio (assuming $^{86}Sr/^{88}Sr$ = 0.1194), and ^{87}Rb was corrected by monitoring the ^{85}Rb signal. Krypton interference coming from the argon supply (^{86}Kr) was subtracted on peak zero before each analysis. Accuracy was evaluated by monitoring the marine region of each otolith and comparing it with a modern seawater value to measure analytical drift for each sample. Data reduction was conducted using Matlab 9.0. Primordial core values were taken as the average of measurements occurring over the entire core (~200 μm), resulting in an average of 20 sequential data points. The freshwater rearing $^{87}Sr/^{86}Sr$ values were taken from an approximately 100 μm region postprimordial on the $^{87}Sr/^{86}Sr$ profile, resulting in an average of at least 10 data points per otolith. When we observed primordial core values that were indicative of a freshwater resident maternal life history, three additional spot analyses (with a 55 μm diameter beam) were conducted on the core for each fish, whereby the laser was focused on a single spot and allowed to drill through the sample.
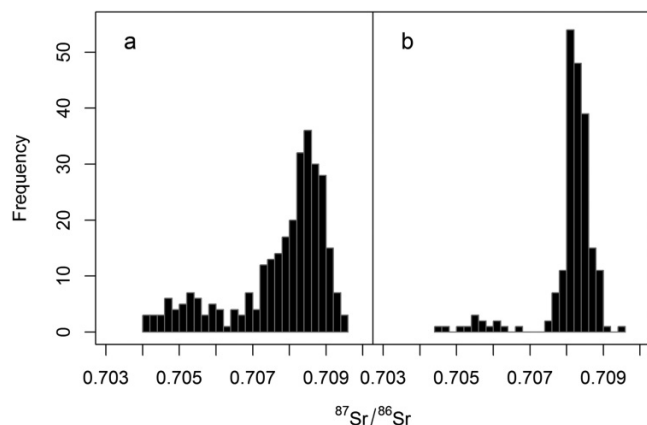
River water samples were transported to a class 100 clean room facility for processing. An aliquot of each water sample was made at volume totaling approximately 1 μg of total Sr. This volume (ranging 3–70 mL) was evaporated to dryness, and Sr was isolated from all other aqueous constituents by selective ion exchange chromatography (Horwitz et al. 1992). Purified solutions were analyzed with the Nu Plasma HR (MC-ICP-MS) to determine the $^{87}Sr/^{86}Sr$ value. Procedural blank was measured and contributed <0.002% of total Sr processed per sample. $^{87}Sr/^{86}Sr$ values were internally normalized and corrected for Kr and Rb interferences. Replicated analyses of NIST SRM 987 (Sr carbonate) were conducted every six samples, normalizing for instrument drift over the course of the day and for analytical artifact among sessions. An in-house modern marine coral standard was processed in parallel with water samples (*n* = 8) and resulted in $^{87}Sr/^{86}Sr$ = 0.709182 ± 0.000017 (mean ± 2 SD).

Data analysis

Measurements of $^{87}Sr/^{86}Sr$ values within primordial core and freshwater rearing strata from each otolith were compared with known marine $^{87}Sr/^{86}Sr$ values (0.70918; Hodell et al. 1990) and those observed in water samples collected throughout the Yakima Basin. Measurements made in the primordial core were used to determine maternal life history, and measurements made in the freshwater rearing portion of the otolith were used to identify the natal origin of each fish (Fig. 2).

Instead of using a predetermined cutoff value to distinguish the maternal life history of each fish, we estimated this value using univariate *K*-means clustering. This procedure separated otolith primordial core signatures into two groups, whereby primordial core signatures less than the estimated cutoff value were assigned

Fig. 3. Frequency of otolith primordial core $^{87}Sr/^{86}Sr$ values measured from adult Yakima Basin steelhead kelts collected in the lower Yakima River in 2010 (*a*) and 2011 (*b*).

Table 2. Summary statistics for $^{87}Sr/^{86}Sr$ values measured within each of the seven water sampling regions at 37 sites throughout the Yakima Basin.

Stream ID	Median (*n* = sample size)	Range
Upper Yakima	0.7053 (*n* = 12)	0.7052–0.7058
Middle Yakima	0.7052 (*n* = 4)	0.7051–0.7052
Lower Yakima	0.7082 (*n* = 4)	0.7060–0.7100
Upper Naches	0.7042 (*n* = 6)	0.7040–0.7043
Lower Naches	0.7047 (*n* = 7)	0.7046–0.7050
Toppenish	0.7053 (*n* = 2)	0.7044–0.7061
Satus	0.7045 (*n* = 2)	0.7039–0.7051

Results

Maternal assignments

Of the 300 steelhead collected in 2010 and the 209 collected in 2011 from the lower Yakima River, 295 and 203, respectively, produced otoliths from which primordial core $^{87}Sr/^{86}Sr$ values could be measured. Bimodal distributions of primordial core $^{87}Sr/^{86}Sr$ values were evident in both 2010 and 2011, emphasizing the presence of a mix of steelhead with resident and anadromous maternal life histories (Fig. 3). In both 2010 and 2011, *K*-means cluster analysis estimated a cutoff $^{87}Sr/^{86}Sr$ value of 0.707. Otoliths with primordial core $^{87}Sr/^{86}Sr$ values greater than 0.707 were classified as anadromous maternal life history, and otoliths with primordial signatures less than 0.707 were classified as resident maternal life history.

The percentage of steelhead predicted to have resident and anadromous maternal life histories varied between sampling years. *K*-means cluster analysis indicated that 20.34% (95% CI: 15.59%–25.08%) of fish from the 2010 sample were assigned to the resident maternal life-history group, whereas 79.66% (95% CI: 74.92%–84.41%) were assigned to the anadromous maternal life-history group. For fish collected in 2011, 6.90% (95% CI: 3.94%–10.84%) were assigned to the resident maternal life-history group, whereas 93.10% (95% CI: 89.16%–96.06%) were assigned to the anadromous maternal life-history group.

All 20 hatchery steelhead from outside the Yakima Basin with known maternal life histories were correctly predicted to have anadromous mothers. Primordial core $^{87}Sr/^{86}Sr$ values for hatchery steelhead ranged between 0.7081 and 0.7114. However, freshwater rearing regions of hatchery steelhead otoliths also produced measured $^{87}Sr/^{86}Sr$ values between 0.7093 and 0.7138.

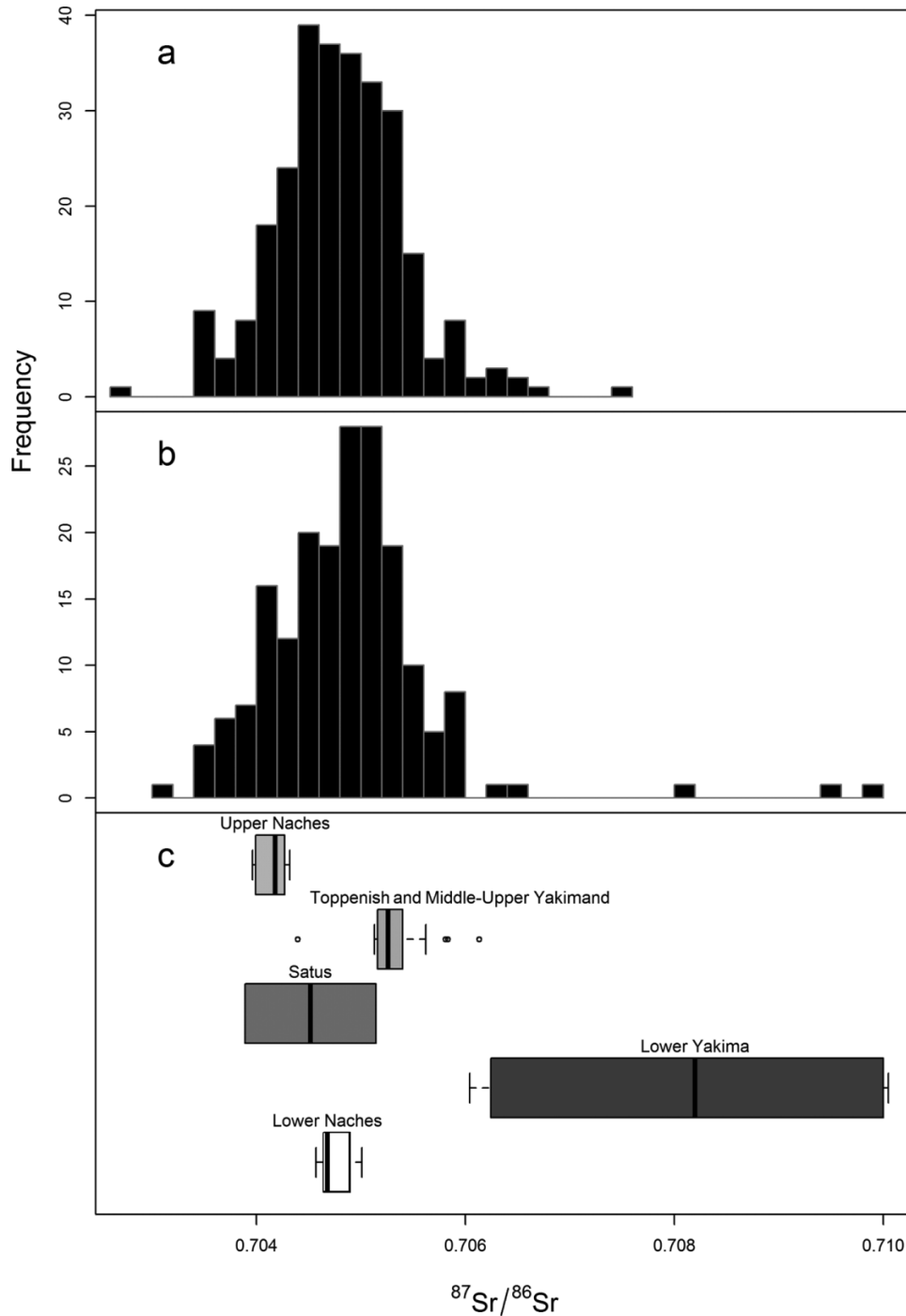### Regional assignments

Water sample $^{87}Sr/^{86}Sr$ values for each of seven geographic regions provided some evidence for distinction between regions (Table 2). The median $^{87}Sr/^{86}Sr$ values for the upper Yakima River, middle Yakima River, and Toppenish Creek basins were nearly identical. Consequently, we pooled water data from the upper Yakima River, middle Yakima River, and Toppenish Creek areas, resulting in five geochemically distinct regions.

Freshwater rearing $^{87}Sr/^{86}Sr$ values collected from native Yakima Basin steelhead otoliths in 2010 and 2011 aligned most frequently with water samples from the Naches River, middle and upper Yakima rivers, Toppenish Creek, and Satus Creek subbasins (Fig. 4). The range in $^{87}Sr/^{86}Sr$ values from water samples collected in the lower Yakima River, though large, overlapped infrequently with otolith $^{87}Sr/^{86}Sr$ values. A high frequency of otolith $^{87}Sr/^{86}Sr$ values corresponded with water samples from the Satus Creek and Naches River subbasin (lower and upper), which might be expected to reduce our ability to differentiate between fish from those regions.

Classification success as determined by the jackknife cross-validation procedure was moderately high with an apparent correct classification rate of 83.79%. The percent correctly classified

a resident maternal life history, and primordial core signatures greater than the estimated cutoff value were assigned an anadromous maternal life history. To quantify the amount of uncertainty in the percentage of fish assigned to each group, a nonparametric bootstrap procedure was used, resampling the primordial core signature database 1000 times. When summarizing results, the median and 95% bootstrap confidence interval (CI), comprising the 2.5 and 97.5 percentiles of observations, are reported.

Summary statistics were used to examine the degree to which a single predefined geographic region provided distinct separation of water $^{87}Sr/^{86}Sr$ values compared with other regions. If two adjacent geographic regions had indistinguishable $^{87}Sr/^{86}Sr$ values, they were pooled. In doing so, the certainty associated with assignments of fish to their natal freshwater region increased, but at the cost of reduced spatial resolution.

Single factor quadratic discriminant function analysis (QDFA) was applied to determine whether $^{87}Sr/^{86}Sr$ values in Yakima Basin water samples were useful for predicting natal origins of steelhead. QDFA was used instead of a linear discriminant function, because it relaxes the assumption that all the variances of the $^{87}Sr/^{86}Sr$ values from geographic regional groups are the same. The QDFA jackknife procedure, which removed a single water sample data point sequentially and recalculated the discriminant function for the remainder of the data, was performed to determine how accurately water sample data could be classified according to its known geographic region. The discriminant function determined by the water sample data was used to identify the unknown freshwater origins of adult fish as determined by the $^{87}Sr/^{86}Sr$ values in the freshwater rearing portion of the otolith. The median and 95% nonparametric bootstrap CI is reported.

To determine the proportion of steelhead with resident maternal life histories from each geochemically distinct region, a two-step approach was taken wherein (*i*) the QDFA procedure and (*ii*) the *K*-means clustering procedure were used sequentially. A two-way contingency table was then calculated to determine the total number of fish with resident and anadromous maternal life histories from each freshwater region. The median proportion of fish classified as having resident and anadromous maternal life histories within each geochemically distinct region and 95% nonparametric bootstrap CI are reported.

All analyses were carried out using the R Statistical Software (R Development Core Team 2012). The "stats" package (R Development Core Team 2012) was used to implement the *K*-means clustering algorithm, and the MASS package (Venables and Ripley 2002) was used to fit the QDFA model.

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Fig. 4. Frequency of freshwater rearing $^{87}Sr/^{86}Sr$ values measured from adult Yakima Basin steelhead kelts collected in the lower Yakima River in 2010 (*a*) and 2011 (*b*) along with boxplots of freshwater $^{87}Sr/^{86}Sr$ values measured at 37 sites throughout the Yakima Basin (*c*).

to each region was 94.44% for the Toppenish and middle–upper Yakima, 75% for the lower Yakima, 100% for the upper Naches, 71.43% for the lower Naches, and 0% for Satus (Table 3).

The discriminant function determined by the water sample data was used to identify the unknown freshwater origins of adult fish as determined by their freshwater rearing $^{87}Sr/^{86}Sr$ value. Of the 300 adult steelhead collected in 2010 and 209 collected in 2011, freshwater rearing $^{87}Sr/^{86}Sr$ values were measured in 275 and 188 otoliths, respectively. The distribution of regional assignments remained relatively consistent for both years, with the majority of steelhead predicted to be natal to the lower Naches

region and upper–middle Yakima region, which included Toppenish Creek. A large proportion of our steelhead were also predicted to be natal to the upper Naches region (Table 4).

In some portions of the basin, rates of cross-life-history form production were noticeably different between sampling years (Table 4). The largest interannual difference in cross-life-history form production occurred in the upper and lower Naches regions, where we observed relatively high proportions of steelhead with resident maternal life histories in 2010 followed by low proportions in 2011. In contrast, the upper–middle Yakima River and Toppenish Creek region had rela-

Table 3. Jackknifed cross-validation accuracy for classification of water data to its known location as determined by ^{87}Sr/^{86}Sr values.

Sample region	Assigned geographic region				
	Upper Naches	Lower Naches	Toppenish and Middle–Upper Yakima	Lower Yakima	Satus
Upper Naches	6	0	0	0	0
Lower Naches	0	5	2	0	0
Toppenish and Middle–Upper Yakima	1	0	17	0	0
Lower Yakima	0	0	1	3	0
Satus	1	0	1	0	0

tively stable proportions of steelhead with resident maternal life histories in both years.

Discussion

This study represents the first successful attempt to quantify steelhead production rates from female resident rainbow trout across a large watershed. Results demonstrated the occurrence of cross-life-history form production, confirming that resident and anadromous forms of *O. mykiss* are not reproductively isolated in the Yakima Basin. This finding supports the conclusion that resident trout and steelhead, where they coexist, are members of a reproductively mixed population (Pascual et al. 2001). Examples of sympatric, reproductively isolated, or genetically divergent *O. mykiss* polymorphisms are rare (e.g., Zimmerman and Reeves 2000; Docker and Heath 2003; Narum et al. 2004) and can typically be explained by segregation in spawn timing or location, physical barriers, or out-of-basin stocking (Wilzbach et al. 2012).

Mortalities from the Yakima Nation's kelt reconditioning program provided ideal samples for our study because they were naturally produced adult steelhead. Previous studies either relied on relatively small sample sizes of adult fish (Zimmerman and Reeves 2000) or focused on juvenile fish collections (Zimmerman et al. 2009; Korman et al. 2010; Mills et al. 2012), which can be confounded by the presence of diverse migratory freshwater life histories (Mellina et al. 2005; Tattam 2006; Wilzbach et al. 2012). Partially anadromous salmonids produce offspring predominantly of the same life-history form, and rates of cross-life-history form production can vary throughout a watershed. Therefore, a robust sample of adult fish across a large area is necessary to accurately determine whether cross-life-history form production is occurring among female spawners.

Maternal assignments

The primary source of uncertainty in our predictions of maternal life history was the potential for depuration of marine Sr while female steelhead finished maturing in freshwater. Complete depuration of marine Sr during oocyte maturation could result in offspring with otolith primordial core ^{87}Sr/^{86}Sr values that do not infer anadromous maternal life history. A study by Zimmerman and Reeves (2002) verified that the Sr/Ca ratio in steelhead otoliths could be used to accurately predict maternal life history, which provided evidence that geochemical signatures in otoliths are reliable. Donohoe et al. (2008) later found the utility of otolith Sr/Ca values to predict steelhead maternal life history varied depending on the Sr/Ca in surface water and the length of time fish spent in fresh water before spawning. Similar variation has been observed with spring Chinook salmon (*Oncorhynchus tshawytscha*) and sockeye salmon (*Oncorhynchus nerka*) otoliths (Rieman et al. 1994; Bacon et al. 2004).

Further testing of steelhead with known maternal life histories would be needed to elucidate the potential bias caused by marine Sr depuration. In lieu of such data, the difference between Yakima

Table 4. Proportion of adult steelhead kelts collected in the Yakima Basin during 2010 and 2011 assigned to each of five geochemically distinct regions, and the proportion within each region derived from resident and anadromous females.

	Total	Resident	Anadromous
2010 (*n* = 275)			
Upper Naches	0.19 (0.15–0.24)	0.26 (0.14–0.38)	0.74 (0.62–0.86)
Lower Naches	0.38 (0.32–0.44)	0.21 (0.13–0.29)	0.79 (0.71–0.87)
Toppenish and Middle–Upper Yakima	0.32 (0.27–0.38)	0.19 (0.11–0.28)	0.81 (0.72–0.89)
Lower Yakima	0.03 (0.01–0.05)	0.38 (0.00–0.78)	0.62 (0.22–1.00)
Satus	0.08 (0.05–0.12)	0.17 (0.04–0.35)	0.83 (0.65–0.96)
2011 (*n* = 188)			
Upper Naches	0.19 (0.13–0.24)	0.03 (0.00–0.10)	0.97 (0.90–1.00)
Lower Naches	0.34 (0.27–0.40)	0.02 (0.00–0.05)	0.98 (0.95–1.00)
Toppenish and Middle–Upper Yakima	0.38 (0.30–0.44)	0.13 (0.05–0.23)	0.87 (0.77–0.95)
Lower Yakima	0.03 (0.01–0.05)	0.17 (0.00–0.67)	0.83 (0.33–1.00)
Satus	0.07 (0.04–0.12)	0.07 (0.00–0.23)	0.93 (0.77–1.00)

Note: Data are represented by median and 95% bootstrap confidence interval (reported in parentheses), comprising the 2.5 and 97.5 percentiles of observations.

steelhead otoliths with primordial core signatures indicative of anadromous and resident maternal life-history forms and the lack of otoliths with intermediate primordial core ^{87}Sr/^{86}Sr values provided some assurance that maternal assignments were accurate. The proportions of Yakima steelhead estimated to have resident maternal life histories were also similar to estimates from genetic parentage and breeding studies from other watersheds, which were not subject to these same potential biases (Thrower and Joyce 2004; Christie et al. 2011).

The maternal life history of middle Columbia River hatchery-origin steelhead with known anadromous maternal life histories were identified correctly based on comparisons of primordial core and freshwater rearing regions of the otolith. The primordial core ^{87}Sr/^{86}Sr values from hatchery steelhead differed from marine values by approximately 0.001, but these fish could not be used to adequately examine depuration rates because the freshwater ^{87}Sr/^{86}Sr values in the areas where hatchery fish were sampled exceeded marine values. Some hatchery summer steelhead spend a substantial amount of time maturing in fresh water before returning to collection facilities, which leads us to believe that they can be used to estimate depuration rates of marine Sr, if samples are collected appropriately, from regions where freshwater ^{87}Sr/^{86}Sr values are markedly less than marine values.

Two of the water samples collected in the lower Yakima River revealed ^{87}Sr/^{86}Sr values that exceeded marine values. ^{87}Sr/^{86}Sr values reported for the middle Columbia River main stem also exceed marine values (Miller et al. 2011). For this reason, the potential for bias in our dataset due to collection of potamodromous (freshwater migratory) rainbow trout from the lower Yakima River, or mainstem Columbia River, mistakenly identified as steelhead kelts, deserved careful consideration. The probability that potamodromous rainbow trout would have been collected in our kelt sample is presumed to be small because there is no evidence that this life history occurs in the lower Yakima River. *Oncorhynchus mykiss* are not abundant in the lower Yakima River, an area dominated by warm-water fish species (Patton et al. 1970; Fritts and Pearsons 2006), and rainbow trout greater than 350 mm have not been observed downstream of Prosser Dam (Karp et al. 2007; J. Hubble, US Bureau of Reclamation, unpublished data; A.L. Fritts, Washington Department of Fisheries and Wildlife, unpublished data). This is because the lower Yakima River does not provide suitable summer habitat for salmonids (Patton et al. 1970;

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Fritts and Pearsons 2006). Moreover, none of our otolith ^{87}Sr/^{86}Sr transects, which document the entire life history of each fish, revealed evidence of potamodromy.

Though we suspect it is unlikely that potamodromous rainbow trout migrate above Prosser Dam from the lower Yakima or Columbia rivers, if such a fish were mistakenly collected in our steelhead kelt sample, they would have been identified as anadromous maternal origin because the freshwater ^{87}Sr/^{86}Sr values from these regions mimic marine values. Therefore, our reported estimates of the proportion of steelhead with resident maternal life histories should, in that case, be regarded as conservative because of bias caused by freshwater migratory fish assumed to be steelhead and later assigned an anadromous maternal life history.

Regional assignments

While maternal life history of Yakima Basin steelhead could be predicted with reasonable confidence, predictions of their natal origins within geochemically distinct habitat areas were less certain. Geochemical differentiation between water samples collected throughout the basin was small, which made our analysis sensitive to perturbations in ^{87}Sr/^{86}Sr values within the freshwater rearing portion of the otolith used to predict each fish's natal origin. This resulted in higher uncertainty about regional assignments. Obtaining additional trace elements from water samples and otoliths would be useful for making more accurate assignments of steelhead to their natal habitat areas. For example, Muhlfeld et al. (2012) relied on both Sr/Ca and ^{87}Sr/^{86}Sr to predict movements of cutthroat trout between natal and non-natal streams.

Despite these uncertainties, proportional assignments of fish to different regions within the Yakima Basin aligned well with anecdotal information about the distribution of steelhead spawners and adult steelhead tracking data (C. Frederiksen, Yakama Nation Fisheries, unpublished data). For example, very few fish assigned to the lower Yakima River and large numbers of fish assigned to the Naches River, consistent with expected steelhead distribution in the basin. This suggested that large sample sizes used in our study may have overcome some of the bias caused by geochemical similarities between water sampling regions and variations in freshwater rearing ^{87}Sr/^{86}Sr values derived from otoliths. The Satus Creek region was the apparent exception. Only 8% of steelhead collected in both years assigned to Satus Creek, which was far less than expected. Our inability to accurately assign fish to Satus Creek was related to the large difference in observed ^{87}Sr/^{86}Sr values measured in the two Satus Creek water samples.

Steelhead with resident maternal life histories were predicted to occur in all five geochemically distinct regions evaluated in this study, with the highest numbers of resident-derived steelhead produced in the upper and lower Naches River subbasins and the region encompassing the Toppenish, middle Yakima, and upper Yakima subbasins. This provides some evidence that cross-life-history form production may be spatially structured such that areas with abundant resident trout produce larger numbers of steelhead with resident maternal life histories. There was also evidence for annual variation in cross-life-history form production, most notably in the Naches subbasin where rates were quite high in 2010 (21%–26%) and low in 2011 (2%–3%). Conversely, cross-life-history form production rates in the upper–middle Yakima and Toppenish Creek region remained relatively stable during both years (13%–19%).

Comparison with other sources of data

Rainbow trout populations with ocean access are typically found to be partially anadromous (Pascual et al. 2001; Docker and Heath 2003; Olsen et al. 2006). These findings are supported by evidence from throughout the Columbia Basin, including the Hood River (Christie et al. 2011), Grande Ronde River (J.R. Ruzycki, Oregon Department of Fish and Wildlife, unpublished data), Imnaha River (Berntson et al. 2011), Touchet River (Narum et al. 2004), and Yakima River (Pearsons et al. 2007). A study in the Deschutes River Basin indicated that of the 20 steelhead sampled, none had resident maternal life histories (Zimmerman and Reeves 2000), suggesting that there could be some rare cases where resident rainbow trout populations with ocean access do not produce anadromous offspring.

Reproductive exchange between different life-history forms appears to be an important component of partially anadromous fish population biology that likely has an important effect on viability of anadromous life-history forms, such as steelhead. Codependence of multiple life-history types makes salmonid populations more resilient (Bisson et al. 2009) and may explain their ability to persist despite detrimental impacts from numerous, compounding sources of mortality. In the same way that a small amount of immigration from source populations can dramatically reduce extinction risk of stream-resident trout (Hilderbrand 2003), a small amount of cross-life-history form production may substantially reduce the probability of steelhead extinction.

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