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Identification of Steelhead and Resident Rainbow Trout Progeny in the Deschutes River, Oregon, Revealed with Otolith Microchemistry

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Abstract.—Comparisons of strontium:calcium (Sr:Ca) ratios in otolith primordia and freshwater growth regions were used to identify the progeny of steelhead *Oncorhynchus mykiss* (anadromous rainbow trout) and resident rainbow trout in the Deschutes River, Oregon. We cultured progeny of known adult steelhead and resident rainbow trout to confirm the relationship between Sr:Ca ratios in otolith primordia and the life history of the maternal parent. The mean (±SD) Sr:Ca ratio was significantly higher in the otolith primordia of the progeny of steelhead (0.001461 ± 0.00029; $n = 100$) than in those of the progeny of resident rainbow trout (0.000829 ± 0.000012; $n = 100$). We used comparisons of Sr:Ca ratios in the primordia and first-summer growth regions of otoliths to determine the maternal origin of unknown *O. mykiss* juveniles ($n = 272$) collected from rearing habitats within the main-stem Deschutes River and tributary rearing habitats and thus to ascertain the relative proportion of each life history morph in each rearing habitat. Resident rainbow trout fry dominated the bimonthly samples collected from main-stem rearing habitats between May and November 1995. Steelhead fry dominated samples collected from below waterfalls on two tributaries in 1996 and 1998.

Rainbow trout *Oncorhynchus mykiss* is a polytypic species characterized by populations of resident, adfluvial, and fluvial rainbow trout and anadromous steelhead (Scott and Crossman 1973; Behnke 1992). Similar migratory polymorphism is observed in several other species of salmonids, including brown trout *Salmo trutta* (Skaala and Nævdal 1989), Atlantic salmon *S. salar* (Verspoor and Cole 1989), sockeye salmon *O. nerka* (Foote et al. 1989), coastal cutthroat trout *O. clarki clarki* (Trotter 1989), Arctic char *Salvelinus alpinus* (Nordeng 1983), and brook trout *S. fontinalis* (White 1940). Migratory polymorphism may result from phenotypic plasticity within a single gene pool or from fixed differences between sympatric but reproductively isolated populations. The relationships between alternative life history forms vary among species and locations. Nordeng (1983), for example, demonstrated through rearing studies that resident and migratory Arctic char were from the same gene pool and that migration was under environmental control. Reproductive isolation between life history morphs has been identified in some locations for Atlantic salmon (Verspoor and Cole 1989) and sockeye salmon and kokanee (lacustrine sockeye salmon; Taylor et al. 1996; Wood et al. 1999). Analysis of the maternal origin of adult resident rainbow trout and steelhead suggested that these life history forms are reproductively isolated in the Deschutes River, Oregon, because adult steelhead of resident origin and resident trout of steelhead origin were not observed (Zimmerman and Reeves 2000). This apparent reproductive isolation was reinforced through segregation in the timing and location of spawning between steelhead and resident rainbow trout (Zimmerman and Reeves 2000). Whether resident and anadromous forms constitute a single randomly mating gene pool or exhibit reproductive isolation between life history forms has significant implications for the study and management of these populations.

In locations where sympatric morphs are reproductively isolated and exhibit fixed differences in life history, the morphs have the potential to act as two separate biological species (Wood et al.

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1999). As a result, ecological studies and management of alternative life history morphs must account for this population structure. Accounting for such a structure when working with juvenile resident and anadromous salmonids is complicated by the inability to identify juveniles to life history morph owing to their identical morphology and appearance. Discrimination between anadromous and resident salmonids has been limited to adults (Kalish 1990). Various studies have attempted to differentiate juvenile resident rainbow trout and steelhead, with disappointing results. Rybock et al. (1975) distinguished steelhead from rainbow trout in the Deschutes River, Oregon, based on otolith nuclear dimensions, but a reexamination by Currens et al. (1988) suggested that the method was not reliable. Wood et al. (1999), however, were able to distinguish juvenile kokanee from sockeye salmon using genetic stock identification based on allele frequencies at two loci. In the absence of genetic methods or as an independent confirmation, otolith microchemistry can be used to identify the progeny of anadromous and resident salmonids (Kalish 1990; Rieman et al. 1994; Volk et al. 2000; Zimmerman and Reeves 2000).

Otolith microchemistry can be used to identify maternal origin through examination of the ratio of strontium (Sr) to calcium (Ca) within the otolith. Strontium, an element with binding characteristics similar to those of calcium, is substituted for calcium in the calcium carbonate matrix of the otolith at levels relative to the ratio of Sr to Ca in the environment (Kalish 1990). Since the ratio of Sr to Ca is generally greater in seawater than in freshwater, analysis of Sr:Ca ratios across the otolith of a fish can reveal the migrational history of that fish (Kalish 1990). Further, comparison of Sr:Ca ratios in the primordia and freshwater growth region can be used to determine maternal origin (resident or anadromous) on the assumption that the composition of the primordia reflects the environment in which the yolk precursors develop (in the ocean for anadromous forms) (Kalish 1990; Volk et al. 2000). This ability provides a powerful tool for studying the freshwater ecology of sympatric resident and anadromous salmonids.

In this study, we describe the use of otolith microchemistry to compare the relative proportions of juvenile resident rainbow trout and steelhead in rearing habitats within the Deschutes River. We first examined Sr:Ca ratios in the otolith primordia of known progeny from steelhead and resident rainbow trout to confirm the relationship between those ratios and life history. We then examined otoliths from unknown *O. mykiss* juveniles collected in rearing habitats in the main-stem Deschutes River and in two tributaries to determine the relative proportions of steelhead and resident rainbow trout progeny.

Methods

Site description.—The Deschutes River, a Columbia River tributary located in northcentral Oregon, drains a watershed of approximately 27,200 km^2 (Figure 1). Although most of the Deschutes River lies in an arid region, the western portion is primarily spring fed and mean monthly discharge near its confluence with the Columbia River ranges from 124 m^2/s in August to 212 m^2/s in February (1957–1997 U.S. Geological Survey data; Hubbard et al. 1999). There are only four perennial tributaries along the lower 160 km of the river, along with many intermittent tributaries.

Main-stem rearing sites were located in the 21 km of main-stem river between the Pelton Reregulating Dam at river km 160 (measuring from the confluence of the Deschutes and Columbia rivers) and the Trout Creek campground at river km 139 (Figure 1). In addition to these sites, we focused on rearing sites in two tributaries of the Deschutes River. Tenmile Creek is a tributary of Trout Creek that encompasses a watershed of 5.7 km^2 (Figure 1). The steam is approximately 18 km long. A falls consisting of three plunge pools separated by several steep drops is located approximately 2 km upstream from the confluence with Trout Creek. Although the falls have been modified to allow passage of fish, passage is dependent on flow conditions, which may not occur in all years. Several portions of the stream are intermittent, including the lower 200 m. Summer water temperatures in Tenmile Creek ranged from 18°C to 24°C during the study. Nena Creek is a tributary of the Deschutes River located 93 river km upstream from the confluence of the Deschutes and Columbia rivers. The Nena Creek basin encompasses 11.5 km^2, and the stream is approximately 20 km long (Figure 1). Like Tenmile Creek, the lower portion of Nena Creek is intermittent. A small waterfall approximately 1 km upstream from the confluence with the Deschutes River prevents upstream migration.

Validation with known samples.—To confirm the relationship between life history (maternal origin) and Sr:Ca ratios in otolith primordia, we spawned and reared fry from both adult steelhead and resident rainbow trout. The experimental fish were the progeny of wild steelhead (four females and

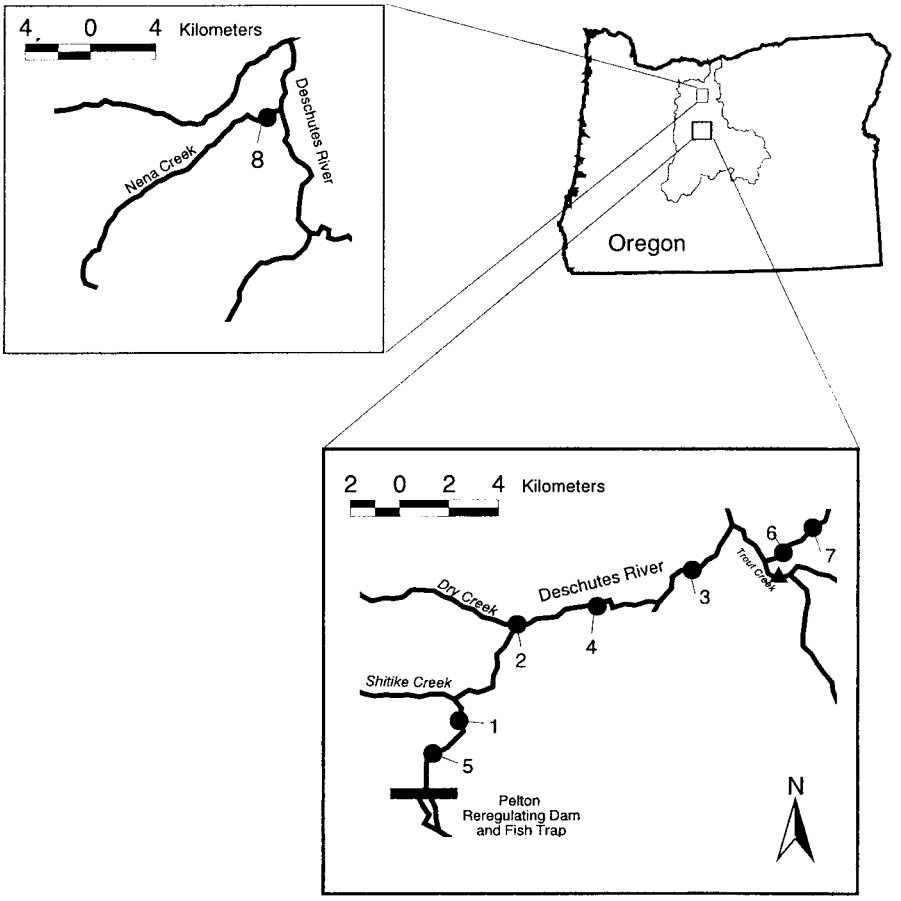

FIGURE 1.—Location of sampling sites in or near the Deschutes River, Oregon. Sites are designated as follows: 1–5 = main-stem sites, 6 = Tenmile Creek below the falls, 7 = Tenmile Creek above the falls, and 8 = Nena Creek.

four males) and resident rainbow trout (two females and six males) collected at the Pelton fish trap. Adult steelhead and resident rainbow trout were initially identified based on coloration, body shape, and size. The steelhead were larger and more fusiform and had less spotting than the resident rainbow trout. In the Deschutes River, adult steelhead range in length from 48 to 80 cm, with more than 90% of the population being longer than 54 cm (Olsen et al. 1994). Adult resident rainbow trout range in length from 16 to 50 cm, with more than 70% of the population between 20 and 35 cm (Schroeder and Smith 1989). To confirm field identification based on the above criteria, otoliths from the broodfish were analyzed according to the methods of Zimmerman and Reeves (2000). Each steelhead was characterized by ocean growth based on otolith growth rates and elevated Sr:Ca ratios in these regions. Neither increased otolith growth rates nor elevated Sr:Ca ratios across otolith life history scans characterized the resident rainbow trout.

Eggs and milt were transported 17 km upstream to the Round Butte Hatchery in plastic bags, mixed, treated with iodine, and placed in incubation trays according to standard hatchery procedures. The eggs of steelhead and resident rainbow trout were incubated in separate trays within the same rack, so that incubation conditions were identical. When the fry reached a size corresponding to emergence size we haphazardly selected and killed 20 steelhead and 20 resident rainbow trout fry with an overdose of anesthetic. The remaining fry were part of another experiment that will be reported elsewhere. We removed sagittal otoliths and stored them in dry vials to await preparation and microchemical analysis.

Juvenile sampling.—We collected unknown ju-

TABLE 1. Mean (±SD) fork length and weight of steelhead and resident rainbow trout collected for analysis of the Sr:Ca ratios of otoliths in main-stream (M) and tributary (T) habitats in the Deschutes River, Oregon, along with the proportion of steelhead. See Figure 1 for an explanation of the location codes.

Date	Location	Habitat	Age-class	*N*	Length (mm)	Weight (g)	Proportion steelhead
30 May 1995	1	M	1	10	103 ± 16	15.8 ± 9.0	0
27 Jun 1995	2	M	0	23	31 ± 5	0.2 ± 0.1	0
28 Jul 1995	3	M	1	10	132 ± 18	34.0 ± 15	0.1
			0	61	41 ± 1	0.8 ± 1.1	0
25 Sep 1995	4	M	1	10	137 ± 32	39.0 ± 25	0.1
			0	41	51 ± 13	1.6 ± 1.5	0
29 Nov 1995	5	M	1	10	115 ± 30	18.8 ± 14.6	0
			0	48	60 ± 14	2.6 ± 1.6	0
2 Jun 1996	6	T	0	7	38 ± 3	0.4 ± 0.1	1.0
24 Apr 1998	7	T	2	5	153 ± 18	27.8 ± 8.0	0
28 Oct 1998		T	0	10	86 ± 10	6.5 ± 1.8	0
12 Jun 1998	6	T	0	3	37 ± 2	0.32 ± 0.1	1.0
10 Jul 1998		T	0	10	69 ± 8	3.3 ± 1.1	0.9
28 Oct 1998		T	0	5	79 ± 7	4.9 ± 1.1	1.0
10 Jul 1998	8	T	0	9	73 ± 9	2.7 ± 1.3	1.0

venile *O. mykiss* from rearing habitats in the mainstem Deschutes River by electrofishing in May, July, September, and November of 1995. Juvenile rearing habitats included edge habitat and side channels. Snorkel surveys indicated that these habitats were the primary rearing habitats for juvenile *O. mykiss*. Nine side channels were identified as rearing habitats within the study reach based on these surveys. One side channel was randomly selected by a drawing in each collection period, and 10 age-1 and all young-of-year *O. mykiss* were collected for otolith analysis. We measured (fork length) and weighed each of these fish, removed their sagittal otoliths, and preserved them in alcohol. No side channel was sampled more than once so that the composition of juveniles would represent the natural mixture of steelhead and resident rainbow trout progeny. An additional collection was done on 27 June 1995, the first week of emergence of steelhead and resident rainbow trout as determined by direct observation using mask and snorkel and emergence trapping (C. E. Zimmerman, unpublished data).

In 1996 and 1998, we collected unknown juvenile *O. mykiss* from below and above Tenmile Creek falls and from the lowermost 200 m of Nena Creek (Table 1). During each survey, we collected up to 70% of the juveniles present within a 200-m length of stream. We measured (fork length) and weighed each of these fish, removed their sagittal otoliths, and preserved them in alcohol. Each fish was aged by examination of otolith banding patterns.

Otolith preparation and microchemical analysis.—Otolith preparation and analysis of microchemistry followed the methods of Zimmerman and Reeves (2000). With the otoliths from the known steelhead and resident rainbow trout fry, five primordia were sampled in each fish so that 100 points were sampled in primordia of each life history morph. With the otoliths collected from fish in the wild, all primordia and an equal number of points along a transect in the first summer of growth and outside the nucleus were sampled. A fish was determined to be of anadromous maternal origin if the mean Sr:Ca ratio in the primordia was significantly higher than that in the first-summer growth region based on an unpaired one-tailed *t*-test with $\alpha = 0.05$. Based on these results, each fish was classified as the progeny of steelhead or resident rainbow trout.

Results

The distribution of the Sr:Ca ratios measured in five primordia in the sagittae of 20 steelhead fry and 20 resident rainbow trout fry ($n = 100$ sample points in each case) did not show any overlap. The Sr:Ca ratios in the 100 primordia from steelhead fry ranged from 0.001055 to 0.002607, with a mean (±SD) of 0.001461 ± 0.00029; those in the 100 primordia from resident rainbow trout fry ranged from 0.000547 to 0.000972, with a mean of 0.000829 ± 0.00012. These mean ratios were significantly different (unpaired two-tailed *t*-test: $t = 20.20$, $P < 0.0001$).

In all, 272 juvenile *O. mykiss* were collected from rearing habitats in 1995, 1996, and 1998 (Table 1). Of these fish, 35 were determined to be the progeny of anadromous females (steelhead) because the mean Sr:Ca ratios were significantly

higher in their primordia than in their first-summer growth regions (unpaired one-tailed *t*-test for each fish; all $P < 0.01$). The remaining 237 fish were determined to be the progeny of resident females because the mean Sr:Ca ratios were not significantly higher in their primordia than in their first-summer growth regions (unpaired one-tailed *t*-test for each fish; all $P > 0.05$). The frequency distributions of the Sr:Ca ratios in primordia and first-summer growth regions were either unimodal or bimodal with little overlap (Figure 2). In 223 fish collected from main-stem rearing habitats, the Sr:Ca ratios in primordia ($n = 1,759$) and first-summer growth regions ($n = 1,973$) overlapped, with a small number of higher Sr:Ca ratios in primordia corresponding to the two yearling steelhead progeny in that collection (Figure 2A). The Sr:Ca ratios in the primordia ($n = 181$) and first-summer growth regions ($n = 205$) of the otoliths from 25 juveniles collected from below the falls on Tenmile Creek were bimodal and did not overlap except for the few low Sr:Ca ratios in primordia associated with the single progeny of resident rainbow trout in the collection (Figure 2B). Similarly, the Sr:Ca ratios in the primordia ($n = 63$) and first-summer growth regions ($n = 70$) of the otoliths from 9 juveniles collected from lower Nena Creek were bimodal and not overlapping (Figure 2D). In contrast, the Sr:Ca ratios in the primordia ($n = 99$) and the first-summer growth regions ($n = 99$) of otoliths from 15 juveniles collected above the falls on Tenmile Creek were low (<0.0012) and unimodal, indicating that no steelhead progeny were present in that sample (Figure 2C).

The progeny of steelhead and resident rainbow trout were not equally divided among samples (Table 1). Main-stem Deschutes River samples contained only two steelhead juveniles in a total sample of 223 fish (Table 1). In contrast, only one progeny of resident rainbow trout was found in a sample of 34 juveniles collected from the lower reaches of Tenmile Creek and Nena Creek (Table 1). All juveniles collected upstream of the falls on Tenmile Creek were the progeny of resident rainbow trout (Table 1).

Discussion

Comparison of the Sr:Ca ratios in the primordia and freshwater growth regions of otoliths is an appropriate method for determining the maternal origin of steelhead and resident rainbow trout juveniles in the Deschutes River and provides an important tool for the study of the freshwater ecology of sympatric steelhead and resident rainbow trout. Through analysis of fry from known matings of steelhead and resident rainbow trout, we confirmed that the Sr:Ca ratios within the primordia of steelhead progeny are greater than those in the progeny of resident rainbow trout. Volk et al. (2000) found similar results when they examined the Sr:Ca ratios in the core or primordia regions of otoliths from fish produced by experimental matings of coho salmon *O. kisutch* and sockeye salmon. The mean Sr:Ca ratio in the core region of the progeny of captive coho salmon broodstock was 0.00042 ± 0.00011, compared with 0.00180 ± 0.00023 for the progeny of coho salmon that had migrated to the ocean (Volk et al. 2000). Similarly, the mean Sr:Ca ratio was 0.00044 ± 0.00007 in the core of the progeny of kokanee and 0.0021 ± 0.00031 in those of sockeye salmon (Volk et al. 2000). Kalish (1990) reported mean Sr:Ca ratios in primordia of sea-farmed (0.00313 ± 0.00068) and freshwater (0.00114 ± 0.00024) rainbow trout progeny. The differences among studies reflect analytical differences and variation in ambient Sr:Ca ratios among locations.

High ambient Sr:Ca ratios in some freshwater environments can confound identification of maternal origin based on these ratios (Rieman et al. 1994). As a result, Rieman et al. (1994) suggest including water chemistry data in studies of otolith microchemistry. In 13 quarterly samples collected between April 1983 and June 1986, the Sr:Ca ratios of river water in the main-stem Deschutes River ranged from 0.0016 to 0.0030 (Alexander et al. 1996). By contrast, Rieman et al. (1994) reported a Sr:Ca ratio of 0.0061 at Alturas Lake, Idaho, which precluded using Sr:Ca ratios to identify maternal origin at that location. We assumed ratios of 0.008643–0.00874 in the ocean based on the data of Bruland (1983) and Nozaki (1997). Thus, the Sr:Ca ratio within the main-stem Deschutes River appears to be low enough to allow the use of otolith microchemistry to determine maternal origin. We do not have data for Tenmile and Nena creeks, but analysis of the Sr:Ca ratios across the otoliths of fish from these streams showed that they were low and similar to that expected from fish in environments with a low Sr:Ca ratio. If the Sr:Ca ratio had been too high within these streams to allow identification of maternal origin based on the value in the primordia, the high ratio would have been evident in the life history scans (across the otoliths) of fish from these streams.

Our initial survey of main-stem rearing sites in 1995 was intended to examine the proportion of steelhead and resident rainbow trout progeny in

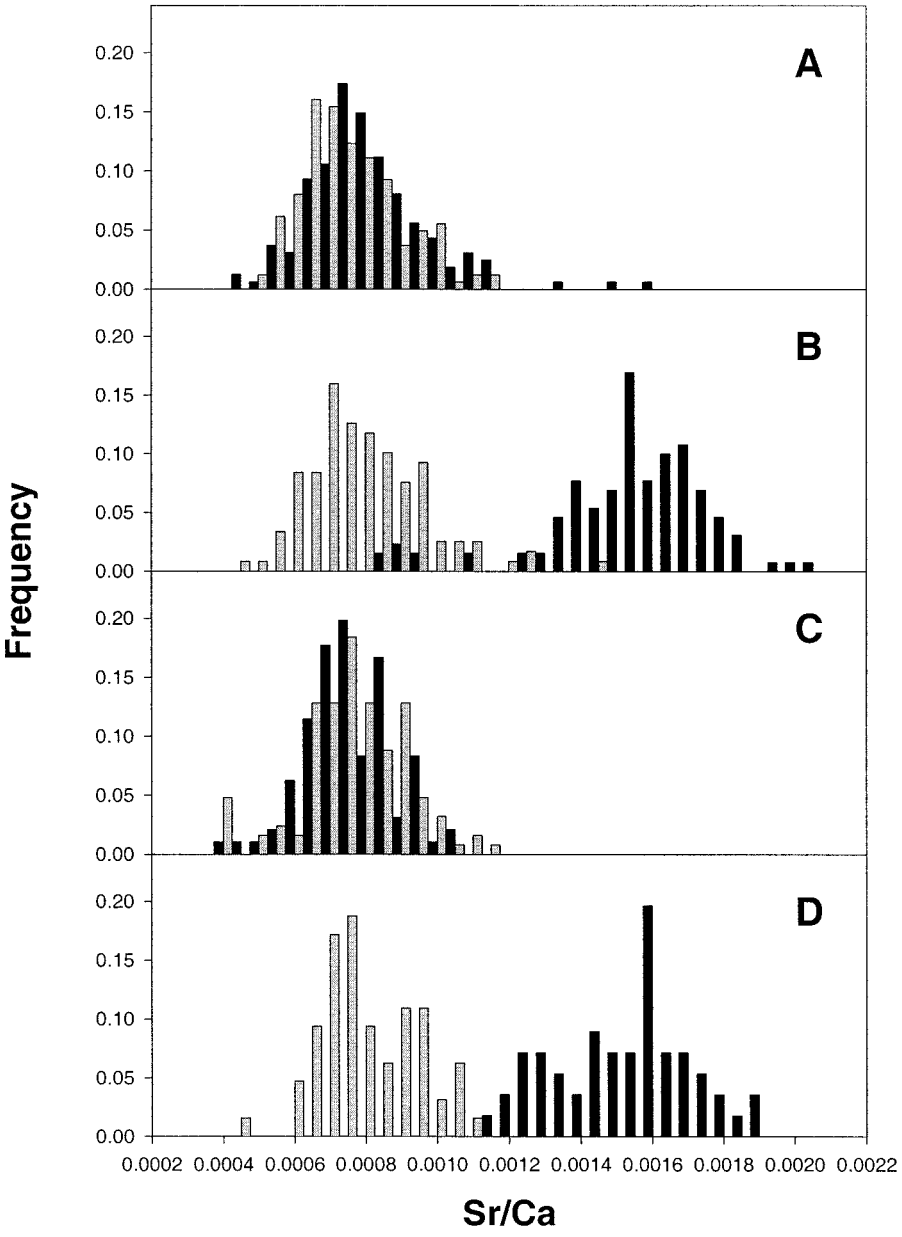

FIGURE 2.—Distribution of Sr:Ca ratios in the primordia (black bars) and first-summer growth regions (gray bars) of otoliths of juvenile steelhead and resident rainbow trout collected from **(A)** the main-stem Deschutes River, **(B)** Tenmile Creek below the falls, **(C)** Tenmile Creek above the falls, and **(D)** Nena Creek.

rearing habitats over time. The lack of steelhead progeny in the 1995 sample motivated our sampling efforts in tributary habitats in later years. Because we did not sample tributary and main-stem habitats simultaneously, we are unable to draw conclusions concerning the relative importance of these habitats to steelhead and resident rainbow trout. It appears from our data, however, that steelhead and resident rainbow trout juveniles are not equally distributed among rearing habitats and that further work concerning the importance of intermittent tributaries to steelhead in the Deschutes River is warranted. Everest (1973), for example, reported that many tributaries of the Rogue

River, Oregon, were utilized by spawning steelhead in winter but were completely dry by summer. Similarly, Erman and Hawthorne (1976) reported disproportionate use by rainbow trout of an intermittent tributary in a High Sierra stream in California. Use of this tributary was related to earlier peak flows resulting from snow melt and a lack of competing brook trout. The downstream movement of fry was highly correlated with discharge, and large numbers of fry emigrated from the stream before it was dry (Erman and Leidy 1975).

The distribution of spawning by steelhead and resident rainbow trout may play an important role in the distribution of juveniles of each life history form. Wood et al. (1999) examined diet and competition between progeny of reproductively isolated and genetically distinct sockeye salmon and kokanee in Takla Lake, British Columbia. Sockeye salmon progeny were predominant in one arm of the lake and kokanee progeny were predominant in another arm; this pattern was attributed to the distribution of spawning adults. From 1996 through 1998, we conducted monthly spawning surveys of Tenmile Creek. The total number of steelhead redds encountered was 7, 2, and 2 in the three years, respectively. No resident rainbow trout redds or adult resident rainbow trout were observed in the lower 4.5 km of Tenmile Creek in any of the years studied. Steelhead spawning in Tenmile Creek was restricted to the area downstream of the falls. In 1998, both steelhead redds were located in the lowermost 150 m of the stream. Steelhead carcasses were observed in 1996 and were associated with a redd just below the falls. A basinwide survey examining the life history of juvenile *O. mykiss* through analysis of otolith microchemistry would aid in determining the distribution of streams used by spawning steelhead.

We have demonstrated the potential use of otolith microchemistry to identify the maternal origin of juvenile *O. mykiss* among sites within a watershed. Owing to the relatively small sample sizes within the main-stem Deschutes River and the sampling of tributaries in different years, we are unable to make direct comparisons of tributary and main-stem habitat use. We have, however, demonstrated that the method is useful in the ecological study of sympatric life history morphs. Most studies using the Sr:Ca ratios in the otoliths of salmonids have focused on migration between freshwater and salt water (e.g., Radtke 1995) or the identification of mixed populations of migratory and nonmigratory individuals (e.g., Howland et al. 2001). Using this method to determine maternal origin has the potential to substantially improve our understanding of the juvenile freshwater ecology of sympatric life history morphs.

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