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[Article]

Use of Otolith Chemistry and Radiotelemetry to Determine Age-Specific Migratory Patterns of Anadromous Bull Trout in the Hoh River, Washington

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Abstract.—The complementary use of otolith chemistry and radiotelemetry demonstrates that bull trout *Salvelinus confluentus* from the Hoh River, Washington, exhibit considerable life history variability. Adult bull trout lived exclusively in the river, inhabited freshwater for prolonged periods and later became anadromous, or were anadromous and made multiple migrations between freshwater and salt water. Twenty of 40 radio-tagged juvenile bull trout emigrated to the ocean at lengths ranging from 243 to 360 mm (mean, 287 mm), which is the first published verification of anadromy at this life history stage. Otolith chemistry analyses of 105 bull trout that were incidentally killed in commercial gill-net fisheries revealed that 85% had migrated from freshwater to the sea at least once and that 75% had migrated multiple times. Anadromous females produced 95% of all individuals examined, but both anadromous and nonanadromous females produced progeny that were anadromous. Age at first seaward migration ranged from 3 to 6 years, 88% first emigrating to sea in their third or fourth growth year. For ages 3 and 4, anadromous individuals were larger than those that remained in freshwater. A wide size range (287–760 mm, 0.2–4.9 kg) of bull trout were killed in commercial fisheries; ages 3–5 composed 88% of the total bycatch. Relocation data from radio-tagged juvenile and adult bull trout provided important insights on anadromous movements that helped to validate inferences drawn from widely oscillating strontium levels in otolith chemistry. In view of the direct mortality in gill-net fisheries, an understanding of the age-specific movements and life history variability of anadromous bull trout will be crucial to future conservation efforts, which should focus on improved monitoring of recreational and commercial bycatch in Pacific salmon fisheries.

Pacific salmonids are known to exhibit a high degree of life history variability, which arguably is most evident in the genus *Salvelinus* (Jonsson et al. 1988; Nelson et al. 2002). Arctic char *S. alpinus*, brook trout *S. fontinalis*, Dolly Varden *S. malma*, and whitespotted char *S. leucomaenis* are all known to be anadromous and exhibit irregular periods of freshwater and marine residence (Randall et al. 1987; Arai and Morita 2005). The anadromous form of bull trout *S. confluentus* is generally unrecognized in the published literature, despite numerous populations that have direct access to the Pacific Ocean along western North America.

A recent study verified anadromy as a primary life history form in coastal bull trout and revealed that adult (>400-mm) bull trout inhabit a diverse range of freshwater, estuarine, and marine habitats (Brenkman and Corbett 2005). The use of radiotelemetry provided an understanding of the timing and spatial extent of anadromous bull trout movements along coastal Washington, and determined that adults inhabited five coastal estuaries up to 47 km south of their original tagging locations (Brenkman and Corbett 2005). The sampling design in that study focused on bull trout larger than 400 mm and did not include information on movements of juvenile bull trout that may emigrate to the ocean. No information has been published on movements of juvenile bull trout from anadromous populations, and knowledge of their movements is restricted to investigations of potamodromous populations (Thurow 1997; Bonneau and Scarnecchia 1998; and Muhlfeld et al. 2003).

Recognition of anadromy in bull trout of the Hoh River, Washington, raises important population questions about age-specific movements between freshwater and marine habitats, such as age and size at first seaward migration and the frequency of migrations over an individual life span. Although telemetry studies provide key insights from documented individual movements, they cannot provide complete life history information because pretagging life history is un-

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known. Telemetry studies are also very expensive, and meaningful data may require years of effort. Another approach is the use of strontium abundance patterns in otoliths to retrospectively view individual past migrations between freshwater and seawater and to link these migratory events to fish age via the record of annual markers in otoliths.

A number of studies have recapitulated individual migratory histories for diadromous fish species using Sr/Ca profiles in otoliths. The species studied include sockeye salmon *Oncorhynchus nerka* (Rieman et al. 1994), Japanese eel *Anguilla japonica* (Tzeng and Tsai 1994; Otake et al. 1994), American shad *Alosa sapidissima* (Limburg 1995), Arctic char (Radtke et al. 1996), striped bass *Morone saxatilis* (Secor and Piccoli 1996), and whitespotted char (Zimmerman et al. 2003; Arai and Morita 2005). These profiles are based on typically higher strontium levels in marine environments compared with those generally found in freshwater habitats (Rosenthal et al. 1970; Kalish 1990). Although a number of factors may influence incorporation of strontium into fish otoliths besides environmental concentrations (see Campana 2005; Bath Martin et al. 2004), the strong relationship between water and otolith Sr/Ca values is well recognized (Bath et al. 2000; Schroder et al. 1995; Zimmerman 2005), and where fish migrate through disparate salinities, the transition is often clearly depicted in otolith strontium profiles. Otolith core strontium may also effectively discriminate between the progeny of anadromous or freshwater resident female salmonids based on marine strontium values passed on to developing embryonic otoliths by maternal parents (Kalish 1990; Rieman et al. 1994; Volk et al. 2000).

The analysis of otoliths from Hoh River bull trout that were incidentally killed in legal gill-net fisheries directed at other Pacific salmonids represented a unique opportunity to study life histories because lethal sampling of federally threatened bull trout is typically precluded. Complementary studies using radiotelemetry and otolith chemistry offer a means to provide detailed information on age-specific migrations of bull trout among the Hoh River, Pacific Ocean, and coastal Washington. Information obtained from radio-tracking of juvenile anadromous bull trout and new relocation data on adult bull trout attained since Brenkman and Corbett (2005) provide important insights that help to validate inferences drawn from otolith chemistry.

The primary objectives of this research were to (1) determine the movements and extent of anadromy in radio-tagged juvenile bull trout and provide examples of movements of radio-tagged adults that support inferences drawn from otolith chemistry, (2) use otolith chemistry to determine the extent of anadromous individuals, age at first seaward migration, and frequency of movements to salt water throughout the life history of individual fish captured in gill nets, (3) determine whether maternal parents of individual fish were anadromous or nonanadromous, and (4) develop a general model of the life history patterns of anadromous bull trout in the Hoh River. We also discuss conservation implications associated with bull trout encounters in commercial gill-net fisheries in the Hoh River.

Study Area

This study was primarily focused on Washington State's Hoh and South Fork Hoh rivers and Kalaloch Creek but also included the lower Queets, Raft, and Quinault rivers and related nearshore waters of the Pacific Ocean (Figure 1). Most of the upper watersheds in the study area occur within Olympic National Park and are managed as a natural area by the U.S. National Park Service. The Hoh River basin drains 894 km^2 and is a glacially influenced river located on the western slopes of the Olympic Mountains in Washington State. The river flows 91 km from glaciers and ice fields on the slopes of Mount Olympus and descends 1,216 m in elevation to its confluence with the Pacific Ocean. Anadromous salmonids have access to at least 84 river kilometers (rkm) below the headwaters of the Hoh River. The South Fork Hoh, the major tributary to the Hoh River, drains 130 km^2 and flows westward until it joins the main stem Hoh at rkm 49. The Hoh Basin has a maritime climate and receives an annual mean precipitation of 358 cm, most of which occurs from November to April. The annual median daily flow of the Hoh River is 51 cm/s and mean daily flow is 71 cm/s (England 2003). Kalaloch Creek is located 17 km south of the Hoh River, drains 45 km^2, and descends in elevation from 320 m to its confluence to the Pacific Ocean.

The Hoh River provides a popular sport fishery for Pacific salmonids and supports self-sustaining populations of coho salmon *O. kisutch*, spring–summer and fall Chinook salmon *O. tshawytscha*, chum salmon *O. keta*, summer and winter steelhead *O. mykiss*, and cutthroat trout *O. clarkii*. The Hoh River offers diverse fishing opportunities: bait fishing in the lower river, single barbless hooks and artificial lures in the middle river, and fly-fishing only in the upper portions of the river in Olympic National Park. In 1994, the National Park Service and Washington Department of Fish and Wildlife implemented catch-and-release regulations for bull trout caught in recreational fisheries. Gill-net fisheries exist for steelhead and Chinook and coho salmon in the lower Hoh River outside Olympic

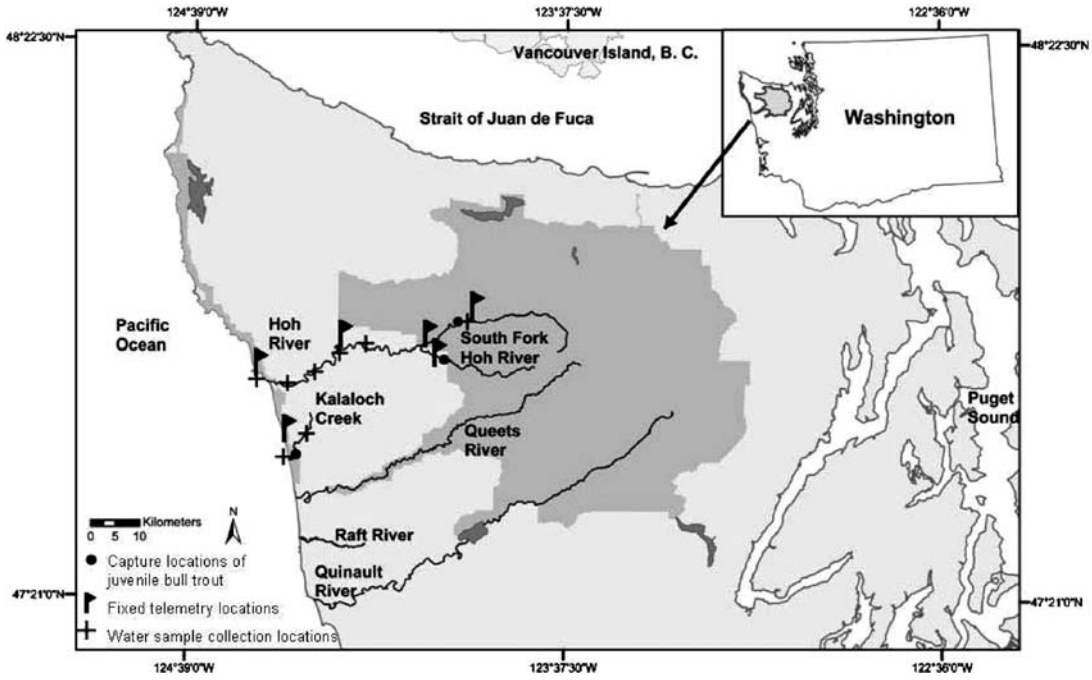

FIGURE 1.—Map of the coastal Washington study area showing the locations where 40 juvenile bull trout were tagged and the locations of six fixed telemetry stations and seven water chemistry collection sites.

National Park during most weeks of the year (Brenkman and Corbett 2005).

Methods

Radiotelemetry.—The radiotelemetry portion of the study was designed to track the movements of juvenile (<360-mm) bull trout fitted with individually coded radio transmitters. Surgical procedures and tracking and relocation of all radio-tagged fish was accomplished using fixed telemetry stations, mobile tracking, and aircraft (as presented in Brenkman and Corbett 2005). We examined movements of juvenile bull trout from September 2004 to January 2005. A total of 40 juvenile bull trout were captured by angling with spinners and single barbless hooks and were surgically implanted with radio transmitters (NTC-6–2, Lotek Wireless) in the Hoh River (rkm 56), South Fork Hoh River (rkm 3), and Kalaloch Creek (rkm 0.5) (Figure 1). Captured bull trout were anesthetized in 80 mg/L solution of tricaine methanesulfonate for up to 7 min, measured for total length (mm), and weighed (g). Each transmitter was tested for functionality before being inserted into the peritoneal cavity similar to procedures described by Ross and Kleiner (1982). Radio transmitters for juveniles were active for up to 414 d, weighed 4.5 g in air, and were always less than 5% of fish weight (averaged 2%). We also present new relocation and movement data from three radio-tagged adult bull trout that illustrate patterns observed from the analysis of otolith chemistry in gill-net captured specimens.

Age determinations.—We analyzed otolith chemistry and determined age for 105 bull trout that were incidentally killed in legal gill-net fisheries directed at Chinook salmon and winter steelhead in the Hoh River (rkm 0 to rkm 22) from January to June 2002. Analyzed specimens were not a representative population sample from the basin because bull trout were primarily killed in the lower portions of the river by size-selective gear. Gill-net mesh sizes ranged from 10 to 20 cm. Age determinations were made from each whole otolith before sectioning. Dry otoliths were immersed in tap water, and dark appearing annuli were counted using transmitted light microscopy. Each otolith was sectioned by abrasive grinding and polishing on a rotating lap wheel according to established procedures in the Washington Department of Fish and Wildlife otolith laboratory (Figure 2). The resulting preparation produced a flat, polished sagittal section of the otolith that included the entire life history of the fish from the core to the margin of the otolith. A preferred transect for chemical and structural measurements was selected along a posteroventral axis running from the core to the otolith margin at the corner of the otolith. This axis provided the most consistently clear

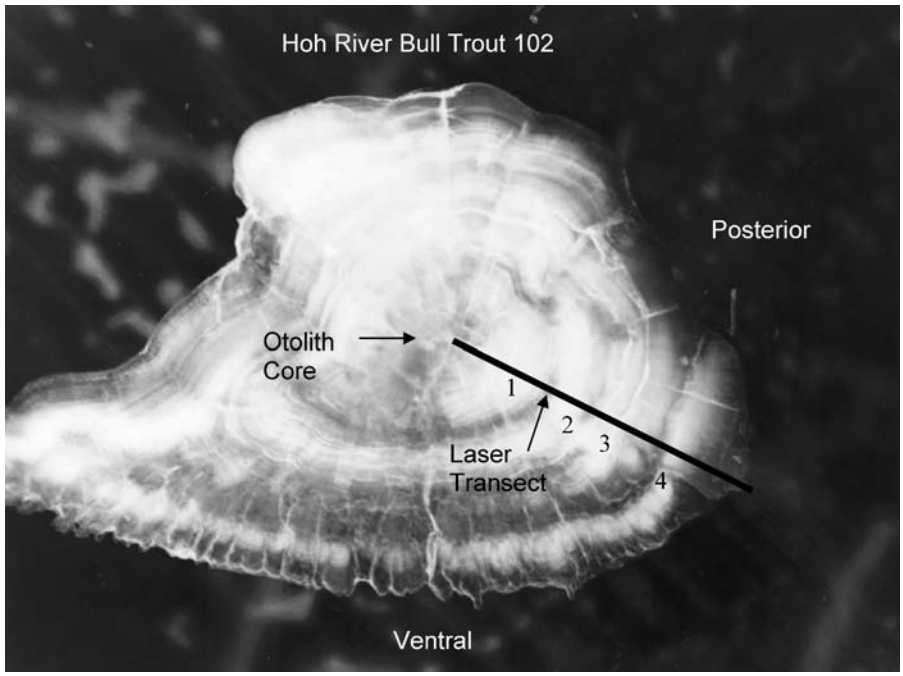

FIGURE 2.—Image of a Hoh River, Washington, bull trout otolith that depicts the analytical transect and locations of annuli (1–4).

and uninterrupted view of otolith microstructure from core to edge.

Using a combination of reflected and transmitted light, we identified annuli as thin, translucent otolith zones (see Secor et al. 1995; glossary), which appear as darker regions (Figure 2). These zones are generally thought to represent annual slower growth periods in temperate fishes (Beckman and Wilson 1995) and are commonly interpreted as age in years. Measurements from the core of otoliths to each of these annuli were made using image analysis software on digital images of the sectioned otoliths.

Chemical data were linked to age for individual fish by noting the position of strontium changes relative to annuli locations. When a specific chemical event was tied to age, that age is the previous annulus number (i.e., young of the year would be age zero). In some cases ($N = 14$), we were unable to clearly recognize all annuli in otolith sections and some annuli positions were estimated using the population mean for each annulus.

Water chemistry.—To verify low Sr/Ca values in freshwater, water samples were collected from several sites along the main stem of the Hoh River, South Fork Hoh River, and Kalaloch Creek (Figure 1). We did not use water and otolith chemistry to examine river-specific associations. Water samples were filtered through sterile 0.45-μm membrane filters, then acidified (to a pH <2) with quartz distilled nitric acid. Samples were diluted 1 mL to 6 mL with 1% quartz distilled nitric acid. Concentrations of calcium and strontium were measured using a Prodigy inductively coupled plasma-optical emission spectrometer in radial view. Concentrations were calculated from the emission intensities, and the intensities of standard solutions. Accuracy of the method was verified by running a National Institute of Standards and Technology (NIST) freshwater certified reference material (NIST 1643c).

Otolith chemistry.—Ninety-five specimens collected near the Hoh River mouth were chemically analyzed. All sectioned specimens were analyzed at the Keck Collaboratory for Plasma Mass Spectrometry at Oregon State University. The laser ablation system consists of a New Wave DUV 193-nm ArF laser coupled to a Thermal Elemental PQ Excell quadropole inductively coupled plasma mass spectrometer. The sample chamber has a continuous flow of helium gas that carried the ablated material through vinyl tubing to the mass spectrometer. Analytical transects were conducted from a point near the otolith core to a point beyond the margin of the otolith along the preferred ventro-posterior radius (Figure 2). Each otolith analysis was paired with an analytical transect on a polished sample

of NIST 612 glass standard. Laser transects were conducted at a pulse rate of 8 Hz and beam diameter of 30 μm. Time-resolved data were examined visually following each analysis, and element integrated counts per second at a particular location on the otolith transect were used to calculate element concentrations following Longerich et al. (1996) as outlined by Russo (2001). We used a mean calcium concentration (38.3%) from nearly 500 microprobe analyses on bull trout from the nearby Queets and Quinault rivers, Washington (E.C.V., unpublished report) as an internal standard. The Sr/Ca values are recorded as atomic ratios.

For strontium profiles, we visually marked the positions of all count rate peaks as well as the beginning and end of each transect. Age at first seaward migration was marked as the inflection point where Sr values steeply rose to the first peak. Once the location of any of these points of interest was recognized on raw count plots, we noted the time in the analytical transect where they occurred and determined their position on the otolith by multiplying elapsed time by 5 μm, the speed of the ablating laser. For each specimen, we calculated Sr/Ca values at each count rate peak in the plot as well as for the early plateau of relatively low count rates during juvenile life history, which provided us with a benchmark of Sr/Ca values experienced by fish living in freshwater. Subsequent peak values were compared against the range of values recorded in this region. Those that exceeded that range were assumed to represent contact with water characterized by elevated Sr/Ca values. Determining whether adjacent peaks represented separate migratory events was subjective and based upon discernable separation of the peaks by large decreases (at most, half of the surrounding peak values) in Sr/Ca values. Where strontium concentrations were significantly higher in the otolith core than periods of known freshwater residency, we inferred that maternal parents were probably anadromous.

Results

Movements of Radio-Tagged Bull Trout

Typical movements of radio-tagged adult bull trout included exclusive residence in the Hoh River (i.e., no migration to marine habitats), a single migration to the ocean after a prolonged freshwater residence, and multiple movements between freshwater and salt water along coastal Washington (Figure 3, right panel). One adult bull trout exhibited a fluvial life history form in the Hoh River for 18 months, including two complete in-river migrations and subsequent emigration to the ocean (Figure 3, right and middle panels).

Radio-tagged juvenile bull trout averaged 287 mm in total length (range, 205–360 mm) and 0.44 kg (0.29–0.65 kg) in weight. Twenty of 40 juveniles moved from freshwater to the ocean (Figure 4, upper panel), and 20 fish remained in the river during their tracking history. Anadromous juveniles that emigrated from the Hoh basin to the ocean were 243–360 mm in total length at time of tagging, and entered the ocean from September to December. Juveniles emigrated from the river to the ocean at a mean rate of 3.4 km/d (SD = 2.7, range = 0.7–7.4 km/d) and entered the ocean up to 86 d after tagging (Figure 4, lower panel). Three juveniles tagged in the Hoh River were relocated in January 2005 in freshwaters other than the Hoh River: one in Kalaloch Creek, one in the Queets River, and one in the Quinault River (Figure 4). Sixteen juvenile fish entered the ocean and were not relocated. Juveniles that were tagged in Kalaloch Creek emigrated to the ocean in February and March, and one fish was relocated in the Queets River (Figure 4).

Age Determinations

The bull trout killed in gill nets averaged 559 mm in length, ranging from 287 mm (0.2 kg) to 760 mm (4.9 kg). There was no significant difference (*t*-test, $P > 0.05$) in mean size at age for males or females (Table 1). Among 105 bull trout captured in the Hoh River net fishery, whole otolith age determinations ranged from ages 3 to 7, age 4 predominating (69%). There were discrepancies between whole otolith age determinations and the number of annuli we were able to measure in sectioned otoliths. Among the 84 specimens for which annuli could be reliably identified in both preparations, 57% of the ages agreed with whole ages. Where they did not agree, age determinations from whole otolith sections typically identified one more (61%) or one less (28%) annuli than we observed in sections. Age discrepancies of more than a year occurred in only four specimens. We produced a general picture of annulus position in Hoh River bull trout otolith sections by calculating a mean distance to each annulus (ages 1–6) among measured annuli for all specimens in the study (Figure 5). Means for each annulus position were significantly different (analysis of variance, $F = 751$, df = 5, 322, $P < 0.01$), and for the first four annuli, the ranges of annular measurements did not overlap. Data for fish size at age are shown in Table 1.

Water Chemistry

Mean water Sr/Ca values among all sites in the Hoh River were low and ranged narrowly between 0.0022 and 0.0034. The highest values occurred near rkm 6 and lowest values near the mouth of the river.

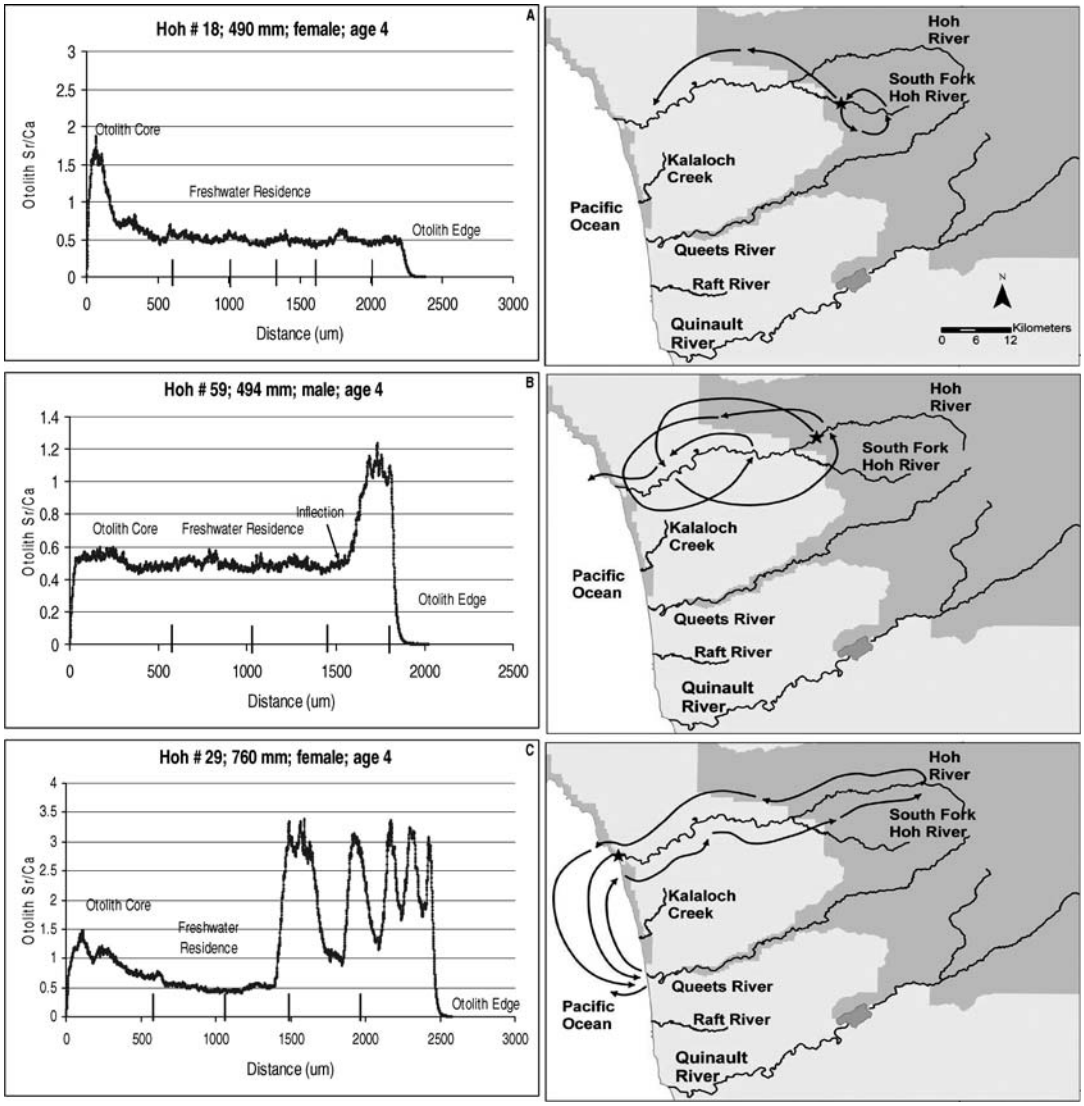

FIGURE 3.—Otolith chemistry profiles from nontagged bull trout specimens killed in terminal gill nets and movements of radio-tagged adult bull trout. The left panels depict typical strontium profiles for Hoh River bull trout, showing **(A)** no migration to marine habitats, **(B)** a single migration to the sea, or **(C)** multiple migrations to and from marine habitats. The data are moving averages of 10 points; the vertical bars indicate the locations of the annuli in sectioned otoliths. The right panels depict the movements and relocations of three radio-tagged adult bull trout, showing no migration to marine habitats (top panel), a single migration to the sea after two complete in-river migrations (middle panel), or multiple migrations to and from marine habitats (bottom panel). Stars indicate tagging locations.

Age-Specific Migrations from Otolith Chemistry

Strontium profiles associated with specific Hoh River bull trout revealed the following general life history patterns: (1) a potamodromous specimen with no marine migrations to sea, (2) an individual with a single emigration from freshwater to marine habitats, and (3) a bull trout showing multiple migrations between freshwater and marine waters (Figure 3, left panels). For all specimens, calculated Sr/Ca values during the period of freshwater residence (before any large increases in otolith strontium) ranged from 0.40 to 0.72 and averaged 0.54. Among 95 specimens analyzed chemically, 15 showed no evidence of marine migrations, maximum otolith Sr/Ca values being within

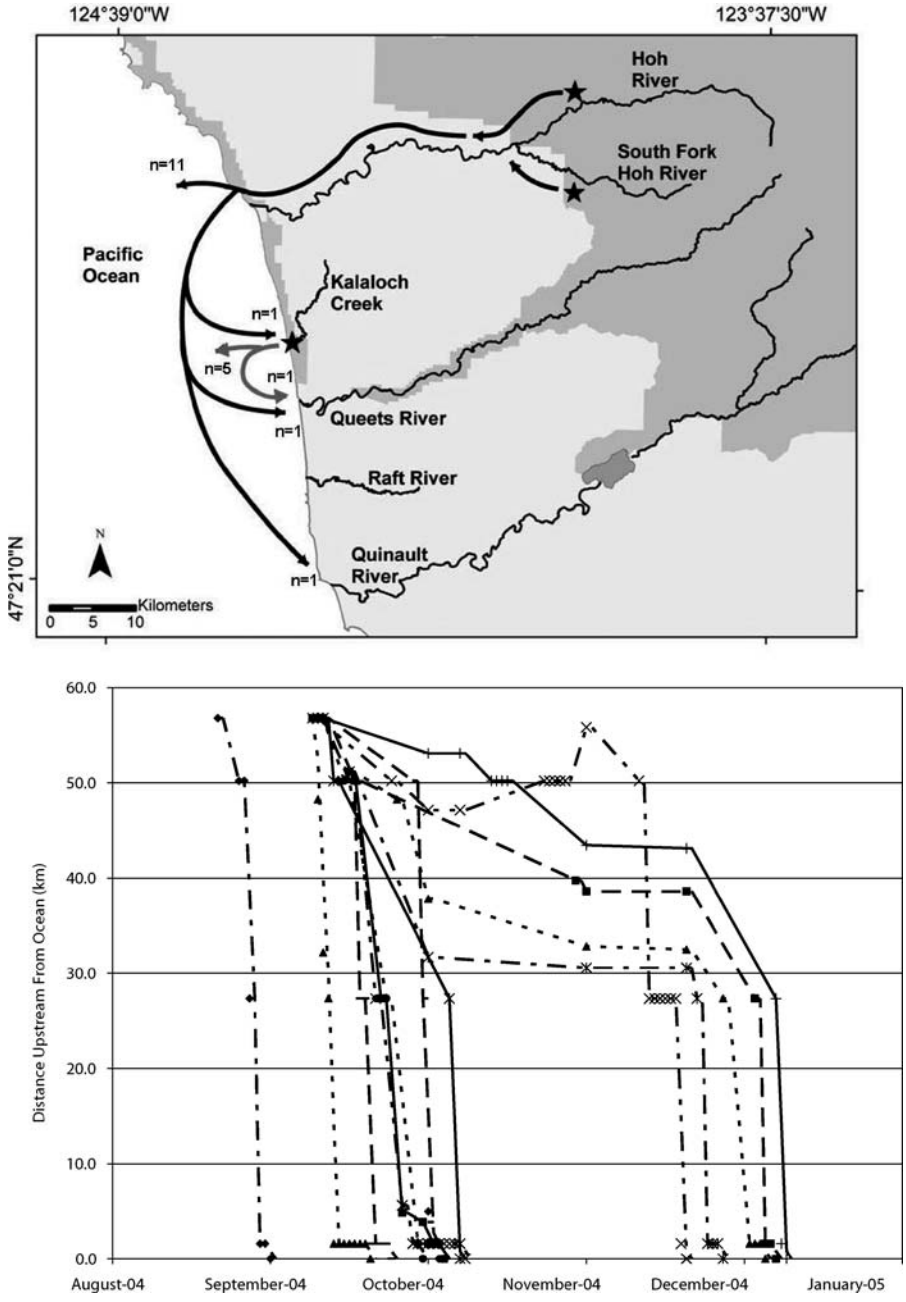

FIGURE 4.—The upper panel shows the movements of 20 anadromous juvenile (<360-mm) bull trout that were radio-tagged and released in the Hoh River (dark lines), South Fork Hoh River (dark lines), or Kalaloch Creek (gray lines), Washington, and their relocations in nearby watersheds. The lower panel shows the timing of the movements and relocations for individual juvenile fish that emigrated from the Hoh River to salt water.

this freshwater range (Table 2). Twelve of these fish were age 4, and the remainder were age 3. Mean total lengths for nonanadromous individuals were significantly less than those for anadromous fish, both for age 3 (317 mm versus 431 mm) and age 4 (516 mm versus 573 mm; *t*-test, $P < 0.05$).

For the remaining 80 specimens, it seemed clear that migrations out of freshwater rearing habitats occurred

TABLE 1.—Mean and range of total lengths (mm) by whole-otolith age and sex of bull trout captured in the Hoh River, Washington, gill-net fishery. Lengths for males and females within age classes were not significantly different (t-test); not all fish captured were sampled for length and age.

Fish group and statistic	Age				
	3 ($N = 12$)	4 ($N = 72$)	5 ($N = 20$)	6 ($N = 0$)	7 ($N = 1$)
Both sexes combined					
Mean (*N*)	388 (8)	562 (63)	651 (17)		695 (1)
Range	287–489	390–760	415–740		
Males					
Mean (*N*)	437 (3)	565 (33)	680 (10)		
Range	403–489	400–731	625–740		
Females					
Mean	393 (3)	560 (30)	654 (7)		
Range	337–454	390–760	415–728		

because the range of peak otolith Sr/Ca values (0.87 to over 4), exceeded those recorded before any large increases in otolith strontium. For the 80 fish that showed evidence of one or more emigrations from fresh to marine waters, most (88%) made their first at age 3 or 4 (some at age 6), none emigrating at younger ages. Males and females were nearly equally represented among age-3 and age-4 first-migrants, but females represented eight of nine fish migrating for the first time at age 5 (Table 2). Multiple migrations between marine and freshwaters were evident in 60 fish, with most fish migrating seaward two times (Table 2). Male and female specimens distributed fairly evenly among migrating fish, but females represented six of the seven nonmigrants (Table 2). Otolith core Sr/Ca values indicated that only four fish in the study were spawned by nonanadromous female parents, all of which eventually migrated to marine waters as juveniles. In contrast, all fish with no sign of marine migrations were apparently spawned by anadromous females.

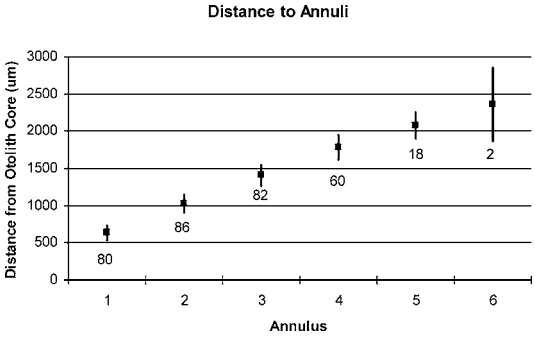

FIGURE 5.—Mean radial distance ± SD from the otolith core to each annulus for bull trout captured in Hoh River, Washington, gill-net fishery. The numbers below bars are samples sizes.

Discussion

The complementary use of radiotelemetry and otolith chemistry offered a unique opportunity to study bull trout life histories and provided a more complete understanding of age-specific movements of fish among freshwater and saltwater habitats along the Washington coast. We propose the following general life history pattern for anadromous bull trout in the Hoh River. Juveniles typically inhabit the river for 3 or 4 years before their first seaward migration. Anadromous juvenile and adult bull trout inhabit in the mouths of nearby coastal rivers, creeks, and nearshore marine environments. Adults then return to the Hoh River from April to July, swim upstream at rapid rates through the lower portion of the river in the summer, and spawn in the uppermost portions of the Hoh and South Fork Hoh rivers from October to December (Brenkman and Corbett 2005). These spawning areas are up to 78 rkm from the marine areas and typically are located upstream of spawning Pacific salmon and steelhead. Postspawned anadromous survivors return to the ocean and to nearby coastal streams from December to March to overwinter (Brenkman and Corbett 2005).

The results from this study illustrate diverse life history strategies in Hoh River bull trout and considerable individual variation in the frequency of movements between riverine, estuarine, and marine habitats. Otolith analyses made it clear that multiple saltwater migrations were common for Hoh River bull trout, most individuals migrating to sea two or three times (Table 2). Bull trout less than age 5, appeared to move annually between the river and the sea, once their first migration to sea was completed. Evidence suggested that anadromous and nonanadromous fish co-occur within the Hoh River basin and that both types of females produced anadromous progeny. This life history plasticity is consistent with observations of Arctic char populations (Nordeng 1983; Radtke et al.

TABLE 2.—Age at first saltwater entry and the estimated number of movements to salt water for male, female, and all bull trout captured in the Hoh River, Washington, gill-net fishery, based on analysis of otolith chemistry. The numbers of males and females do not equal the totals because there were head samples only in some specimens and therefore no sex determinations were made.

Fish group	First saltwater entry at age							Number of movements to salt water						
	0	1	2	3	4	5	6	0	1	2	3	4	5	6
All Fish	0	0	0	35	35	9	1	15	20	33	22	4	1	0
Males	0	0	0	17	14	0	0	1	9	18	6	1	0	0
Females	0	0	0	13	13	8	1	6	9	15	10	3	1	0

1996), and such life history variation has adaptive significance that is important for long-term persistence of populations (Den Boer 1968; Healey 1986; Gresswell et al. 1994).

Age at first seaward migration for Hoh River bull trout ranged from 3 to 6 years, which is consistent with the ranges reported for Dolly Varden (2–6 years), brook trout (1–7 years), and Arctic char (1–8 years) (Randall et al. 1987), but anadromous whitespotted char migrated to sea mainly at age 3 (Morita 2001). Radtke et al. (1996) found a substantially larger range of age at first seaward migration in Arctic char from a Norwegian lake system (4–13 years, mean 6.7), perhaps due to much smaller sizes at age for far northern populations.

We conclude from water and otolith chemistry data that the patterns of oscillating otolith strontium commonly observed in bull trout otoliths most likely represented migrations between the Hoh River and marine waters. Water chemistry analyses from the Hoh River showed uniformly low Sr/Ca values, well below typical values (about 8) reported for marine waters. For all specimens, otolith Sr/Ca values were consistently lowest in otolith regions that represented early juvenile life history, when fish must have occupied the river (Figure 3). In contrast, otolith Sr/Ca peaks observed in most specimens were, with rare exception, twofold to sixfold greater than the freshwater regions and similar to values observed in other salmonids during residence in estuarine or nearshore marine environments (Volk et al. unpublished data). Observed water and otolith Sr/Ca values made it unlikely that these high values could have been recorded in the Hoh River upstream from tidal influence. A number of studies support a broad relationship between otolith strontium and environmental salinity (Bath et al. 2000; Zimmerman 2005; Schroder et al. 1995; Volk et al. 2000), and migrations through salinity gradients are often reflected in otolith Sr/Ca profiles. The association of strontium reductions with return to freshwater was less definitive because Sr/Ca values often exceeded those recorded from fish that did not migrate to the ocean. Also, as growth rates declined with age, the otolith structural and chemical record became more compressed near the margin, making spatial resolution of peaks and valleys more challenging (Figure 2). Similar phenomena were apparent in anadromous Arctic char strontium profiles (Halden et al. 2000; Figures 2, 3). It was not always possible to reliably associate otolith annuli with chemical signals in older fish because we could not clearly recognize every annulus in all specimens. For example, we strongly suspect that specimen 29 (Figure 3) was at least 1 year older than indicated from otlith annuli; however, no additional annuli were recognized in either whole or sectioned otoliths. Though most otolith strontium profiles suggested that younger specimens typically migrated between freshwater and the sea on an annual basis, we cannot be certain of that frequency in older specimens, for which recognizing distal otolith annuli was unreliable.

Relocation data from radio-tagged fish provide the first verification that juvenile bull trout enter salt water and that anadromous juveniles use nearby coastal tributaries, which are similar to patterns observed in adults (Brenkman and Corbett 2005). The complementary use of radiotelemetry and otolith chemistry revealed that anadromous bull trout emigrate to the ocean at larger sizes and older ages than Pacific salmon. Radio-tagged juveniles emigrated to the ocean at lengths of 243–360 mm, first saltwater entry occurring at ages 3–6. These older ages at first seaward migration are more similar to patterns observed in anadromous cutthroat trout than in Pacific salmon or steelhead (Quinn and Myers 2004). Also, ages 3 and 4 anadromous individuals were larger than those that remained in freshwater. Hoh River bull trout ultimately attain a larger size at a given age compared with potamodromous populations throughout western North American (see Table 9 in Goetz 1989), and the larger body size of anadromous fish may lead to greater fitness (Thorpe 1987 and Gross et al. 1988).

Conservation Implications

Little attention has been given to the impact of recreational fisheries and commercial bycatch on bull trout, perhaps because bull trout are not typically

recognized as an anadromous species. We confirmed incidental bycatch of primarily anadromous bull trout in terminal gill-net fisheries directed at Pacific salmon and steelhead in the lowermost portions of the Hoh River. We found no published information on the extent of mortality of bull trout in rivers where intensive fisheries exist for other Pacific salmonids. The most frequently encountered bull trout in gill nets were ages 3–5 year old bull trout (up to age 7), and we speculate that fish were caught during (1) their first seaward emigration to the ocean, (2) their first upstream migration to spawn, (3) one of many movements between freshwater and salt water presumably after spawning, or (4) feeding migrations to the mouth of the Hoh River. Multiple emigrations between the Hoh River and ocean in successive years makes individuals particularly vulnerable to commercial fisheries. An understanding of age-specific seaward migrations and life history variability of anadromous bull trout should be considered in recovery planning and conservations efforts, particularly in coastal and Puget Sound, Washington, the Columbia River basin, and British Columbia rivers, where intensive recreational and commercial gill-net fisheries exist for other Pacific salmonids. Clearly, additional information is needed to fully understand the extent of incidental mortality of anadromous bull trout in these fisheries. Although it is difficult to isolate specific factors that influence anadromous bull trout populations, future conservation decisions should address how to reduce direct mortality through improved monitoring of catch and fishing effort in recreational and terminal commercial fisheries.

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