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[Note]

Previously Undocumented Two-Year Freshwater Residency of Juvenile Coho Salmon in Prairie Creek, California

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Abstract.—Over 2,000 juvenile coho salmon *Oncorhynchus kisutch* were tagged with passive integrated transponder (PIT) tags during the fall of 1998 and 1999 in Prairie Creek, California, as part of a study on individual winter growth rates and movement of juvenile coho salmon. During this study, age-2 out-migrants were incidentally observed. Previously, it had been generally assumed that all juvenile coho salmon in northern California streams spend only 1 year in freshwater before out-migrating at age 1 and that a 2-year freshwater life history pattern was found only in the more northerly portions of the species' range. Subsequently, scale analysis of PIT-tagged fish recaptured during spring out-migration was used as a basis for estimating the proportion of out-migrants displaying a 1- or 2-year freshwater residency life history. Twenty-eight percent (28%) of out-migrants captured in spring 2000 displayed a 2-year freshwater residency life history, apparently related to low winter growth rates documented in related research in the study stream.

In addition to influencing freshwater and marine survival (Scrivener and Anderson 1984; Quinn and Peterson 1996), freshwater growth rates may affect timing of and age at smoltification in anadromous salmonids (Hogasen 1998). Økland et al. (1993) found that faster growing juvenile Atlantic salmon *Salmo salar* and brown trout *S. trutta* smolted at smaller sizes and younger ages than did their slower growing counterparts. Svenning et al. (1992) found that when food availability for Arctic char *Salvelinus alpinus* was low, growth rates were reduced and only a small fraction of the population reached the threshold size for smoltification. Increased summer growth rates of individual juvenile coho salmon in British Columbia were cited as an explanation for an observed increase in the proportion of juveniles smolting at age 1 instead of age 2 (Holtby 1988). Previous research in the southern portion of the species' range has not found evidence of coho salmon smoltification at age 2 (Shapovalov and Taft 1954; Bradford et al. 1997). In British Columbia and farther north, however, coho salmon generally smolt at age 2; in some streams, age-3 smolts are common (Sandercock 1991; Bradford et al. 1997). In this study, we assessed the relationship between low growth rates and the incidence of age-2 smolts in a nearly pristine California stream within the southern range of coho salmon. As Mobrand et al. (1997) noted, salmon life history diversity, including variation in age at out-migration, increases a population's resilience to disturbance and thus is an important measure of population performance.

Methods

The study took place in a 6-km reach in the headwaters of Prairie Creek in northwest California. Prairie Creek is a third-order coastal stream contained almost entirely within Redwood National Park and Redwood State Park. Vegetation in the watershed is primarily old-growth redwood *Sequoia sempervirens* forest; red alder *Alnus rubra* and big-leaf maple *Acer macrophyllum* form a nearly continuous band of riparian vegetation in the study area. The drainage area above the study reach is 10 km^2, and base discharge in the study reach between October and March is approximately 0.56 m^3/s (R. Klein, Redwood National Park, Orick, California, personal communication). Gradient in the study reach averaged 1.2%. Weather in the region is characterized by wet, mild winters; rainfall between 135 and 200 cm; and relatively dry summers. Prairie Creek has been found to support consistently high densities of juvenile coho salmon since studies began in the early 1990s. Fish movement is not restricted by barriers within the study reach, and the reach has been little altered from its pristine condition.

Sampling for fish consisted of multiple-pass removal electrofishing in early winter (mid-November to mid-December) and later winter (mid-February to mid-

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TABLE 1.—Number of PIT-tagged juvenile coho salmon that were recaptured in Prairie Creek, California. Gear type 1 is electrofishing and gear type 2 is out-migrant trapping.

			Number of fish	
Year	Gear	Month	Tagged	Recaptured
1998	1	Nov	619	—
1999	1	Jan	422	187
	1	Mar	—	169
	2	Mar–Jun	—	172
	1	Oct	819	—
	1	Nov	520	135
2000	1	Mar	—	97
	2	Mar–Jun	—	115
Total			2,380	875

TABLE 2.—Results of scale analysis of PIT-tagged juvenile coho salmon from Prairie Creek, California; FL = fork length..

		FL (mm)	
Interpreted age	*n*	Mean	SD
1	99	88.6	9.2
2	52	101.9	9.9

March) during 1998–1999 and 1999–2000. We attempted to remove all juvenile coho salmon from habitat units (alcoves, backwaters, and main channel pools) by making multiple passes with one or two backpack electrofishers (Smith Root Inc., Vancouver, Washington; model 12). Before sampling, we blocked each habitat unit with 6-mm-mesh netting at the upstream and downstream ends and then electrofished the areas to near depletion using a minimum of four passes.

We anesthetized all captured juvenile coho salmon with tricaine methanesulfonate (MS-222) before recording their size (fork length [FL], nearest 1 mm; wet weight, nearest 0.01 g) and tagging a subsample of fish. All juvenile coho salmon of at least 55 mm FL were tagged with 11.5-mm-long passive integrated transponder (PIT) tags. The PIT tags were inserted into the body cavity anterior to the pelvic fin with a 12-gauge hypodermic needle (Prentice et al. 1985). We sealed the needle entry wound with Vetbond adhesive glue (3M Corp., Saint Paul, Minnesota) to reduce risk of infection and tag loss. After inserting PIT tags, we recorded the tag number for each fish and clipped the adipose fin to aid future identification and allow tag loss to be estimated. Fish were allowed 30–45 min to recover and then were returned to the habitat unit from which they were captured. On subsequent sampling dates, all adipose-fin-clipped fish were scanned with a tag reader; the tag number, FL, and wet weight were recorded.

A downstream migrant trap was located 7,450 m downstream of the study reach, allowing data to be collected from fish emigrating or displaced from the study reach. The trap was operated continuously from 5 February through 21 June during all years, except for 13 d in 1998–1999 and 4 d in 1999–2000. In 1999, the trap consisted of a rotary screw trap (1.5 m in diameter). The rotary screw trap was ineffective when discharge fell below about 0.14 m^3/s; in March 2000, the screw trap was replaced with a fyke trap that spanned the channel width. Adipose-fin-clipped fish that were captured at the trap were scanned to record PIT tag numbers and were measured and weighed. We used *t*-tests to compare the size of 1- and 2-year-old coho salmon on specific dates. A significance level of 0.05 was used in all statistical comparisons.

To determine the proportion of smolts out-migrating at age 2 in the spring, we measured the length and collected scales from around 20% (n = 151) of the juvenile coho salmon captured at the downstream migrant trap by systematic sampling. Fish age was determined by scale analysis using the methods of DeVries and Frie (1996) and was aided by recapture of known age-2 fish from the PIT-tagged population. The mean and SD of FL were calculated for fish with estimated ages of 1 or 2 years . We used Mix 3.1A software (MacDonald and Pitcher 1979) to determine the proportion (±SE) of 1- and 2-year-old coho salmon among the total captured at the downstream migrant trap in spring 2000 ($n = 759$). Mix 3.1A software uses a maximum likelihood estimator to analyze age-groups based on size-frequency data—in this case, a fixed mean and SD for age-1 or age-2 fish based on scale analysis.

Results

We tagged a total of 2,380 juvenile coho salmon with PIT tags during the study (Table 1). No mortalities resulting from handling were observed in either year, and tag loss was 3–5% in both years. We recaptured 24.7% of all juvenile coho salmon tagged during electrofishing efforts and recorded an additional 12.1% in a downstream out-migrant trap during March–June (Table 1).

Twelve coho salmon tagged in 1998 were recaptured during the spring 2000 downstream migration, and 55 fish tagged in 1999 were recaptured during the spring 2001 downstream migration, confirming a previously undocumented expression of 2-year stream residence by juvenile coho salmon in Prairie Creek. Based on scale analysis ($n = 151$), the mean length of age-1 out-migrants during spring 2000 was 88.6 mm (SD = 9.2), and the mean length of age-2 out-migrants was 101.9 mm (SD = 9.9; Table 2). Applying these to the length-

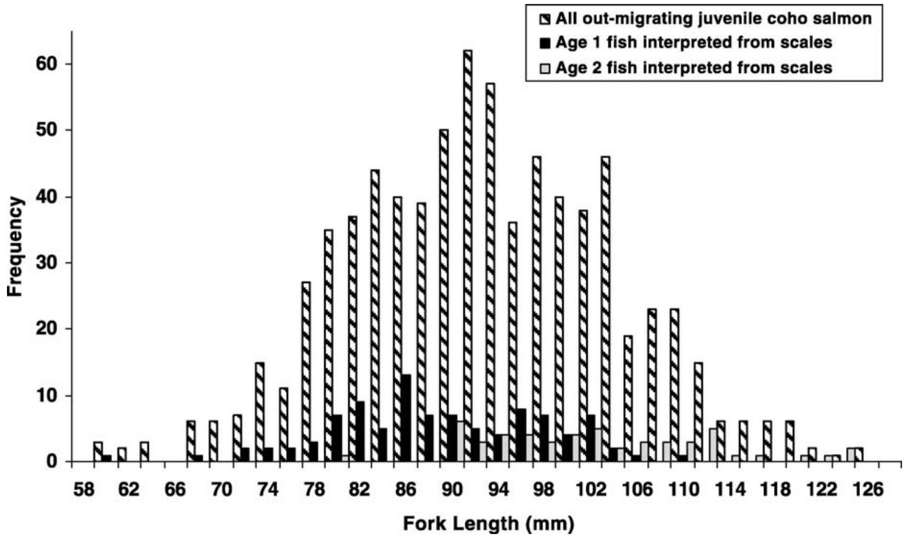

FIGURE 1.—Length frequency (FL, mm) of juvenile coho salmon that out-migrated from Prairie Creek, California, during spring 2000. Juveniles identified as age 1 or 2 from scale analysis are also shown.

frequency distribution of the whole population of out-migrating coho salmon (Figure 1), 28.2% (SE = 2.9%) of the 759 smolts caught at the downstream migrant trap in spring 2000 were age 2.

The size of juvenile coho salmon that out-migrated at age 2 differed from that of juveniles that out-migrated at age 1. Juvenile coho salmon that delayed their out-migration were smaller in November 1998 and January and March 1999 than other juveniles of the same cohort ($t_{42} = 2.02$, $P < 0.001$; Figure 2). During February–May 2000 out-migration, however, the average FL of age-2 smolts (102 mm, SE = 1.37) was larger than that of age-1 smolts (89 mm, SE = 0.92; $t_{24} = 5.709$, $P < 0.001$). Sample sizes of individually marked juvenile coho salmon recaptured in both November 1998 and March 1999 that did not out-migrate at age 1 were too low to allow statistical comparisons with growth rates of smolts out-migrating at age 2. Although winter growth rates appeared to be low overall (Bell 2001), juveniles that out-migrated at age 1 displayed positive growth in both years of the study (average absolute growth: 2.2 mm in winter 1998–1999, 5.4 mm in 1999–2000). In contrast, juveniles that extended their stream residency displayed notably weak growth during their first winter in freshwater (average relative growth: 0 mm in winter

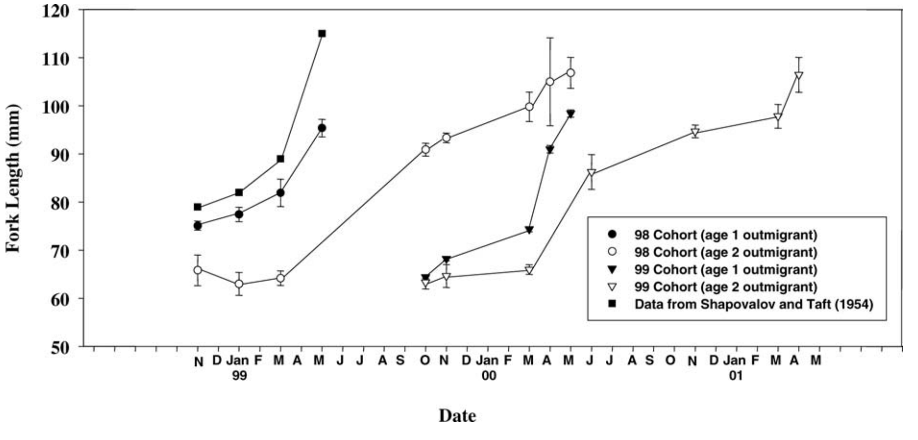

FIGURE 2.—Mean FL (±SE) of PIT-tagged juvenile coho salmon that out-migrated during spring 1999–2001 at ages 1 and 2 from Prairie Creek, California. Data from Waddell Creek, California (Shapovalov and Taft 1954), are shown for comparison.

1998–1999, 1.3 mm in 1999–2000; Figure 2). This trend appeared despite the more general pattern of higher growth rates typically observed for juveniles of smaller initial size.

Discussion

Coho salmon exhibit a variable life history, spending from 1 to 4 years in freshwater (Sandercock 1991). The mean age at out-migration has been previously reported at 1.0 year in California streams, generally increasing with latitude to 1.5 years or more in British Columbia and Alaska (Bradford et al. 1997). A similar pattern of increasing smolt age with latitude has been observed in Norwegian streams by Øakland et al. (1993). Information about the life history of coho salmon in California has largely been drawn from research conducted in Waddell and Scott creeks, very near the southern extent of the species' range (Shapovalov and Taft 1954). Although Prairie Creek is located at latitude 41°N, the average age at out-migration (1.3 years) is more typically observed at latitudes north of 48°N, around 800 km further north (Bradford et al. 1997). Investigations into the life history of coho salmon in other northern California streams since this study began have documented the occurrence of a 2-year freshwater juvenile residency elsewhere in the region (W.G.D., unpublished data).

Low growth rates of juvenile coho salmon in Prairie Creek, as documented in related research (Bell 2001), may increase the proportion of juveniles remaining in freshwater for a second year, as has been observed for coho salmon in British Columbia by Holtby (1988), Atlantic salmon by Utrilla and Lobon-Cervia (1999), and Atlantic salmon and brown trout by Økland et al. (1993). Although Shapovalov and Taft (1954) did not measure individual growth rates of juvenile coho salmon in Waddell Creek, where only age-1 smolts were observed, they compared mean sizes of juveniles and found that growth averaged 10 mm between November and March—much higher than was observed in Prairie Creek in winter 1998–1999 (2.17 mm) or 1999–2000 (5.38 mm) (Bell 2001). Our data appear to support the observations of others that a minimum size threshold is required for smoltification (Øakland et al. 1993; Svenning et al. 1992, as cited in Hogasen 1998) and that smaller, slower growing fish are more likely to spend a second year in freshwater than are larger fish (Figure 2). Variable growth rates appear to be related to variable stream residence time, as was hypothesized by Grand (1999) and observed by Thorpe et al. (1990) in Atlantic salmon. Clearly, life history patterns should be considered when interpreting potential population-level effects of low growth rates rather than presuming that low growth rates of juvenile coho salmon have only negative consequences. Different population of salmon may have adapted various alternative strategies, such as the 2-year stream residence seen in the study.

The benefits of extended stream residency time for coho salmon are unclear. Age-2 smolts must survive a second year in freshwater before out-migrating, though Brakensiek (2002) found that age-2 fish in Prairie Creek appeared to have high (>60%) apparent winter survival rates. In streams where mortality rates are high, whether because of poor habitat quality, high predation rates, or other factors, extended residency may be selected against. Conversely, extended stream residency that results in smoltification at a larger size may enhance marine survival (Bilton et al. 1982; Mathews and Ishida 1989; Holtby et al. 1990), resulting in attendant population-level consequences. Mobrand et al. (1997) suggested that conserving life history diversity of Pacific salmon (e.g., variable age of out-migrants) is critical for maintaining healthy populations.

The 2-year stream residency exhibited by a proportion of the juvenile coho salmon population is probably an important component of the population's adaptation to this particular system. One potential source of bias in our results is that trap efficiency was not measured and was probably size based. If smaller fish were captured at a higher rate than larger fish, which is often the case, the proportion of age-2 smolts may be biased low. A second caveat to our results is that the calculated life history of age-2 fish is not based on following a cohort through the juvenile stage (which was not feasible for this study) but rather on calculating the percentage of smolts in a particular year that exhibit the age-2 life history. The potential problem is that this calculation is confounded by year-class strength. An unusually large year-class might have unusually low growth (possibly from increased density) and thus produce an unusually large number of age-2 fish. If this large cohort is followed by another strong year-class, the percentage of age-2 out-migrants might appear small, masking the importance of this life history type. Conversely, a small number of age-2 fish from a large cohort might then constitute a relatively large proportion of total smolt production in a single year if the large year-class is followed by a very weak year-class. We believe that further studies should be pursued to determine the percentage of age-2 fish within cohorts and the potential causes, consequences, and extent of this life history strategy for coho salmon throughout northern California. Findings of such studies could prove extremely valuable for documenting changes resulting from habitat disturbance, climate change, or other factors that affect salmon population health and resilience.

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