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ARTICLE

Relocation and Recolonization of Coho Salmon in Two Tributaries to the Elwha River: Implications for Management and Monitoring

Martin Liermann* **and George Pess**
National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Fish Ecology Division, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

Mike McHenry
Natural Resources Department, Lower Elwha Klallam Tribe, 2851 Lower Elwha Road, Port Angeles, Washington 98363, USA

John McMillan
Trout Unlimited, 484 Dodger Lane, Port Angeles, Washington 98363, USA

Mel Elofson
Natural Resources Department, Lower Elwha Klallam Tribe, 2851 Lower Elwha Road, Port Angeles, Washington 98363, USA

Todd Bennett
National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Fish Ecology Division, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

Raymond Moses
Natural Resources Department, Lower Elwha Klallam Tribe, 2851 Lower Elwha Road, Port Angeles, Washington 98363, USA

Abstract

In 2012 the lower of two Elwha River dams was breached, restoring access of anadromous salmonids to the middle Elwha River (between the two dams), including two distinct tributaries, Indian Creek and Little River. While comparable in size, Indian Creek is considerably less steep than Little River (mean slope of 1.0% versus 3.5%, respectively) and has a warmer stream temperature regime due to its source, Lake Sutherland. During and after breaching, Coho Salmon *Oncorhynchus kisutch* were relocated to these tributaries from lower Elwha River hatcheries (below the dams) to determine if individuals from a hatchery-dominated population would successfully spawn and seed the systems with juveniles and to assess differences in recolonization between the streams. Transplantation led to immediate spawning, which resulted in levels of smolt out-migrants per stream kilometer comparable with other established Coho Salmon populations in the Pacific Northwest. During the first 2 years of the relocation, redd densities in the two systems were similar but Indian Creek produced four to five times as many smolts per kilometer as Little River. In addition, fry out-migration occurred 2 to 4 weeks earlier in Indian Creek, as predicted by the warmer incubation temperatures. In the first years of the study, there was little evidence of natural colonization of the two tributaries by adults. However, in 2016 over half of the observed adults returning to the two tributaries were not transplanted, suggesting that the progeny from

*Corresponding author: martin.liermann@noaa.gov
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the transplanted fish were returning to their natal waters. This work demonstrates that transplanting hatchery-dominated Coho Salmon adults into newly available habitat can result in immediate freshwater production that is comparable to other systems and that density and timing of juvenile out-migrants can differ dramatically based on the seeded habitat.

Dams and other artificial in-river obstructions have truncated the migration of many anadromous fish species in Atlantic and Pacific river systems (NRC 2004), resulting in the severe reduction or extirpation of many populations (NRC 2004; McClure et al. 2008). As dams have aged and the awareness of their impacts have increased, such barriers are increasingly being removed to facilitate the recovery of threatened fishes, leading to opportunities for reintroduction of salmonid populations (Anderson et al. 2014). Anadromous salmonids have been reintroduced in dam-removal projects using a variety of strategies, including natural colonization, planting of hatchery juveniles and adults, relocation of natural-origin and hatchery adults, and a combination of the preceding actions (Anderson et al. 2014). Scientists and managers have observed how recolonization by different migratory fishes is shaped by the first colonizing adults and their habitat (Berdahl et al. 2014; Pess et al. 2014).

The success of natural salmonid recolonization, particularly during the early stages, depends on the tendency of individuals to stray from the source population and the availability of habitat that is accessible and satisfies the specific requirements of the species. Of the Pacific salmon *Oncorhynchus* spp., Coho Salmon *O. kisutch* tend to have one of the lowest stray rates, demonstrating high fidelity to their natal streams (Pess 2009). While Coho Salmon utilize a range of habitats, adults often spawn in small streams and juveniles tend to prefer pools and other slow-water habitat (Bisson et al. 1988; Rosenfeld et al. 2000; Sharma and Hilborn 2001) common in low-gradient wetland watersheds. The success of Coho Salmon in these habitats also depends on water temperature, with optimal incubation and rearing temperatures ranging from 2.5°C to 6.5°C and 12°C to 15°C, respectively (Edsall et al. 1999; Richter and Kolmes 2005). Understanding these and other preferences in the context of newly available habitat can

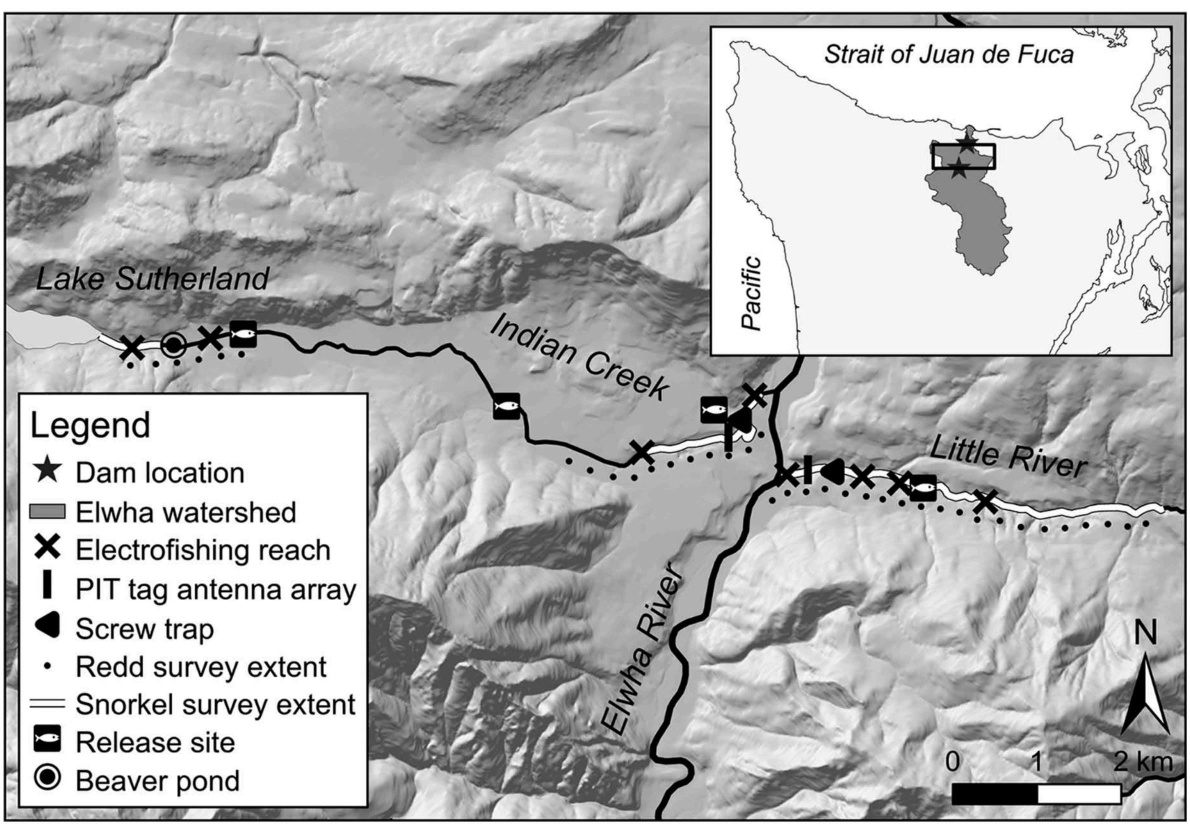

FIGURE 1. Map of Little River and Indian Creek in Washington. The middle release site on Indian Creek was only used in 2012 when it replaced the lower site. The displayed snorkel survey extent and redd survey extent represents the maximum extent of the surveys across all years.

help guide managers tasked with evaluating and implementing measures to speed recolonization, particularly when deciding if and how to use fish relocation.

The Elwha River dam removal project provides an opportunity to evaluate the effectiveness of the relocation of hatchery-dominated adult Coho Salmon as a tool for accelerating recolonization and to compare the productivity of these relocated fish in two very different tributaries. Two dams (Elwha Dam and Glines Canyon Dam, 33 m and 64 m high, built in 1913 and 1927, at river kilometer [rkm] 7.9 and 21.6 [measured from the river mouth], respectively) in the Elwha River (Figure 1) blocked access to over 70 km of freshwater aquatic habitat for anadromous species (Duda et al. 2008). The removal of both dams was initiated in September 2011 and by April 2012 the Elwha Dam was removed, providing access to the Middle Elwha River between rkm 7.9 and 21.6. Starting in 2011, as the Elwha Dam was being removed but was not passable to fish, adult Coho Salmon from hatcheries in the lower Elwha River were moved to two tributaries of the middle Elwha River—Little River and Indian Creek. The impetus for this relocation was to initiate the recolonization process in tributaries that provide refuge from the high suspended sediment loads (up to 5,000 mg/L) created by the removal of the upper (Glines Canyon) dam (Magirl et al. 2015).

Little River and Indian Creek are the first major tributaries above the lower dam site (Elwha Dam) and were some of the first sites naturally recolonized by anadromous fish (McMillan et al. 2012). Although the tributaries enter the Elwha River at almost the same location, they have very different stream characteristics, temperature regimes, and resident fish assemblages (Brenkman et al. 2008). Little River enters the Elwha River from the east side of the watershed and is a steep-gradient mountain channel that drains snowfields in Olympic National Park. Indian Creek is a low-gradient and low-elevation stream that drains from the west side and originates at Lake Sutherland and its associated wetlands. The differences in habitat characteristics and fish communities provide a unique opportunity to study how Coho Salmon, derived from a population confined to the lower river for over 100 years and heavily influenced by hatchery practices, respond to two very different habitats.

From the winter of 2011 to the summer of 2015, we characterized Coho Salmon abundance, distribution, and diversity using several enumeration techniques, including surveys of adult redds, juvenile snorkel surveys, juvenile parr estimates with electrofishing, tagging with passive integrated transponder (PIT) tags combined with downstream antennas, and rotary screw traps to estimate fry and smolt out-migration. The combination of techniques allowed us to generate stream-specific estimates of abundance and movement for different life stages of Coho Salmon in Indian Creek and Little River. We used this data to compare spawning densities and juvenile production in these tributaries with those metrics in other established regional populations. In addition, we contrasted the two tributaries based on stage-specific densities and the extent and timing of juvenile movement. Results of these comparisons will not only improve knowledge about how recolonization may be shaped by an interaction between Coho Salmon and their habitat during and closely following dam removal but will also help elucidate the effectiveness of relocating adults and clarify the benefits and limitations of different monitoring techniques.

METHODS

Study sites.—Little River and Indian Creek are located 5 km above the former Elwha Dam site and enter the main-stem Elwha River from opposite sides of the watershed (Figure 1). They drain approximately 52 and 60 km^2, respectively. Little River is relatively steep (mean gradient ~3.5%), and its headwaters originate on Hurricane Ridge (elevation 1,615 m) in Olympic National Park. With its north aspect and snowmelt-driven hydrology, Little River is a coldwater stream with a mean yearly temperature of 7.5°C (SD, 2.2) (Washington Department of Ecology 2016). At rkm 4.4 a series of three waterfalls act as either partial or full barriers to adult and juvenile Coho Salmon passage. Prior to dam removal, the fish community was dominated by resident Rainbow Trout *O. mykiss* (Brenkman et al. 2008).

In contrast, Indian Creek empties from Lake Sutherland (elevation 155 m), flows through a low-gradient valley (~0.6%) with an extensive wetland complex for 8 km, and then steepens in its lower 1 km (~2.5%) before emptying into the Elwha River main stem. All 9 km of channel are accessible to anadromous fish and contain suitable salmonid spawning and rearing habitat. Given its lake influence and low elevation, Indian Creek is a relatively warm stream with a mean yearly temperature of 9.0°C (SD, 2.3) (Washington Department of Ecology 2016). Temperatures are warmer close to the lake source and cooler lower in the system, where the lake has less influence (McMillan et al. 2014). The predam fish community was dominated by Coastal Cutthroat Trout *O. clarkii clarkii* and a smaller number of resident Rainbow Trout (Brenkman et al. 2008). Both basins have a history of forestry, and current land use is a mix of residential, commercial, and national park.

Relocation of adult Coho Salmon.—Starting in 2011 and continuing to the present (2017), adult Coho Salmon were relocated from hatchery returns in the lower river to the two tributaries (McHenry et al. 2017). In 2015, hatchery returns were very low and there were no relocations. The relocated fish were either surplus from the Lower Elwha Klallam Tribe's hatchery or caught in the Washington Department of Fish and Wildlife hatchery trap. These fish were used for the relocation because the current population of Coho Salmon in the Elwha River is dominated by hatchery-origin fish (~95%) (McHenry et al. 2017). In response to declines in the Coho Salmon population after dam construction, the lower river was heavily out-planted with out-of-basin fish starting in the

1950s and continuing into the 1970s. In the mid-1970s, a hatchery was constructed in the lower river, relying initially on a mixture of Elwha River and Dungeness River broodstock. Since 1977, broodstock has been taken largely from the Elwha River. While natural spawning occurred in the lower river, prior to dam removal approximately 90% of returning adults were of hatchery origin. Transplanted fish had similar hatchery-origin percentages ranging from 92% in the 2013–2014 season to 86% in the most recent seasons with releases (2014–2015, 2016–2017). Hatchery releases have ranged from close to 2 million smolts in 1985 to approximately 300,000/year over the last decade (2007–2016).

Sex was determined for all fish, except for a small subset of the 2013 releases, and all fish were floy-tagged. Adult Coho Salmon were first relocated to the main-stem Elwha River in brood year 2011 (winter 2011–2012) immediately below the confluences of the two tributaries with the main-stem Elwha River. However, over 55% of those fish fell back to the lower river and the hatchery, presumably because main-stem river conditions were unfavorable and their natal waters were in the lower river. Still, some adults were observed spawning in the tributaries, but conditions for surveys were too poor to generate a rigorous estimate of adults. Consequently, adult Coho Salmon relocations in brood years 2012–2015 were focused in the tributaries, after which fewer than 5% of the adults were observed falling back to the lower river and hatchery.

Data collection.—Data was collected from October 2011 through October 2016 to estimate daily temperature, redd abundance, summer parr densities, and timing and extent of movement out of the tributaries. We were not able to access all portions of both tributaries equally, a limitation that impacted basinwide survey techniques such as redd enumeration and snorkel surveys. For example, while we surveyed over 70% of the anadromous fish habitat in Little River, surveys in Indian Creek were typically restricted to the lower 1.5 km and upper 2.8 km of anadromous fish habitat (<40%) due to a combination of private land ownership, poorer water clarity, and difficulty accessing and moving within the heavily vegetated channel.

Redd and adult surveys.—Redd surveys were attempted every 7–10 d during the Coho Salmon spawning season (October to January) in all accessible reaches of the two tributaries (Figure 1) (McHenry et al. 2017). Surveyors walked upstream to enumerate redds, which were identified as disturbed areas in the streambed where gravels were overturned. Each redd was identified with a distinct location (latitude and longitude) and number and flagged to avoid recounting on subsequent visits. For three brood years (2012, 2013, and 2016), the proportion of live and dead spawners with floy tags (all relocated adults were floy-tagged) was recorded. Fish for which the tagging status was unknown due to visibility were not included.

Juvenile snorkel surveys.—Snorkel surveys were conducted in late July to early August of 2012 and 2014 for both tributaries to characterize the spatial distribution of juveniles. Traditional juvenile snorkel survey techniques were used to estimate the abundance of salmonids in all habitat units greater than 0.2 m in depth (Dolloff et al. 1993; Thurow 1994). All units were sampled by the same experienced diver and habitat recorder to reduce bias associated with multiple surveyors (Hankin and Reeves 1988; Thompson and Mapstone 1997).

Juvenile electrofishing and PIT-tagging.—Electrofishing was conducted once a year during spring and summer in four 100-m reaches each in Little River and in Indian Creek, from 2011 to 2015. Reaches were distributed throughout each stream longitudinally to capture as much environmental variability as possible. Surveys were conducted to estimate juvenile Coho Salmon density and to insert PIT tags for estimating the extent and timing of movement in and out of the tributaries and between sites. Each 100-m reach was block-netted at the upper and lower end, and three electrofishing passes (500 v, unpulsed DC) were performed in an upstream direction with two to three netters (Temple and Pearsons 2007). After each electrofishing pass, captured Coho Salmon juveniles were anesthetized (tricaine methanesulfonate [MS-222]), counted, and checked for PIT tags (12.5 mm in length, 2.1 mm in diameter; Digital Angel, St. Paul, Minnesota). All untagged Coho Salmon larger than 55 mm and 2.0 g received a PIT tag in the peritoneal cavity (Prentice et al. 1990). The PIT tags were unique identifiers that were detected during recapture events at sample reaches or at stationary receivers. The fish were retained until they had recovered and then released into the same reach. If fish had previously been tagged, the tag number and capture location were recorded.

Antenna detections of PIT tags.—Permanent PIT tag antenna arrays were located at the lowest possible access points in both tributaries. Antenna arrays were installed in spring of 2013 in Little River at rkm 0.5 and in Indian Creek in the fall of 2012 at rkm 0.75. Periodic efficiency trials were conducted from late winter to early summer when fish captured in the screw traps were available. For each trial, PIT tags were inserted in a group of Coho Salmon juveniles that were subsequently released 50–100 m above the antenna arrays. The combined detection efficiency (the proportion of released individuals detected at the array) for the Indian Creek and Little River antenna arrays over the course of 3 years was 89% (SD, 13). Mean annual efficiency at Indian Creek was higher (97%; SD, 4) than at Little River (73%; SD, 9).

Screw trap out-migrant data.—Screw traps were installed on both tributaries to enumerate the Coho Salmon fry and smolt out-migration (e.g., Volkhardt et al. 2007). Screw trap operation started in April 2012 in Little River and in February 2013 in Indian Creek, with a typical season starting in February and ending in July (McHenry et al. 2016). Screw traps were placed at the lowest possible access points in the two tributaries (in Little River at rkm 0.5, in Indian Creek at rkm 0.7) close to the PIT tag antenna arrays. Both traps were floated on pontoons. The cone sizes were 1.5 m and 1.2 m for Little River and Indian Creek, respectively. Trap efficiency was estimated with marked releases of 25–100 fish caught in the trap. The release sites were approximately 100 m above the traps. Due to the availability of fish, only one size-class and species of fish was generally released during each 1–2-week period. This choice was based on the most abundant fish migrating past the trap during the period. Fish used in the trials tended to be similar in size to age-0 and age-1 Coho Salmon during their periods of out-migration. Efficiency estimates averaged 35% (SD, 24), with Indian Creek tending to have a higher efficiency (48%; SD, 30) than Little River (26%; SD, 17). All passage estimates were adjusted for efficiency and missing days (McHenry et al. 2016).

Temperature data.—Temperature loggers were located at several sites in Little River and Indian Creek from 2011 to 2015, although there were many large temporal gaps in the data for any individual recorder. For Little River, where between-site variability in temperature was minimal, we could construct a composite temperature series for the entire period using data from multiple readers. For Indian Creek, where the upper lake-influenced reaches tended to be substantially warmer than groundwater-influenced lower reaches (McMillan et al. 2014), we constructed two series, one for the lower river (~100 m from the confluence with the Elwha River main stem) and a second for the upper river (~0.5 km from the Lake Sutherland outflow). The lower Indian River site had no data for the first 10 months of the study. We used the relationship between the lower and upper sites for 2 years with complete data to fill in this gap. Because this relationship changed seasonally but was relatively consistent across the 2 years, we fit a loess smoother to the relationship between Julian day and the log ratio of the temperatures at the two sites. This fit was then used to backfill the 10 months using Julian day and the upper site temperatures. The error introduced in this extrapolation will affect the calculations for this site and period but should have little effect on the broader between-stream and between-year comparisons.

Analysis.—We synthesized the different sources of data to quantify characteristics of adult and juvenile Coho Salmon during the early stages of recolonization and to compare these characteristics in Indian Creek, Little River, and other established systems documented in the literature. When describing the results we did not use statistical tests but instead relied on graphical displays of the data supplemented with 95% confidence intervals where possible (e.g., Bradford et al. 2005). However, note that nonoverlapping intervals serve as a conservative test for a difference (e.g., Schenker and Gentleman 2001). To reduce the chances of presenting spurious results, we focus on patterns that are consistent across years and/or sites and avoid highlighting isolated differences. Where possible we display the raw data.

Redd abundance and density.—We characterized the abundance and density of Coho Salmon redds in each stream and year. We summed the weekly redd survey data to calculate the total number of Coho Salmon redds per stream per year as our estimate of abundance and then divided the annual redd total by total accessible kilometers of river in each stream to generate an estimate of linear redd density. All of Indian Creek was assumed to be habitable (9 km), while only the lower 4.4 km of Little River, below a series of falls, was assumed to be habitable. Because large portions of Indian Creek could not be surveyed, total redds and redd densities should be considered lower bounds with planted females serving as an upper bound (since almost all observed adults were relocated and tagged through brood year 2014). We visually compared the annual redd densities in Little River to those in Indian Creek and also compared the densities in the two tributaries to estimated minimum densities at full seeding, N^*, for 13 established populations in the Pacific Northwest (Bradford et al. 2000).

Stream temperatures and time of emergence.—We summarized stream temperatures to determine the extent of variation between the two tributaries and to estimate the mean time of emergence in Little River and upper and lower Indian Creek. For water temperature, we calculated (1) the maximum weekly average temperature as the maximum of average daily temperatures for each 7-d period and (2) the average temperature during the observed core of the incubation period (December 1 through March 1). We also estimated the timing of fry emergence for each redd based on the temperature data and approximate redd construction date (equation 4 in Beacham and Murray 1990):

$$\log_e(D) = \log_e(a) - b\log_e(T - c),$$

where D is the days to emergence after fertilization, and T is the mean incubation temperature. The values of the parameters $\log_e(a) = 7.018$, $b = -1.069$, and $c = -2.062$ were taken from Beacham and Murray (1990). The emergence date for each redd was estimated by iterating forward in time from the estimated date of redd construction and stopping when the mean temperature and time span to that date predicted emergence. For Indian Creek, this procedure was repeated for both temperature series (upper and lower) and the dates were combined. An interval was then created based on the dates by which fry were predicted to emerge for 10% and 90% of the redds. These intervals were compared to the timing of fry out-migrants seen at the screw traps.

Juvenile abundance and density.—We characterized the density (number/100 m) of juvenile Coho Salmon for each electrofishing reach and year (surveyed during late summer). The mean linear densities of juvenile Coho Salmon per 100 m and 95% confidence intervals were estimated based on three-pass electrofishing and a depletion estimator (Carle and Strub 1978). We visually compared the electrofishing estimates of density between streams and to snorkel survey density estimates for the same reaches and years (surveyed in late summer but on different dates from the electrofishing surveys).

Juvenile movements and smolt production.—Movements by juvenile Coho Salmon were estimated using PIT tag detections at the fixed readers and screw trap captures. The PIT tag detections were summarized based on the date of detection (August–November, November–February, and March–July), year, and tagging site. Detections at the antenna arrays were not adjusted due to the low number of efficiency trials and the fact that trials were restricted to the spring season when fish were available from the screw traps. This was noted when comparing the results between the two streams. Fry and smolt out-migrations for each year and tributary were characterized using screw trap catches. Estimates of total fry and smolt out-migrants along with 95% credible intervals were constructed based on catches expanded with efficiency trials using a Bayesian model (McHenry et al. 2016). These estimates were contrasted across tributaries and years. In addition, the smolt numbers were compared to estimates of smolts per kilometer for 39 established populations in Washington State (Bradford et al. 1997).

RESULTS

Redd Abundance and Density, and Adult Origin

Total numbers of relocated adult female Coho Salmon and their redds were quite variable across years due to variation in the supply of fish returning to the hatcheries. The total number of relocated adult female Coho Salmon per year ranged from 0 to 156 in Little River and from 84 to 261 in Indian Creek (Table 1). Annual total redd abundance ranged from 28 to 126 in Indian Creek and from 5 to 160 in Little River (Table 1). Those totals equated to redd densities that ranged from 6 to 28 redds/km in Little River and from less than 1 to 18 redds/km in Indian Creek (Figure 2). However, redd counts in Indian Creek are likely biased low since redd survey access was limited (Figure 1), and the actual number of redds was likely closer to the number of relocated females. This is also supported by the data. We typically counted almost as many redds as relocated females in Little River, while the number of redds we observed in Indian Creek was much lower than the numbers of relocated females (Figure 2). With this in mind, in most cases, redd densities likely fell within the range of previously reported values necessary to achieve full seeding (N^* in Bradford et al. 2000; Figure 2). The percent of observed adults in the two tributaries with floy tags (all transplanted fish were floy-tagged) was 94% (17 out of 18) for brood year 2012 and 97% (253 out of 260) for brood year 2013. In 2016, this percentage more than halved to 45% (48 out of 107).

Water Temperature and Emergence Timing

We observed large differences in average daily stream temperature between upper and lower Indian Creek, between Indian Creek and Little River, and across brood years during key Coho Salmon incubation and rearing stages (Figure 3; Table 2). The upper Indian Creek site, immediately below the outlet from Lake Sutherland, was by far the warmest, especially in the summer when the maximum weekly average temperature was 8–10°C degrees higher than the other sites (Figure 3; Table 2). The lower Indian Creek site and Little River were more similar, although at both Indian River sites

TABLE 1. Life stage specific numbers of Coho Salmon by brood year and tributary. The total kilometers of Coho Salmon habitat in Little River and Indian Creek are 4.4 km and 9.0 km, respectively. The "relocated" measurement is the number of adult females relocated to the tributaries. The "tagged/total" measurement is the number of tagged fish divided by the number of fish whose tagging status could be determined.

		Brood year					
Tributary	Measurement	2011	2012	2013	2014	2015	2016
Indian Creek	Relocated		102	261	84	0	175
	Redds	28	36	126	30	1	82
	Tagged/total		3/4	131/136			48/106
	Fry migrants		17,494	19,268	3,570		
	Parr (electrofishing)	6,120	1,290	5,265	3,668		
	Parr (snorkel)	6,552		2,160			
	Smolt migrants	9,534	9,030	7,330	10,393		
Little River	Relocated		21	156	0	0	0
	Redds	58	10	160	5	0	21
	Tagged/total		15/15	122/124			0/1
	Fry migrants	26,110	16,262	7,422	6,220		
	Parr (electrofishing)	2,310	1,419	2,629	2,112		
	Parr (snorkel)	1,553		1,923			
	Smolt migrants	872	1,272		183		

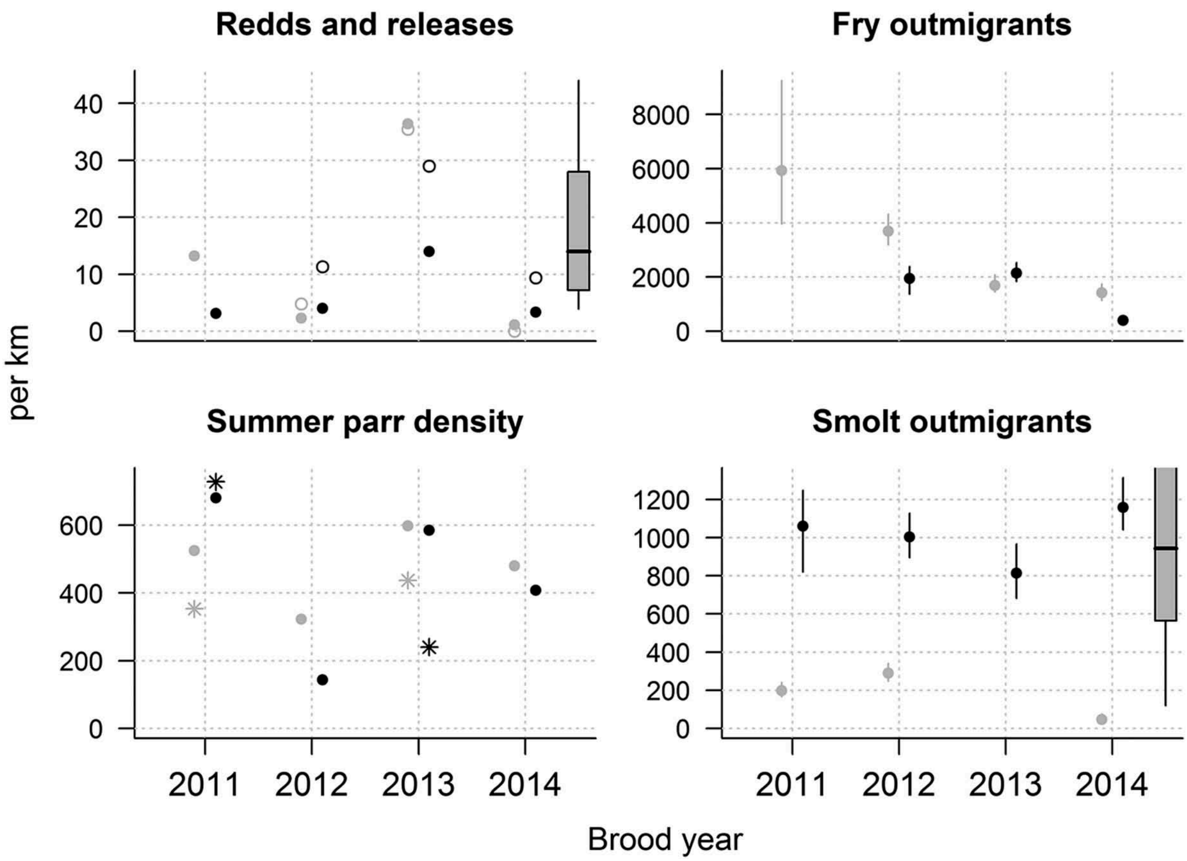

FIGURE 2. Estimated density of Coho Salmon redds, fry out-migrants, summer parr, and smolt out-migrants (each per km) by stream and year. Little River points are in gray and Indian Creek points in black. In the top left panel, open circles represent relocated female fish released into the stream and the filled circles represent observed redds. Asterisks in the bottom left panel represent parr densities estimated from the 2012 and 2014 snorkel surveys (excluding the beaver pond in Indian Creek). Brood year 2013 smolts were not reported because the trap was not operating during most of the smolt migration period in 2015. The gray box in the upper left panel is a box plot of estimates of the minimum number of female spawners per kilometer at full seeding for 13 populations in the Pacific Northwest (Bradford et al. 2000). The gray box in the lower right panel represents the average number of smolts per kilometer for 39 populations in Washington State (Bradford et al. 1997).The line in each box represents the median, the box dimensions represent the 25th and 75th percentile ranges, and the whiskers show the range of the data.

the increase in temperatures during the spring occurred earlier than in the Little River (Figure 3). This along with slightly warmer winter temperatures in Indian Creek resulted in warmer mean temperatures in both Indian Creek sites during the incubation period (Figure 3; Table 2).

Different stream temperatures in the two tributaries translated into pronounced differences in predicted fry emergence timing. Spawning timing was similar for the two tributaries, but fry were predicted to emerge 2–4 weeks earlier in the warmer Indian Creek (Figure 4). This aligned well with the observed differences in fry out-migration timing between the two tributaries (Figure 4). Fry (<75 mm) out-migration occurred predominantly from mid-March to mid-April in Indian Creek, and from late March to mid-May in Little River. Fry migration timing also varied among years, which was in part explained by among-year differences in incubation temperatures (Figure 4). For example, in 2014 when mean incubation temperatures were over a degree warmer than other years (Table 2), fry out-migration was also earlier than in other years (Figure 4). Smolt out-migration timing, however, was much more consistent with little observed difference between streams or years, regardless of temperature differences (Figure 4).

Juvenile Abundance and Density

Summer densities of juvenile Coho Salmon in the eight electrofishing reaches were variable across years and between sites (Figure 5), with no clear temporal or between-stream patterns. Densities ranged from 10 to 1,930 fish/km but tended to fall between 200 and 800 fish/km. Average densities ranged from 143 to 680 fish/km in Indian Creek and from 323 to 598 fish/km in Little River (Figure 2). Expanding for the total length of the

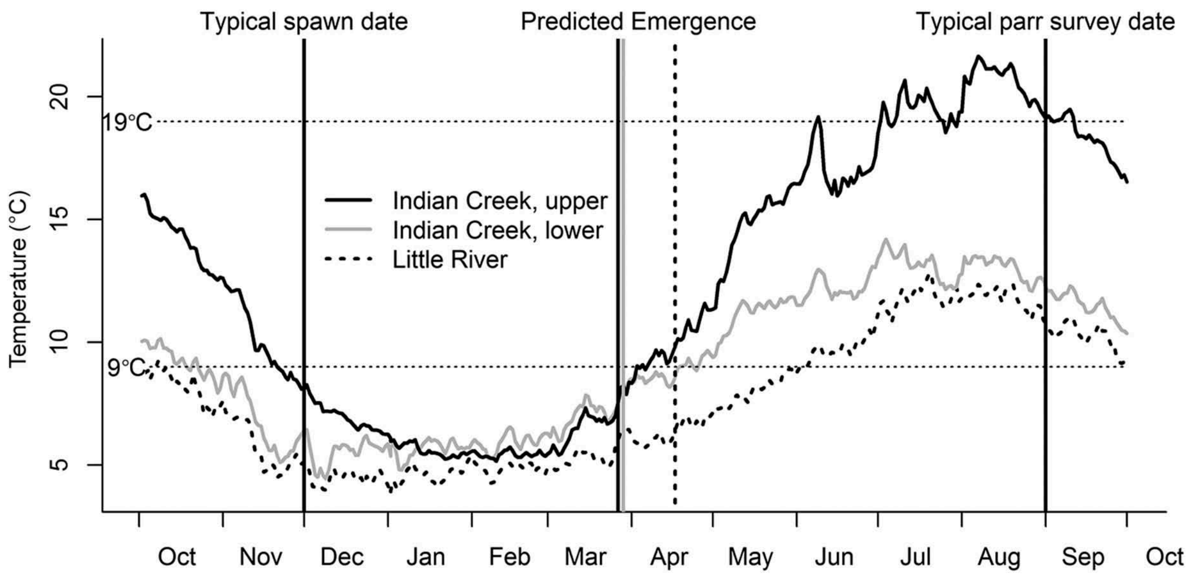

FIGURE 3. Daily temperature (°C) averaged across 4 years in three locations. In Little River the temperature varied little across sites and therefore is represented by a single temperature trajectory. For Indian Creek there were large differences in temperature by location due to the variable influence of water from Lake Sutherland (the initial source) and groundwater inputs lower in the system. Vertical lines indicate a typical spawn date, predicted emergence dates (see Figure 4), and a typical date at which parr were sampled in late summer. The two horizontal dashed lines represent a predicted optimal range of maximum weekly average temperatures for rearing (9–19°C; Sullivan et al. 2000).

tributary produced ranges of 1,290–6,120 fish for Indian Creek and 1,419–2,629 fish for Little River (Table 1).

For brood years 2011 and 2013, snorkel surveys were also conducted in the two tributaries. In Little River, where most of the stream accessible to juveniles was snorkeled, the mean densities of juvenile Coho Salmon were higher in the lower reaches, where the electrofishing sites were located, and lower in the upper reaches (Figure 1). Therefore expanding the electrofishing estimates from the lower river to the entire river will likely result in overestimation. In the lower river the densities for the two methods were comparable; thus, the snorkel survey estimate of the total abundance is probably more accurate. Snorkel surveys of Indian Creek were much less extensive and likely unrepresentative (Figure 1).

TABLE 2. Temperature (°C) statistics by year and site.

		Temperature		
Statistic	Brood year	Lower Indian Creek	Upper Indian Creek	Little River
Average incubation temperature Dec 1 to Mar 1	2011			4.3
	2012	5.5	5.8	4.4
	2013	5.0	5.5	3.9
	2014	6.9	6.8	6.1
Maximum weekly average temperature	2011			11.8
	2012	14.1	22.6	12.8
	2013	14.9	22.9	12.6
	2014	15.5		16.2

Extent and Timing of Juvenile Emigration and Smolt Production

The number of PIT tag detections and the timing of movement downstream through the antenna arrays tended to differ between the two tributaries (Figure 5). The total unadjusted detections for fish tagged at an individual site and year ranged from 0% to 100%. For reaches above the antennas (the upper three in each tributary), detections tended to be higher in Little River (40–60%) than in Indian Creek (10–30%). Adjusting for antenna efficiencies would likely accentuate the differences between the tributaries since Indian Creek tended to have higher estimated efficiencies based on the limited trials. Timing of out-migration also differed. Except for 2012, when the Little River reader was not in place until spring, the proportion of smolt out-migrants (March–July) was higher in Indian Creek. In fact, for the upper two Indian Creek reaches, all observed detections occurred as smolts. In Little River, the majority of the detections were in the fall or winter.

There were large differences in fry out-migrant densities among years but no consistent difference in densities between tributaries (Figure 2; Table 1). Conversely, smolt out-migrant densities were relatively consistent across years but over four times larger in Indian Creek than in Little River for the 3 years of available data. The number of smolts per kilometer in Indian Creek ranged from several hundred to over a thousand, which is well within the range of densities documented in other Washington

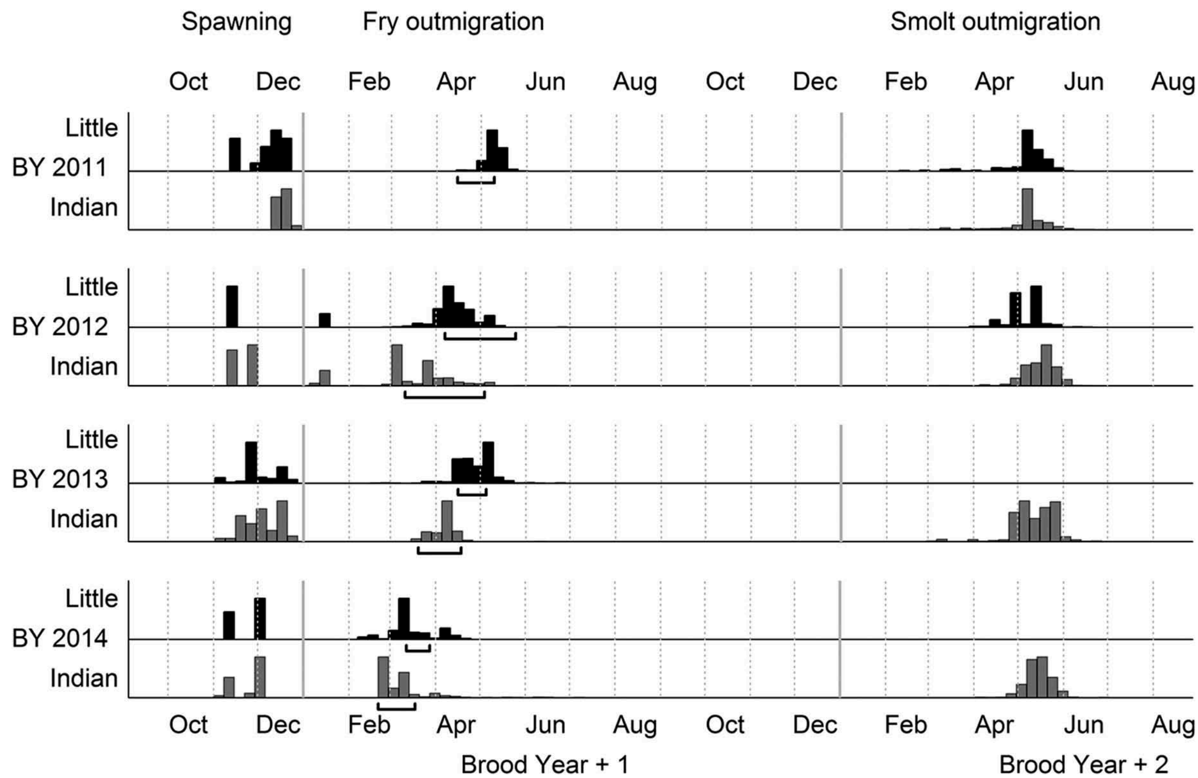

FIGURE 4. The timing of Coho Salmon spawning, fry out-migration, and smolt out-migration in Little River (Little) and Indian Creek (Indian) for brood years (BYs) 2011–2014. Each histogram is scaled so that the tallest bar is the same height. Therefore, the height of bars cannot be compared across years, streams, or life stages. All bars before February 1 of the first year are spawning. The horizontal bars under the fry out-migrants represent the period in which 80% of the redds are predicted to have reached their median emergence date. Smolt out-migrant timing was not reliable for fish from brood years 2013 and 2014 in Little River due to very low discharge in 2015 and a small total catch (11 fish in 2015 and 19 in 2016). The plot does not depict the migration out of and into the streams from summer through winter.

streams (Bradford et al. 1997; Pess et al. 2011; Figure 2; Table 1). However, the smolt densities observed in Little River, 200–300 fish/km, fell within the lower tail of this regional distribution.

DISCUSSION

The transplanting of over 1,600 adult Coho Salmon from the Elwha River hatcheries into Indian Creek and Little River during and after the removal of the lower Elwha River dam immediately resulted in successful spawning and fry and smolt out-migrant densities comparable to those in other Coho Salmon streams in the Pacific Northwest. During the first 4 years of relocations, adults that were examined for tags in the two tributaries were almost exclusively relocated fish (tagged). However, in 2016 over half of the adult fish for which tag status was determined were untagged, suggesting that the progeny of transplanted fish were beginning to return to the middle river.

While Little River and Indian Creek enter the Elwha River within 0.5 km of each other and were seeded with fish of the same origin, there were large differences in smolt production for the two tributaries. Indian Creek, with a mean gradient of less than 1% and a predominantly unconfined channel, produced over four times as many smolts per kilometer as Little River, which is much steeper and more confined. This is despite similar planting, redd, and fry out-migrant densities during the first 3 years. These differences are not unexpected given Coho Salmon overwintering preference for low-gradient, slow-water habitat (Nickelson et al. 1992; King et al. 2012). Warmer temperatures in Indian Creek, due to its lower elevation and lake source, resulted in earlier predicted emergence timing, which aligned well with the fry out-migration timing at the two traps. In contrast, smolt out-migration timing was relatively similar for the two tributaries. Spawn timing has been linked to stream temperature for Coho Salmon and other species, with earlier spawn timing tending to correspond with colder temperatures (Lister et al. 1981; Quinn 2011). As volitional movement of spawners into the two tributaries supplants the relocation effort, spawn timing may start to diverge in the two systems in response to the different temperature regimes (e.g., Gerson et al. 2016). This may reduce the difference in emergence timing.

Stage-specific freshwater densities in the two streams were generally within the range of densities found in other

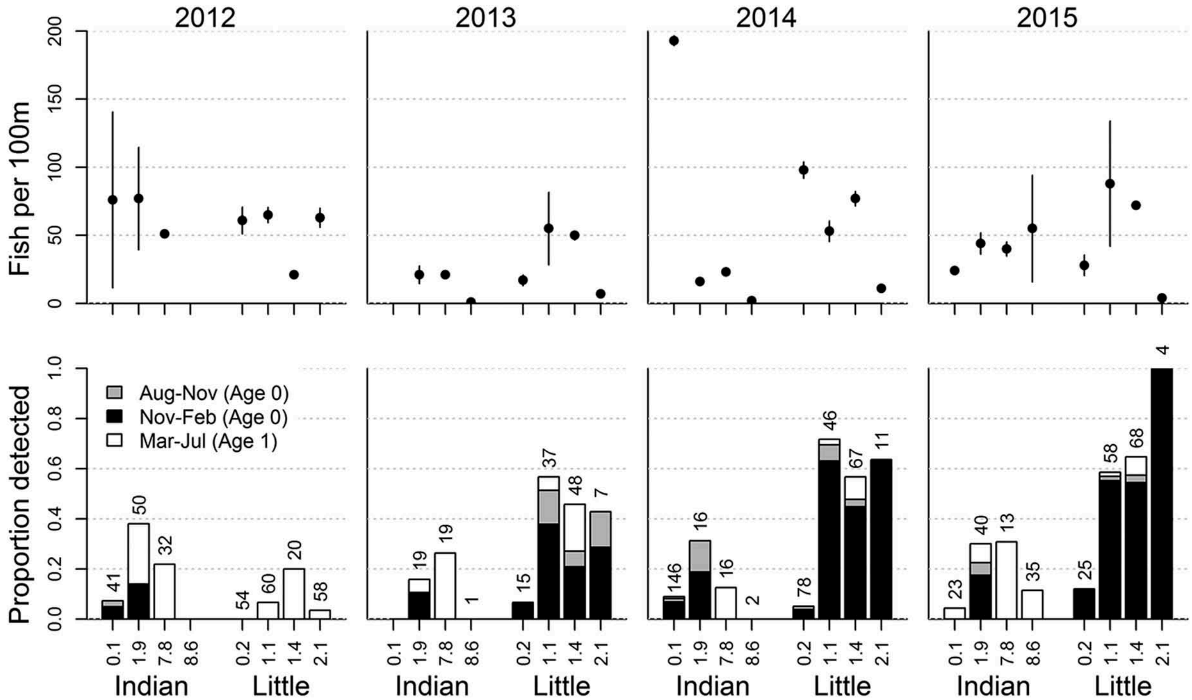

FIGURE 5. Density and proportion of tagged Coho Salmon detected at the instream antenna arrays, plotted by year and by reach (*x*-axis), where reach is designated by river kilometer. The error bars in the top panels show 95% confidence intervals. The proportion detected is the unadjusted proportion of PIT-tagged fish that were detected at the reader. The total number of fish tagged is indicated above each bar. The PIT tag reader was installed in Little River in the spring of 2013, so only age-1 fish were observed from the summer 2012 tagging event. In Indian Creek, the reader was installed in early fall, so some summer and fall migrating fish were likely not detected.

established Coho Salmon populations described in the literature (Bradford et al. 1997, 2000). Indian Creek smolt densities were comparable to the densities seen in other Washington streams, while Little River smolt densities were among the lowest (Bradford et al. 1997; Pess et al. 2011). We hypothesize that these lower densities in Little River may be attributable to a scarcity of protected low-velocity overwinter habitat in this high-gradient tributary (Nickelson et al. 1992). Tripp and McCart (1983), for example, found lower smolt densities when hatchery fry were planted in steeper headwater streams. We observed considerable variability among years for all Coho Salmon life stages except smolt out-migrants, suggesting that habitat may be limiting in both tributaries for the observed densities of spawners (Nickelson et al. 1992). Although redd density estimates in our two study tributaries fell within the lower range of those observed for other fully seeded systems (N* in Bradford et al. 2000), redd density estimates in Indian Creek are almost certainly underestimates due to problems with access.

On average, 1,000–2,000 fry/km left each of the tributaries in the spring. This constituted a relatively large proportion of the total fish leaving these systems (approximately two times the number of Indian Creek smolt out-migrants and 5–10 times the number of Little River smolt out-migrants). The overall contribution of these tributaries to Coho Salmon production will depend on the fate of these fry. The two tributaries flow into a section of the Elwha River that has an abundance of floodplain habitat, which has been recently augmented with the transformation of the former Lake Aldwell into a free-flowing river. Because floodplain habitat can be ideal habitat for rearing juvenile Coho Salmon (Morley et al. 2005; Rosenfeld et al. 2008), these fish may experience good survival. Leaving a tributary in the first year has been demonstrated to be a successful Coho Salmon strategy in other systems on the Olympic Peninsula (Peterson and Reid 1984).

During the first years of relocation (2011–2013), sediment released from the upper reservoir during deconstruction of the upper dam resulted in very high levels of turbidity in the main-stem river during spawning, incubation, and rearing. As the first major clear-water habitats above the former Elwha Dam, Indian Creek and Little River served as refuges where Coho Salmon could begin the recolonization process while the main stem was largely unsuitable. This strategy of relocation may be especially appropriate for Coho Salmon due to their lower rates of straying or exploration of new habitat when compared with other Pacific salmon species (e.g., Pess 2009; Westley et al. 2013). Burke et al. (2008), for example, found that none of 49 radio-tagged Coho Salmon adults came closer than 2.4 km to the lower dam when tagged on entry to the river prior to dam removal. This contrasts with Chinook Salmon *O.*

tshawytscha that were regularly seen in large numbers immediately below the dam. During the initial 3 years of relocation, almost all the fish observed in the tributaries were floy-tagged, indicating that they were relocated and not the product of natural recolonization. In addition, when relocation of adults to Little River was stopped after the 2013 brood year, redd densities fell dramatically and have remained low. However, in 2016 over half of the adult fish with identified tag status were untagged, suggesting a substantial volitional movement of spawners into the middle watershed. Many of these fish are likely progeny of the initial transplanted fish although the continually evolving habitat in the middle river could also be attracting more fish. Continued monitoring will be essential for characterizing the population of nontransplanted fish. This, in turn will inform decisions about future relocation of Coho Salmon in the Elwha River.

Bringing together data collected using different approaches and from multiple life-stages and locations allowed us to construct a more complete picture of freshwater residence and reduced the sensitivity of our results to a single source. However, there were still gaps in our knowledge. Specifically, where were the bulk of Indian Creek juveniles rearing and what was the fate of the of fry out-migrants from the two systems? In addition, high flows and turbidity during the winter season resulted in aborted redd surveys, and large portions of Indian Creek were not surveyed for redds or juveniles due to access and turbidity. Working in this complex and changing environment, our approaches to monitoring will necessarily adapt as our understanding of the system evolves.

After over 100 years of absence, Coho Salmon are now reproducing and rearing in the middle section of the Elwha River between the two former dams. The effort to accelerate recolonization through the relocation of adults from the lower-river hatchery returns into Little River and Indian Creek immediately produced levels of spawning and juvenile production that were comparable to other established Coho Salmon populations in the Pacific Northwest. While natural recolonization of the tributaries was negligible during the first years of relocation, in the most recent spawning season (2016–2017) more than half of the observed spawners in the tributaries with confirmed tagging status were not relocated. Given that the tributaries together produced over 35,000 fry and 7,500 smolts in 2013, many of these colonizers are likely progeny of fish that spawned in the tributaries. Differences in the response of the two tributaries to similar levels of transplantation reinforces established knowledge of Coho Salmon habitat preferences and highlights the importance of using this knowledge when setting expectations for projects like this. This work provides further evidence that behavioral plasticity sufficient to exploit new and varied habitat can remain viable even in a population heavily influenced by a hatchery environment for several decades. Such plasticity provides the flexibility necessary for successful recolonization of complex habitats that require diverse life history strategies to exploit fully. As habitat conditions throughout the Elwha River basin continue to evolve in response to dam removal and the Coho Salmon population expands into its new environment, the diversity of life history trajectories will likely increase conferring greater resiliency to the reestablishing population (Waldman et al. 2016). A suite of evolving methods will be necessary to monitor these complex dynamics to inform basin-specific decisions, such as when and where to relocate additional fish and how to adjust hatchery management, as well as provide guidance for future dam removal planning and monitoring.

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