

Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/utaf20>

Juvenile Coho Salmon in the Elwha River Estuary Prior to Dam Removal: Seasonal Occupancy, Size Distribution, and Comparison to Nearby Salt Creek

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Published online: 21 Jun 2013.

To cite this article: Thomas P. Quinn, Nicole Harris, J. Anne Shaffer, Chris Byrnes & Patrick Crain (2013): Juvenile Coho Salmon in the Elwha River Estuary Prior to Dam Removal: Seasonal Occupancy, Size Distribution, and Comparison to Nearby Salt Creek, Transactions of the American Fisheries Society, 142:4, 1058-1066

To link to this article: <http://dx.doi.org/10.1080/00028487.2013.793614>

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NOTE

Juvenile Coho Salmon in the Elwha River Estuary Prior to Dam Removal: Seasonal Occupancy, Size Distribution, and Comparison to Nearby Salt Creek

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Abstract

In addition to the downstream migration of smolts in spring, Coho Salmon *Oncorhynchus kisutch* also enter estuaries throughout the year but especially in the spring as fry and in the fall as parr. The removal of two large dams on the Elwha River, Washington, has increased the area accessible to salmon and is affecting many aspects of the system. For comparison with the postdam period, when the Elwha River estuary will likely expand in size and complexity, monthly sampling was conducted in the estuary during 2007–2011 to determine patterns of Coho Salmon presence and size prior to dam removal; Salt Creek, a nearby undammed stream, was also sampled to allow comparison of fish size and seasonal timing patterns. The spring smolt migration in the Elwha River included a large fraction of unmarked fish (primarily of natural origin) as well as marked fish from the Lower Elwha Klallam Tribe Fish Hatchery. Subyearlings entered both estuaries during much of the year, exhibiting a peak in September. Coho Salmon from the Elwha River (including wild and hatchery-origin fish) were larger and more heavily represented in the fall relative to the spring smolt migration compared to those from Salt Creek. Future patterns in the Elwha River may include reduced presmolt use of the estuary if the center of distribution is farther upriver,

but improved estuarine habitat may make it more suitable for presmolts.

Pacific salmon *Oncorhynchus* spp. and trout populations are a vital component of commercial, recreational, ceremonial, and subsistence fisheries around the Pacific Rim (NRC 1996; Augerot 2005) and are keystone species in their ecosystems (Willson and Halupka 1995). However, overall abundance and population diversity of salmonids in the southern end of their distribution have declined for decades, and many populations are extinct or in jeopardy (Nehlsen et al. 1991; Gustafson et al. 2007). Impassable dams have contributed to these losses (Lichatowich 1999), and removal or modification of dams is increasingly viewed as an option for restoring salmonid populations and their ecosystems (Hart et al. 2002). Dams can block fish movements, but they also alter temperature and flow regimes and reduce transport of sediment and woody debris, thus affecting the habitat that is available to fishes and other biota (Bednarek 2001). The trajectory of fish recovery therefore

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Received November 21, 2012; accepted April 3, 2013

depends on complex combinations of intraspecific and inter-specific population dynamics in the context of changing habitat quantity and quality. Accordingly, documentation of alternative migration and life history patterns may be important in assessing the recovery process.

The removal of two large dams on the Elwha River in the Olympic Peninsula, Washington, provides exceptional opportunities for studying the processes of fish life history and ecology, as anadromous fishes can expand their ranges upstream and formerly landlocked populations can resume anadromy or interact with anadromous fishes (Duda et al. 2008; Pess et al. 2008). Since the construction of Lower Elwha Dam in 1910–1913, migratory fishes have been blocked and sediment transport and other physical and ecological processes have been altered. Removal of Lower Elwha Dam (at river kilometer 7.9) and Glines Canyon Dam (at river kilometer 21.6) began in September 2011. Surveys prior to dam removal indicated that the numerically dominant salmonid above the dams was the Rainbow Trout *O. mykiss* (Brenkman et al. 2012). Coho Salmon *O. kisutch* were restricted to the section below Lower Elwha Dam, and adult escapements were estimated at 2,900, of which 76% were hatchery produced (Pess et al. 2008). However, the density of juvenile Coho Salmon was roughly comparable to that of steelhead (anadromous Rainbow Trout) below the dam (Pess et al. 2012); based on habitat capacity, Coho Salmon abundance might expand 10-fold during the postdam period (Pess et al. 2008).

Coho Salmon typically spawn in streams during late fall and early winter; fry emerge in spring, reside in freshwater for a full year (or 2 years in environments that are less conducive to growth), and then migrate to the sea as smolts in spring (Sandercock 1991; Weitkamp et al. 1995; Quinn 2005). During the fall, when streamflows increase in coastal, rain-dominated systems, parr often move downstream and overwinter in wetlands, beaver ponds, and other off-channel habitats (Bustard and Narver 1975; Peterson 1982; Swales et al. 1988). However, the downstream movement of fry in the spring and parr in the fall can take them into marine waters as well (Hartman et al. 1982; Miller and Sadro 2003; Bennett et al. 2011); these fish can represent a substantial fraction of the total population (Bennett et al. 2011; Roni et al. 2012). The fall migrants, which are missed by typical spring smolt sampling operations, may be numerically important and also reflect important aspects of the species' ecology in streams. Coho Salmon smolts tend to move through estuaries rapidly and then disperse, but the use of estuaries by fry and parr is less well known and might be important for the survival of individuals and for persistence of the population (Koski 2009).

The estuary of the Elwha River has been greatly reduced in size and complexity due to a series of processes, including (but not limited to) the retention of sediment behind the dams, diking, and channelization (Draut et al. 2008; Shaffer et al. 2008; Duda et al. 2011b), which have disrupted the fish's use of nearshore habitat in the Elwha River (Shaffer et al. 2009, 2012). Future physical changes in the estuary from sediment and wood deposition, and perhaps beaver activity, are likely (Hood

2012), thus affecting riverine and estuarine communities. Here, we report the results of monthly beach seining conducted on the west side of the Elwha River estuary during March 2007 through September 2011, when removal of Lower Elwha Dam began. These pre-dam-removal data will allow for comparisons with future postremoval patterns in (1) the seasonal catch of Coho Salmon representing different life history stages (fry in spring, parr in fall, and smolts in spring) and (2) juvenile Coho Salmon body size. In addition, similar seining efforts were conducted in the estuary of nearby Salt Creek as a comparison. There are three scenarios for future use of the Elwha River estuary by Coho Salmon. First, body size and temporal patterns of estuarine occupancy may be similar to those observed in the period prior to dam removal (i.e., the null hypothesis). Second, the estuary may become more extensive and more complex, leading to increased occupancy (although in the short term, the patterns of sediment transport and deposition might also limit access to some habitats). Third, if the spawning distribution of Coho Salmon shifts farther upstream, fry and parr that move downstream may find suitable habitat in the river, and use of the estuary during fall will therefore decrease. A large fraction of the hatchery-produced Coho Salmon in the Elwha River were externally marked by removal of the adipose fin, allowing us to make some comparisons between natural- and hatchery-origin fish. This is important because full restoration of the ecosystem will require the expansion of natural production.

METHODS

The Elwha River on the Olympic Peninsula, Washington, flows north into the Strait of Juan de Fuca (Figure 1). The estuary's total area is about 35–40 ha, with 25–28 ha on the eastern side and 10–12 ha on the western side, including a pond that is not accessible to salmon (Shaffer et al. 2009; Duda et al. 2011a). Sampling took place in two tidally influenced channels (maximum depth = 2 m) on the western side of the estuary (Shaffer et al. 2009, 2012); these channels were separated from the main channel during low tides. At the higher-elevation northern site, the substrate consisted of sand, flat beach rock (up to 12 cm in diameter), and aggregated woody debris. The southern site was bordered by a rock levee with fine silt substrate and vegetation on the margins, and this site was more closely connected to the river. Tidal amplitudes in this area can exceed 3 m. Between the estuary and Lower Elwha Dam, the river had some floodplain channels that were used by juvenile Coho Salmon, but most of the tributary habitat in the basin was inaccessible to them and to other anadromous fishes prior to dam removal.

Estuaries are challenging habitats in which to sample because they change on complex tidal and lunar time scales and in response to river flow fluctuations. Thus, the two sites in the Elwha River's small estuary were selected for their convenience and consistent access; they were not intended to represent the estuary as a whole but rather to allow seasonal sampling of the fish. In addition, there is no "reference" against which the Elwha River estuary can be paired. A review of the

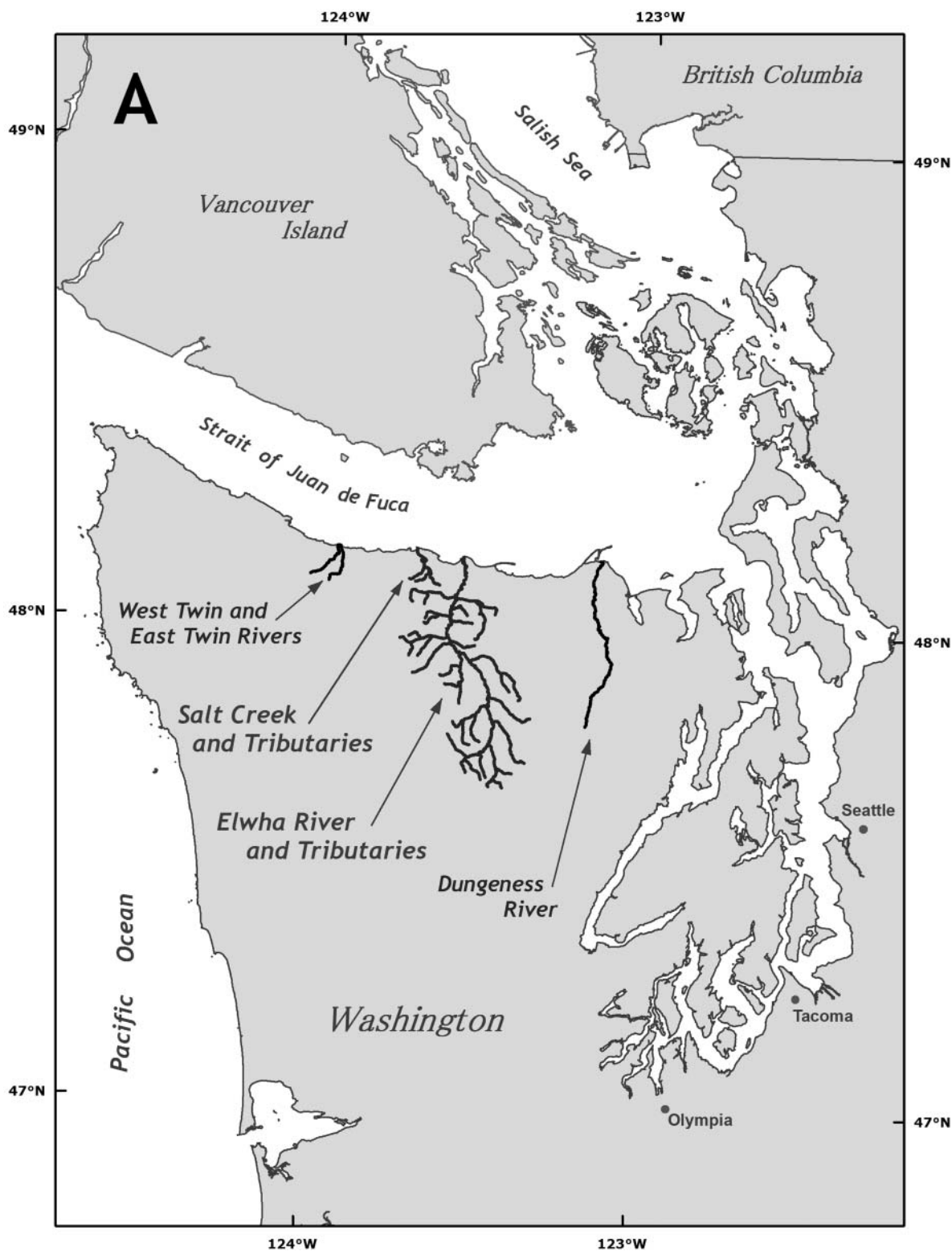


FIGURE 1. (A) Map of western Washington and vicinity, showing the locations of the Elwha River, Salt Creek, and other nearby rivers mentioned in the text; (B) orthophoto of the Elwha River estuary in 2011, showing locations of the sampling sites (X) on the west side; and (C) orthophoto of the Salt Creek estuary in 2011, depicting locations of the sampling sites (X).

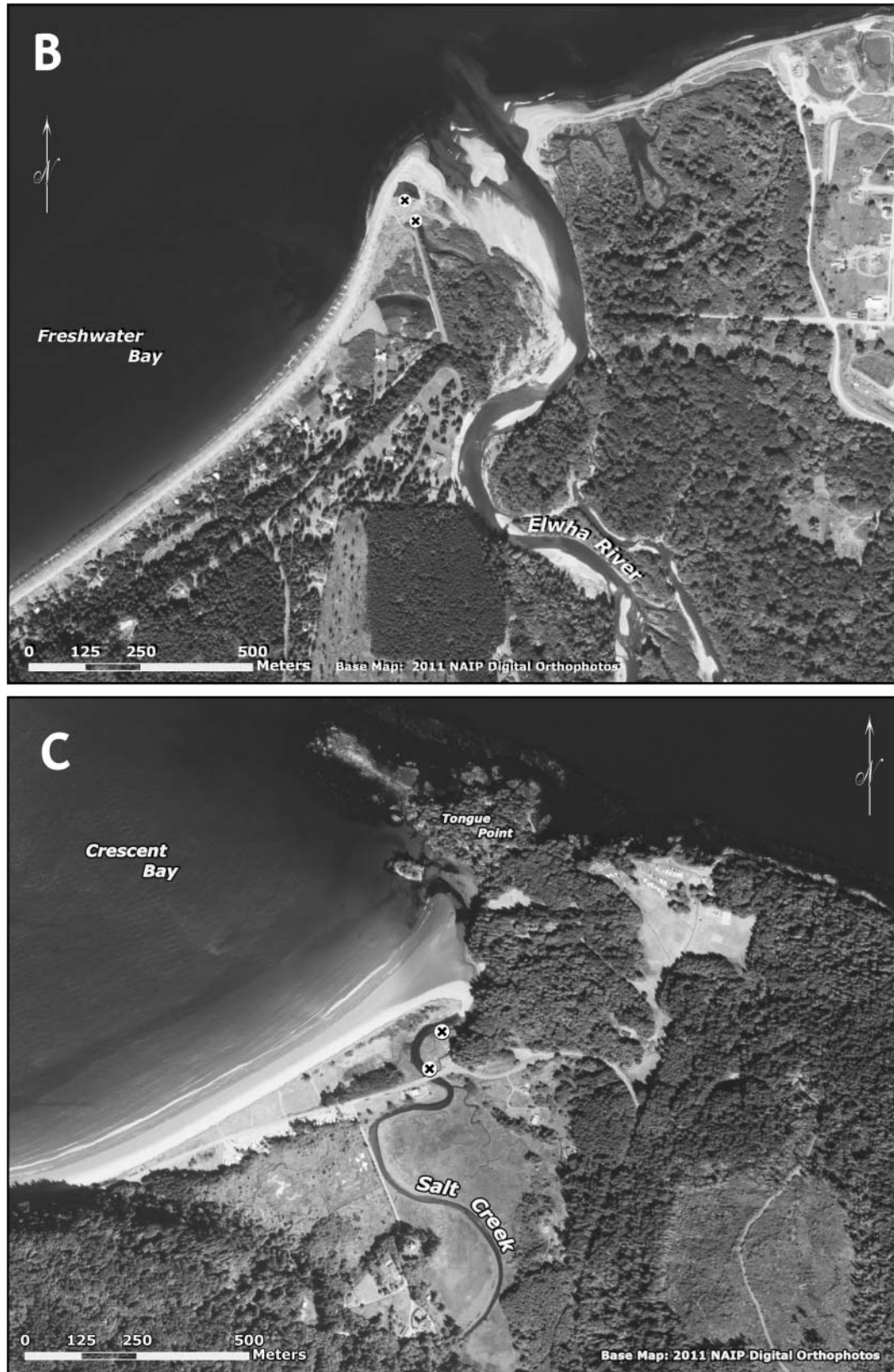


FIGURE 1. Continued.

dam removal evaluation process concluded that "... the most appropriate design for the Elwha River dam removal [is] a BA [before–after] study design" (Roni et al. 2008). The sampling reported here was intended to be used in that manner; however, the estuary of Salt Creek, located approximately 10 km west of the Elwha River, was also sampled at two sites by similar methods to allow comparison of fish size and seasonal timing patterns. The Salt Creek estuary consists of approximately 29 ha of salt marsh and includes the main channel and side channels of lower Salt Creek. The mouth of Salt Creek enters directly into the east end of the highly productive and stable Crescent Bay. The Salt Creek estuary is bisected by a century-old dike that divides the eastern and western portions, although fish are present on both sides as well as in the main channel. The main channel, where the sampling occurred, is shallow, broad, and low energy and has heavy tidal influence upstream from the mouth. Salt Creek has about 38 km that are accessible to salmon and has a basin area of 49 km². The Coho Salmon is the dominant salmonid species in Salt Creek (McHenry et al. 2004). The habitat has been degraded to some extent, and there are some fish passage barriers within the system as described by McHenry et al. (2004), but many of those barriers have been eliminated since that report was completed (Michael McHenry, Lower Elwha Klallam Tribe, personal communication). The flow regime of Salt Creek is dominated by winter rainfall, whereas the Elwha River shows a snowmelt peak in early summer and a rain-dominated peak in winter (Draut et al. 2011).

Sampling was conducted in mid- to late morning on a single day of each month during the first monthly neap tide; we used a 24.4-m-long × 1.8-m-deep beach seine with a cod end of 1.8 m³ and 5-mm knotless mesh. Sampling is ongoing; in this paper, we report only the sampling that occurred during the period when the dams were in place (i.e., March 2007–September 2011). The net was deployed at the 2-m water depth mark parallel to the beach by using a row boat and was brought in by hand. All fish were identified to species; FL was recorded for all Coho Salmon if the catch was small or for about 20 Coho Salmon as a subsample if the catch was very large; and all specimens were then released on site.

The objective was to characterize the overall seasonal patterns rather than to describe interannual variation in or details of habitat use, so the data were pooled by month (i.e., combining all years of sampling) and examined as catch per unit effort (CPUE; fish/set) to account for unequal numbers of sets. Age-classes of juvenile Coho Salmon were separated by inspection of length frequency distributions. For example, in the Elwha River estuary, 90-mm and larger juveniles in April and May collections and 99-mm and larger juveniles in June samples were considered to be yearlings, whereas smaller fish were categorized as young of the year (Figure 2). In Salt Creek, the modes were smaller: 80-mm and larger juveniles in April and May samples and 89-mm and larger juveniles in June samples were categorized as yearlings. The proportions of each age-class among the measured fish at each sampling event were used to estimate the

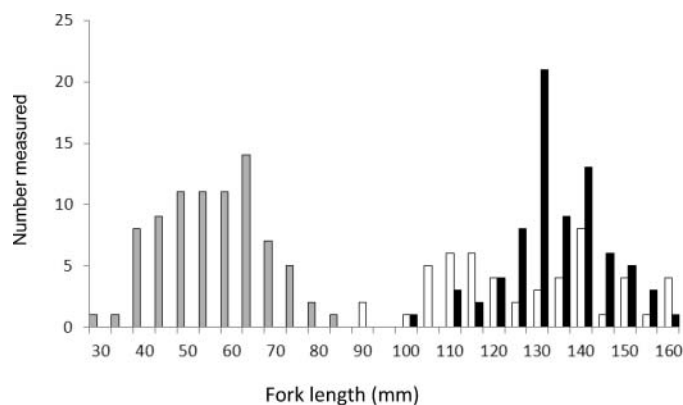


FIGURE 2. Length frequency distribution of juvenile Coho Salmon captured in the Elwha River estuary, Washington, during April and May of 2007–2011, illustrating the sizes of young of the year (gray bars; all fish were unclipped) and yearlings as inferred from the distributions. Black bars represent adipose fin-clipped (i.e., hatchery-origin) yearlings, and white bars represent unclipped yearlings, which include wild fish and unclipped hatchery fish. The final length bin includes all fish that were 160 mm or larger.

numbers of subyearlings and yearlings among the fish that were counted but not measured. Most of the hatchery-origin Coho Salmon were marked externally by removal of the adipose fin (Table 1), in addition to coded wire tagging of a fraction; in late March to early or mid-May of each year, these fish were released volitionally from the Lower Elwha Klallam Tribe Fish Hatchery, which is operated by the Lower Elwha Klallam Tribe. The average mass of 30 g for these hatchery fish (Regional Mark Information System, Pacific States Marine Fisheries Commission, <http://www.rmpc.org/>) indicated a FL of about 136 mm based on unpublished length–weight data for hatchery Coho Salmon (Morgan Bond and Sean Hayes, National Oceanic and Atmospheric Administration [NOAA] Fisheries, Santa Cruz, California).

RESULTS

In total, 239 beach seine sets (127 in the Elwha River estuary and 112 in the Salt Creek estuary, with at least six sets in each

TABLE 1. Numbers of hatchery-produced Coho Salmon smolts that were released into the Elwha River, Washington, by Lower Elwha Klallam Tribe Fish Hatchery from 2007 to 2011 and the annual percentages of hatchery fish that were marked by removal of the adipose fin (source: Regional Mark Information System, maintained by the Regional Mark Processing Center, Pacific States Marine Fisheries Commission, <http://www.rmpc.org/>).

Release year	Number released	Fin clipped (%)
2007	410,866	80.2
2008	323,813	73.7
2009	444,514	64.4
2010	218,720	63.2
2011	506,402	84.2
Total	1,904,315	74.5

TABLE 2. Numbers of beach seine sets and average catch per unit effort (CPUE, fish/set; SD in parentheses) of juvenile Coho Salmon in the Elwha River estuary and the Salt Creek estuary during spring 2007 through fall 2011. The percentage of smolts (i.e., yearlings, as inferred from length frequency distributions) among fish captured at each site during each month is also reported.

Month	Elwha River estuary			Salt Creek estuary		
	Sets	Mean CPUE (SD)	% Smolts	Sets	Mean CPUE (SD)	% Smolts
Jan	6	0.0 (0.0)		6	1.2 (2.9)	
Feb	6	0.2 (0.4)		8	0.1 (0.4)	
Mar	10	0.1 (0.3)		9	1.0 (1.7)	
Apr	17	77.1 (217.0)	80.2	12	8.3 (24.2)	96.6
May	15	42.1 (63.0)	59.5	16	71.6 (162.9)	82.0
Jun	15	3.9 (4.8)	42.3	11	20.0 (45.3)	34.7
Jul	15	1.2 (3.6)	11.1	11	3.6 (6.3)	5.0
Aug	14	5.7 (15.1)	1.7	12	7.7 (14.0)	2.5
Sep	9	34.6 (94.6)	0.0	7	10.7 (14.2)	0.0
Oct	8	2.6 (7.4)	0.0	8	5.6 (10.8)	0.0
Nov	6	5.8 (13.8)	0.0	6	1.7 (3.6)	0.0
Dec	6	0.2 (0.4)		6	0.2 (0.4)	

month at each site) were performed, resulting in a total catch of 4,213 juvenile Coho Salmon (2,469 in the Elwha River estuary; 1,744 in the Salt Creek estuary). Fish were caught during all months of the year, but there were clear modes of CPUE (fish/set) during spring and fall (Table 2). However, the timing and relative magnitude of the modes differed between the two estuaries. In the Elwha River estuary, the spring mode (dominated by smolts; Table 2) was observed in April and to a lesser extent in May, whereas in the Salt Creek estuary the mode was observed in May and more fish were caught during June than during April. The mode of fall migrants relative to the spring smolt migration was greater for the Elwha River estuary than for the Salt Creek estuary. The CPUE of smolts in spring was similar between the two estuaries (Elwha River: 77.1 fish/set in April; Salt Creek: 71.6 fish/set in May), but the peak fall (September) CPUE was higher in the Elwha River estuary (34.6 fish/set) than in the Salt Creek estuary (10.7 fish/set).

Young-of-the-year fish from the Elwha River were larger than those from Salt Creek during spring through fall (Table 3). The Elwha River smolts were also much larger than Salt Creek smolts in April (Elwha River: mean $\pm$ SD = 135.3 $\pm$ 17.5 mm; Salt Creek: 98.6 $\pm$ 17.0 mm; $t = 9.66$, $P < 0.001$) and in May (Elwha River: 129.2 $\pm$ 15.61 mm; Salt Creek: 117.4 $\pm$ 17.5 mm; $t = 4.96$, $P < 0.001$) but not significantly so in June (Elwha River: 116.2 $\pm$ 12.9 mm; Salt Creek: 111.3 $\pm$ 14.7 mm; $t = 1.32$, $P = 0.19$). These size differences between streams were influenced by the mixture of hatchery- and naturally produced fish but did not seem to simply reflect larger, hatchery-produced fish in the Elwha River. In the Elwha River, the adipose fin-clipped (hatchery) smolts varied less in length than the unclipped (mix of hatchery and natural origin) smolts during April (clipped [$N = 37$]: variance = 140.5 mm; unclipped [$N = 12$]: 462.1 mm; $F = 0.304$, $P = 0.003$) and during May (clipped [$N = 39$]:

variance = 109.7 mm; unclipped [$N = 39$]: 354.0 mm; $F = 0.310$, $P < 0.001$). The clipped fish did not differ in length from the unclipped fish during April (clipped: 130.1 mm; unclipped: 133.0 mm; $t = 0.59$, $P = 0.565$), but in May the clipped fish were longer than the unclipped fish (clipped: 134.0 mm; unclipped: 123.2 mm; $t = 3.15$, $P < 0.003$).

Not surprisingly, the fall mode of presmolts in the Elwha River represented fish of natural origin (all 286 examined fish were unclipped), but the smolt migration period also included a substantial fraction of unclipped fish. In April, 60.4% of the 932 examined fish were unclipped, and in May 51.2% of the 561 examined fish were unclipped. Three clipped smolts were caught in the Salt Creek estuary during May (165, 165, and 185 mm; each fish was captured in a different year), and presumably these were from a hatchery program (although not necessarily the Lower Elwha Klallam Tribe Fish Hatchery).

TABLE 3. Fork lengths (mm) of age-0 Coho Salmon sampled in the Elwha River estuary and the Salt Creek estuary from 2007 to 2011; n = number of fish measured. Samples with fewer than 10 fish were omitted.

Month	Elwha River estuary			Salt Creek estuary		
	n	Mean FL	SD	n	Mean FL	SD
Apr	21	47.0	8.4			
May	60	58.2	11.3	24	38.3	7.6
Jun	41	76.9	11.0	49	49.7	9.2
Jul	16	70.9	8.3	38	64.2	6.1
Aug	57	83.6	11.5	77	72.1	7.7
Sep	46	93.7	8.4	49	90.3	7.9
Oct	17	106.5	10.0	41	93.5	7.2
Nov	25	112.3	7.8	10	95.2	10.0

Our power to detect interannual patterns was reduced due to (1) the small number of years ($n = 5$) of data and (2) the fact that seine sets in some month $\times$ site $\times$ year combinations were missing. At both sites, a great deal of among-year variation was detected in CPUE for any given month. For example, catches of Coho Salmon parr in the Elwha River estuary during September (the mode for fall catches; Table 2) varied from 0 to 286 fish/set, and the corresponding catches in the Salt Creek estuary varied from 0 to 28.5 fish/set. In general, CPUEs in both estuaries were low during 2007 (all months combined; Elwha River: 7.17 fish/set; Salt Creek: 6.52 fish/set) and were high during 2010, especially for the Elwha River (51.27 fish/set; Salt Creek: 14.90 fish/set). The expectation that catches in spring would reflect the number of Coho Salmon released from Lower Elwha Klallam Tribe Fish Hatchery was not supported. Indeed, April catch rates of Coho Salmon of all sizes in the Elwha River estuary were negatively correlated with the number released ($r^2 = 0.77$, $P = 0.05$), and the relationship was improved when only the catch rates of smolts were considered ($r^2 = 0.83$, $P = 0.03$). No relationship was detected between the number of hatchery fish released and the catch rates in May.

DISCUSSION

The primary purpose of this study was to document the patterns of juvenile Coho Salmon size distribution and timing in the small, degraded estuary of the Elwha River during the years immediately prior to removal of the two large dams; secondarily, we sought to compare these patterns with those of juvenile Coho Salmon in the nearby Salt Creek estuary. The salient findings were the substantial numbers of presmolt Coho Salmon in the estuaries of both systems, including (1) fry in the spring, which overlapped with the conventional smolt migration in May and June, and (2) parr in the fall (Figure 2; Table 2). These migratory patterns have been documented in other nearby systems, such as the East Twin and West Twin rivers, which are situated along the Strait of Juan de Fuca west of Salt Creek (Bennett et al. 2011; Roni et al. 2012); such patterns have also been documented in British Columbia (Hartman et al. 1982) and Alaska (Koski 2009). The smaller members of the cohort in the East Twin and West Twin rivers were more likely to move downstream and enter estuarine waters during fall than were the larger members of the cohort (Roni et al. 2012), but the factors affecting this downstream movement (e.g., density and competition, high flows, and decreasing temperatures) remain uncertain (Roni et al. 2012). Prior to dam removal, Coho Salmon in the Elwha River were found primarily in the lower 4 km (Pess et al. 2008) compared to the broader range available in Salt Creek. Thus, many Elwha River juveniles may have encountered the estuary in the course of their normal downstream movement because they emerged only a short distance above the estuary and did not find suitable habitat prior to reaching the estuary. If so, an increased upstream distribution of Coho Salmon spawning after dam removal may decrease the proportion of the population that enters the estu-

ary as fry and parr because suitable rearing habitat is present above the sites where the dams were located (Pess et al. 2008), at least until the carrying capacity is reached. The somewhat smaller fraction of the Salt Creek population that was caught during the fall may reflect the greater length of stream available for rearing habitat, although many other factors might affect the proportions of fall versus spring catches and presmolt versus smolt catches, including differences between the two rivers and their estuaries. One additional complication is that the estuaries contained some smolts from other river systems, as indicated by genetic analyses (Shaffer et al. 2012); this occurs because the Strait of Juan de Fuca is a migratory corridor and feeding area for salmon (Weitkamp and Neely 2002). Future changes in the Elwha River estuary's configuration may make it more attractive to smolts from other systems, making comparisons even more difficult.

The Elwha River Coho Salmon presmolts were also larger than Salt Creek presmolts, but information on the size distribution of juveniles residing upstream in each system at the time of estuarine sampling was not available, thus limiting our ability to interpret the difference. Density depresses growth in Coho Salmon (Scrivener and Anderson 1984; Spalding et al. 1995), so the larger size of the Elwha River fish might reflect the lack of competition; however, thermal regimes and other ecological factors also affect size. It will be important to monitor body size in the future as the population expands spatially and numerically and reaches its carrying capacity.

The Lower Elwha Klallam Tribe Fish Hatchery produced an average of 380,863 smolts/year from 2007 to 2011 (Table 1), and these fish probably contributed to the earlier smolt migration in the Elwha River relative to Salt Creek (Table 2). The hatchery's smolt production is probably far greater than would be possible from the few adults spawning naturally (Pess et al. 2008), so the vast majority of Elwha River Coho Salmon smolts were probably of hatchery origin. Indeed, it is likely that the approximately 80,000 unclipped Coho Salmon smolts that were released from the hatchery each year (Table 1) considerably outnumbered the wild smolts based on an estimate of smolt production as a function of stream length (Bradford et al. 1997). However, despite the numerical dominance of hatchery fish in overall production, three lines of evidence indicate that the presence of naturally spawned fish in the Elwha River estuary was disproportionate to their likely abundance. First, unclipped presmolts were caught during periods when hatchery fish would not be present. Second, the length distributions of clipped and unclipped smolts differed significantly. Third, at least half of the smolts sampled in the estuary were unclipped, even though approximately 75% of the hatchery fish were clipped. Thus, fish of natural origin were probably over-represented in estuarine sampling relative to their abundance. The hatchery fish may have moved through the river and into the Strait of Juan de Fuca more rapidly than the wild fish and therefore would have comprised a smaller fraction of the fish sampled in the Elwha River estuary relative to their overall abundance. This is consistent with

the tendency for large Coho Salmon smolts to migrate earlier than small smolts (Shapovalov and Taft 1954; Durkin 1982; Irvine and Ward 1989), the tendency for hatchery Coho Salmon smolts to migrate rapidly (Hayes et al. 2004), and the tendency for hatchery-produced Chinook Salmon *O. tshawytscha* to occupy northern Puget Sound for a shorter period than naturally produced fish (Rice et al. 2011). In addition, the inverse correlation between the number of smolts released from the hatchery and the catches in April but not in May of the same year suggests that there is some tendency for density to affect residence time; however, the limited number of years makes such a conclusion speculative.

The before–after study design has its advantages (Roni et al. 2008) but also has many limitations in this and other cases wherein the goal is to detect the beneficial or harmful effects of a large event. Interannual variation owing to spawner–recruit processes, climate, and other factors greatly complicates this approach (e.g., Holtby and Scrivener 1989). As many authors have pointed out, natural variation hinders the ability to detect changes in salmonid (and other) populations unless the effect is large or unless the period of record is long (e.g., Lichatowich and Cramer 1979; Bisson et al. 2008; Dauwalter et al. 2009). Consequently, the short period of record (5 years) in the present study will inevitably compromise our ability to conduct comparisons with post-dam-removal abundance, size, timing, and other aspects of salmon population biology. However, this information is still an advance over cases of natural or anthropogenic disasters for which the “before” data were even more limited, with serious consequences for the ability to detect change (e.g., the *Exxon Valdez* oil spill in Prince William Sound, Alaska; Paine et al. 1996).

Prior to dam removal, an assessment of salmon production in the region concluded that “Restoration of the Elwha River may represent one of the best opportunities to improve natural production of Coho [in the Strait of Juan de Fuca region]” (PSSSRG 1997). It remains to be seen whether this potential will be realized, but the information in the present study provides some basis for comparison as the population expands spatially and numerically towards its natural carrying capacity in the rapidly changing environment of the Elwha River system.

ACKNOWLEDGMENTS

We thank the many people who helped collect the data for this project. Jack Ganzhorn (director of the Peninsula College Fisheries Program) provided project interns for many years of field sampling, and Terry Johnson (Washington Department of Fish and Wildlife) made the maps. Financial support was provided by NOAA Fisheries, the Environmental Protection Agency, Patagonia, the Olympic Peninsula Chapter of Surfrider, the North Olympic Peninsula Lead Entity (Selinda Barkhuis, coordinator), the Clallam County Marine Resources Committee, and the National Science Foundation (Research Experiences for Undergraduates Grant Number 0452328 to Peninsula College and

Western Washington University). We thank the Lower Elwha Klallam Tribe, Malcom Dudley, and Chuck Janda for providing site access. We are grateful to George Pess and Phil Roni (NOAA) and Michael McHenry, Larry Ward, and Douglas Morrill (Lower Elwha Klallam Tribe) for providing comments on drafts and information on the hatchery program. The analysis and reporting were funded in part by a grant to T.Q. from Washington Sea Grant, University of Washington, pursuant to NOAA Award Number NA10OAR4170075, Project R/LME-7. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies.

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