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Initial response of Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) to removal of two dams on the Elwha River, Washington State, U.S.A.

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Abstract

Large dam removal is being used to restore river systems but questions remain regarding their outcomes. We examine how the removal of two large dams in the Elwha River, coupled with hatchery production and harvest restrictions, affect the population attributes of Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) in the Elwha River. Initial response to dam removal by Chinook salmon and steelhead was an increase in the number of returning adults and their watershed distribution over the pre-removal run size and area. Hatchery production and harvest restrictions have helped to increase Elwha Chinook salmon and winter steelhead abundance, particularly during dam removal. Naturally produced juvenile Chinook salmon and steelhead outmigrant abundance increased three years after adult passage was restored, suggesting that short-term impacts due to downstream sedimentation during and immediately after dam removal were short-lived. We have also observed a natural "reawakening" of the summer steelhead, particularly above the former dams. Our results suggest an integrated set of habitat, hatchery, and harvest actions can result in positive responses for salmonid populations.

Keywords

Dam removal, restoration, salmon, monitoring

Introduction

Dams are a major threat to the connectivity of river ecosystems across the world and have contributed to extinctions and imperiled status of migratory fishes (Pringle et al. 2000). Over the last several decades, there has been an increase in the number of dams that are deemed unsafe or are no longer meeting their intended objectives, resulting in over 1200 dams being decommissioned and removed over the last two decades (O'Connor et al. 2015; Bellmore et al. 2016). Dam removal can lead to a rapid ecosystem response including river channel formation in former reservoirs, restored migration of fish, and downstream changes in physical habitat (O'Conner et al. 2015; Tullos et al. 2016; Bellmore et al. 2019). Initial dam removal efforts focused on small structures (< 8 m in height) (Bellmore et al. 2016), but removal of large dams (> 10 m) has gained momentum, particularly in the Western United States (O'Conner et al. 2015).

Following dam removal fish can move upstream to recolonize former habitats and expand their distribution across a watershed (Bellmore et al. 2019), and habitat loss is a major factor in the decline of many fish species, which is one reason dam removal is increasingly being considered and implemented to assist the recovery of depleted populations of Pacific Salmon (Hare et al. 2019). Salmon can quickly recolonize new habitats and increase their population size exponentially, regardless of whether initial abundance from donor populations is small (i.e., less than 100) or large (i.e., ~ 1 million) (Milner et al. 2007; Kiffney et al. 2009; Pess et al. 2012*a*; Anderson et al. 2015). The rate of recolonization depends on several factors including the size and proximity to source populations in the same or nearby river systems, the types and characteristics of the new habitats, and the life history diversity of each species (Pess et al. 2014). Further, homing and straying are important to successful salmon recolonization, as strays are responsible for initial colonization while homing in future generations can maintain populations and contribute to population growth. Lastly, dam removal can potentially improve resilience by increasing diversity (e.g., Schindler et al. 2010) if unique life histories or habitats are above the dams (e.g., Beechie et al. 2006; Waples et al. 2008) and the adaptive genetic diversity to express those life histories remains

(Thompson et al. 2019). Hence, dam removal could benefit salmon by increasing spatial and temporal distribution, population size, and diversity, all of which are fundamental to improving viability of depleted populations of salmon.

In 1992, the Elwha River Ecosystem and Fisheries Restoration Act was signed into law, making it the largest dam removal in the history of the United States at the time (US Public Law 102-495; Winter and Crain 2008). The Act authorized the Department of the Interior to acquire and remove two dams on the Elwha River, Washington State - the Elwha and Glines Canyon dams. The goal of the Act was "full restoration of the Elwha River ecosystem and native anadromous fisheries." The intentional concurrent removal of the two large dams started in 2011 and was finalized in October 2014. Approximately 30 million metric tonnes (Mt) of impounded sediment were ultimately exposed to fluvial erosion, presenting a unique opportunity to simultaneously examine the geomorphic evolution of a river system and the associated ecological response, including the recolonization of upstream habitats by anadromous salmonids (Ritchie et al. 2018).

Approximately 65% of the stored sediment was eroded since dam removal, of which only ~10% was deposited in the fluvial system (Ritchie et al. 2018). The remaining ~90% of the released sediment was transported to the coast; expanding the delta by ~60 ha (Ritchie et al. 2018). This restored fluvial supply of sediment and wood substantially altered the freshwater channel morphology, and habitats within the estuarine and nearshore environment (Foley et al. 2017; Shaffer et al. 2017; Ritchie et al. 2018).

Removing the two dams on the Elwha River has also resulted in ecological responses by anadromous fish species. For example, Liermann et al. (2017) found that hatchery adult Coho salmon (*Oncorhynchus kisutch*) transplanted from the lower Elwha River into two tributaries of the Elwha above the former Elwha dam led to immediate spawning, resulting in levels of smolt outmigrants per stream kilometer comparable with other established coho salmon populations in the Pacific Northwest. Further, the timing and body size of juvenile outmigrants differed dramatically between two proximate tributaries based on the physical and biological characteristics of the newly occupied habitat (Liermann et al. 2017). Elwha River bull trout, almost entirely landlocked for a century, rapidly resumed anadromy and consumed marine prey (Quinn et al. 2017; Brenkman et al. 2019). However, responses of Chinook salmon and steelhead have not yet been documented.

Our study focuses on the short-term response of Chinook salmon (*O. tshawytscha*) and steelhead (*O. mykiss*) to the reconnection of the Elwha River. In this paper, we compare the abundance, distribution, and productivity of Chinook salmon and steelhead, before, during, and after dam removal. To accomplish this, we first estimated and compared the abundance of adults, smolts, and the proportion of natural and hatchery origin Chinook salmon and steelhead. Second, we estimated productivity of Chinook salmon as juvenile outmigrants per spawner, and as adult-to-adult return rate. Third, to better understand potential sediment impacts we examined whether smolt abundance and productivity differed in relation to sediment transport and river discharge indices during and after dam removal. Fourth, to better understand spatial expansion we estimated the spatial distribution of spawning adults. Fifth, we documented the life history diversity of steelhead to determine if it changed after dam removal. We examine and discuss this information in the context of historical and current studies of salmon recolonization, including natural recolonization of newly created habitats and restoration efforts associated with habitat reconnection through removal of anthropogenic barriers. Lastly, we discuss how multiple management actions in the form of habitat restoration, current hatchery practices, and harvest restrictions combined can positively impact Chinook salmon and steelhead in the Elwha River basin.

Methods

1.1 Study Area

The Elwha River is located on Washington State's Olympic Peninsula, originating in Olympic National Park (Fig. 1). The Elwha drains 833 km^2 and flows 72 km from an elevation of 1,372 m at the headwaters to its mouth on the Strait of Juan de Fuca in the Pacific Ocean. The physical geography of the Elwha River system is characterized as a series of alternating canyons and floodplains, which occur throughout the watershed (Pess et al. 2008). Two hydroelectric dams, which were built without fish passage facilities, eliminated anadromous salmonids' access to 95% of the Elwha River watershed (Brenkman et al. 2019). Elwha Dam, constructed at river kilometer (rkm) 7.9, was completed in 1913 and created Aldwell Reservoir (Fig. 1). Glines Canyon Dam, constructed at rkm 21.4, was completed in 1927 and created Mills Reservoir. The 32-m-tall Elwha Dam was removed over an 8-month period from September 2011 to April 2012, while Glines Canyon Dam (64 m in height) was removed over a 3-year period from 2011 to 2014 (Brenkman et al. 2019). In October 2014, shortly after the Glines Canyon Dam removal was complete, a large rockfall occurred in the canyon immediately downstream of the dam site near rkm 20.0 (Fig. 1). The accumulation of rockfall debris and large boulders created a new barrier to upstream passage of adult salmonids. Rock blasting occurred in October 2015 to improve fish passage, and additional blasting in September 2016 was presumed to have eliminated the barrier (Brenkman et al. 2019).

The salmonids community in the Elwha River consists of wild, natural-origin, hatchery, and nonnative fish (Brenkman et al. 2019). The salmonid species composition in the river includes Chinook, coho salmon, chum salmon (*O. keta*), pink salmon (*O. gorbuscha*), sockeye salmon (*O. nerka*), rainbow trout (*O. mykiss*), summer and winter steelhead (anadromous form of Rainbow Trout), coastal cutthroat trout (*O. clarkii clarkii*), bull trout (*Salvelinus* confluentus), and nonnative brook trout (*S. fontinalis*). Nonsalmonid species include the coastrange sculpin (*Cottus aleuticus*), prickly sculpin (*C. asper*), Pacific lamprey (*Entosphenus tridentatus*), and the presumed non-native redside shiner (*Richardsonius balteatus*).

Records indicate release of hatchery-origin Chinook salmon into the Elwha watershed as early as 1914 (Duda et al. 2018). A dedicated Elwha River origin Chinook salmon hatchery program was initiated in 1930

(Brannon and Hershberger 1984), and in recent years, Chinook releases have been large (annual average number released, 1985 to 2014 = 2.5 M). The current Chinook salmon hatchery program was deemed necessary during and post dam removal because the population has been dependent upon hatchery production for multiple decades and the predicted and realized short-term lethal effects of dam removal. Winter steelhead releases have occurred since 1965 and out-of-basin summer steelhead were released from 1968 to 2008 (Duda et al. 2018). Native Elwha winter steelhead had persisted in low abundances below the dams prior to dam removal, and dam removal disturbance was seen as a potential threat to short-term viability, so a native broodstock winter steelhead hatchery program was developed. For summer steelhead it was hypothesized that such a life history form could occupy and "recolonize" historically re-available upstream habitats (Ward et al. 2008), but specific mechanisms as to how were not identified (Brenkman et al. 2008). A moratorium on fishing for all species within the Elwha River watershed and terminal nearshore area was implemented in 2011 and will continue through June 2021 (Peters et al. 2014). The only exception to the moratorium has been an ongoing fishery targeting kokanee in Lake Sutherland, the headwaters of Indian Creek.

Chinook salmon and steelhead adult relocation

Adult Chinook salmon and steelhead were relocated during and immediately after dam removal (Tables 1 and 2). Adult Chinook salmon were relocated from hatchery facilities and a weir in the lower river to five different locations in the Middle Elwha River, upstream of the Elwha Dam site (Table 1). Relocations occurred in five of nine years during and after dam removal (Table 1). Relocated fish were considered surplus to hatchery broodstock goals, and as a result, they were numerically dominated by males in all years except 2019. The largest number of relocations occurred in 2018 and 2019, which were also the only years in which a considerable number of females were transported (Table 1).

Adult steelhead relocation occurred during the same period as Chinook salmon relocation (2012–2016); however, the number of sites was limited to two Middle Elwha tributaries – Indian Creek and Little River (Table 2). We relocated adult steelhead because they volunteered into the Lower Elwha Klallam Tribe's (LEKT) hatchery trap, likely to avoid elevated sediment loads in the mainstem river during dam removal. Adult steelhead were not captured and released into tributaries in 2015 because the hatchery adult trap was not operational. In 2016 the adult trap was operational, and 32 hatchery origin and three natural origin steelhead were relocated to Indian Creek, while no steelhead were relocated into Little River. No steelhead have been relocated since 2016 (Table 2).

1.2 Returning Adult Chinook salmon and steelhead population size estimates

We used multiple sampling techniques throughout the Elwha basin to monitor adult and juvenile Chinook salmon and steelhead (Fig. 1). Specifically, we enumerated adult spawners and outmigrating smolts, and used that data to produce estimates of abundance, productivity, and spatial distribution. Returning adult Chinook salmon and steelhead were enumerated using two different multi-beam SONAR units, a DIDSON-LR (0.7/1.1 MHz) and an ARIS 1800 (1.1/1.8 MHz) (Sound Metrics Corp., Bellevue, WA). The SONAR units operated from late January or early February through September each year from 2013 to 2018. Chinook salmon were counted from late May or June through September (2012–2020) and steelhead from late January or February through mid-June (2013–2020).

Field methods

Continually changing river conditions and two distinct stream channels (migratory pathways) in the lower Elwha River necessitated two separate SONAR installations to accurately detect upstream movements of Chinook salmon and steelhead (Fig. 1). The primary enumeration site was located in the East Channel (EC) while a secondary site was located in the West Channel (WC). Both sites were located at approximately rkm 0.8. SONAR site selection was based on four criteria: 1) almost all fish would pass the site; 2) the location was downstream of the majority of spawning habitat; 3) the river channel was sufficiently narrow to accommodate the effective range of the SONAR; and 4) fish movement was primarily directed upstream with little milling in the location of the SONAR. Depending on river discharge, the WC site was between 12 and 25 m wide and 1.3 m deep in the thalweg, while the EC site was 15 to 30 m wide and 2 m deep in the thalweg. We estimated that during Chinook salmon migration approximately 80% of the flow was in the EC, while the remaining 20% was in the WC. During the winter steelhead migration, the estimated proportion of adult migrants was 60% EC and 40% WC.

Data analysis

During the upstream Chinook salmon migration, 20 minutes of each hour-long file was reviewed for fish passage at each SONAR site, which is on the upper end of the range of recommended subsampling regimes (Lilja et al. 2008). Due to relatively low spawner abundance during the steelhead season, the full hour was reviewed. Several variables were noted for each fish passage event, including the date, time, direction (upstream or downstream), distance from SONAR head, and body length (mm).

The net upstream fish passage count is tabulated by subtracting downstream passage events from upstream passage events (Xie et al. 2005):

$$N = U - D \tag{1}$$

Where N is the net upstream movement of fish for a given time period, U is the sum of upstream fish for that time period and D is the sum of downstream moving fish for that time period.

To account for downstream migrating steelhead that had already spawned (kelts) we did not subtract downstream moving targets for any 24-hour period that had a net total downstream passage. This adjustment strikes a balance between accounting for kelts leaving the system that should not be subtracted from the total escapement estimate versus subtracting downstream passage events that are likely due to milling or spawning behavior in the vicinity of the SONAR site. This adjustment increases the final escapement an average of 13% in any year over a strict application of equation 1. We were able to calculate this percentage because the Elwha River currently has a unimodal winter steelhead run timing with spawning concentrated in late-April through May, and most kelts leave the system after the majority of the upstream run is over and when Chinook salmon are the predominate species migrating upstream.

To sum upstream and downstream passage events in each file, we also had to establish a minimum threshold length to distinguish adult Chinook or steelhead from other species and life stages. We accomplished this by using field-measured lengths of fish captured during weekly or bi-weekly in-river tangle net sampling conducted at nine different sites within 1 km of the SONAR sites over the entire course of the SONAR operation season. The netting also allowed us to estimate the onset and completion of the Chinook salmon and steelhead run timing, and the proportion of each species present during the period when they overlapped. The size thresholds for adult Chinook salmon and steelhead were 550 mm and 500 mm, respectively. The 550 mm threshold effectively excluded Chinook salmon jacks, smaller bodied bull trout, and pink salmon. For steelhead, we used 500 mm as the minimum size threshold, which excluded most bull trout. We then applied those criteria to all the raw targets to identify and count adult steelhead and Chinook salmon.

To estimate annual escapement, we used four-step (Chinook salmon) and three-step (steelhead) simulation models to adjust the total counts of the raw SONAR targets. In the first step, which was for Chinook salmon only, we expanded the 20-minute counts to full hour counts (Lilja et al. 2008). Second, we adjusted the raw counts to reflect the proportion of SONAR targets that were either Chinook salmon or steelhead. Third, we corrected the species-specific counts to account for observer error. Lastly, we filled in passage data for gaps in the data resulting from periods when the SONAR was not operating in order to expand and correct the data. The simulation also provided season- and year-specific coefficients of variation. Full methods utilized in this study including SONAR installation and performance of simulation is described in Appendix A.

1.3 Origin of returning Chinook salmon and steelhead

We evaluated carcasses for hatchery marks to estimate the proportion of hatchery-origin Chinook salmon returning to the Elwha River. Carcasses were collected via stream surveys, a channel-spanning weir deployed from 2010–2013, and from the hatchery following spawning. We examined Chinook salmon for four different hatchery marks. The primary marking strategy was a thermal otolith mark, with a goal of 100% marking. A subset of hatchery-reared Elwha Chinook salmon also received adipose fin clips and Coded Wire Tags (CWT). Examining for adipose and CWT allowed us to detect Elwha-origin fish in cases where thermal otolith marks were not successfully applied, and identify hatchery-origin fish from other watersheds. Lastly, a small number of fish were considered marked as hatchery-origin based on scale analysis that indicated they had growth patterns indicative of hatchery rearing, despite not carrying otolith, adipose, or CWT marks. We view our estimates of the proportion of hatchery origin as minimum hatchery mark rates because any non-Elwha origin or unsuccessful otolith marks from these fish would only serve to increase the proportion of hatchery-origin Chinook salmon. We used mixed effects models with binomial error structure and return year as a random effect to evaluate the hatchery mark information.

Mark rate information, including adipose clip and CWT, was collected from steelhead captured during SONAR species composition netting in the Lower Elwha River and limited additional sampling upstream of the former dam sites from 2014–2018. The vast majority of the samples were collected within 1 km of the Lower Elwha River hatchery where hatchery steelhead were reared and released. Consequently, there is likely a bias towards hatchery fish in our sampling effort, and the data were therefore only used to illustrate spatial differences in hatchery:natural origin proportions from 2014–2018. In 2019, a more intensive effort was undertaken to produce an unbiased estimate of basin-wide and reach-specific (Lower Elwha, Middle Elwha between the former dams, and Upper Elwha above both dams) hatchery:natural proportions which took into account spatial and temporal differences as well as differences in catch per unit effort (CPUEs) between sites (Peters et al. 2020).

1.4 Abundance of subyearling and smolt outmigrants

Juvenile Chinook salmon and steelhead outmigrants were enumerated using rotary screw traps in three locations of the Elwha River – the mainstem (rkm 0.3 and 3.3 in 2014–2018 and 4.0 in 2019–2020), Little River (rkm 0.2), and Indian Creek (rkm 0.7) (Fig. 1). Mainstem trapping operations were typically initiated by February 15th and completed by July 26th. Tributary operations in both Little River and Indian Creek were initiated on January 27th, with Little River ending on average by June 22nd and Indian Creek by September 5th. Monitoring in Little River typically ceased before Indian Creek due to low flows. Trap operation on the mainstem trap was 73% (~118 days) of all potential days, while for the tributary operations it was closer to 95% (Little ~139 days, Indian ~211 days) of all potential days.

Field methods

The traps were inspected and cleaned either daily or every other day at all sites. All captured fish were removed from the trap box using dip nets and transferred to plastic buckets for identification. Each fish was individually examined for tags or marks, identified to species, counted and immediately released downstream of the trap. We utilized plexiglass fish viewers to facilitate fish identification. A weekly subsample of all species caught was measured and weighed throughout the outmigration period. Salmon produced at hatcheries were distinguished and identified by adipose clip and/or scanning for CWT and enumerated separately from natural-origin fish. See Appendix B for details on determining the origin of smolts.

We estimated trap catch efficiency (proportion of total outmigrants captured) using multiple mark recapture tests across the trapping season at all three trap sites. On the tributaries, weekly samples of 50 to 100 fish, representative of the species migrating at any given time (i.e., Chinook salmon subyearlings or smolts, Coho salmon parr or smolts), were given a distinctive mark (Bismarck Brown) and released approximately 100 m upstream of the trap site. For the mainstem trap, we used small-bodied (0+) Chinook salmon or Chum salmon obtained from the LEKT and Washington Department of Fish and Wildlife (WDFW) fish hatcheries and released approximately 1000 m upstream for trap efficiency trials. For the small-bodied fish, we typically attempted multiple trials between late March and late May. Mainstem trap efficiency for 1+ fish was estimated using 1+ Coho salmon clipped at either the Indian Creek or Little River traps or 1+ hatchery Coho salmon released the same distance as 0+ fish in the mainstem.

Data analysis

We combined daily catch data with efficiency trials to estimate total production for each season. To incorporate uncertainty due to periods of missing data and expansion based on trap efficiency, we applied a flexible Bayesian model. Daily passage was assumed to follow a negative binomial distribution with a mean constrained to change smoothly with time - a random walk. Catch was modeled as a binomial distribution where the probability of capture was estimated from efficiency trials. Period-specific efficiencies were assumed to be independent due to observed temporal trends in efficiency for some traps. The estimates only incorporate passage during the trap operation. Therefore, if the trap was not in place during fish passage, these fish were not included in the estimate. We summarize the results with the median and 95% credible interval for total passage. We also include the CV and the geometric CV, which is more appropriate for skewed distributions. See Appendix B for details of the smolt data analysis.

1.5 Examination of Chinook 0+ production per spawner vs. flow and sediment events during the egg incubation phase

We evaluated the relationship between river discharge and sediment transport on Chinook salmon outmigration productivity (age-0 migrants/spawner) from 2011 to 2018. We used daily discharge data (2011–2018) from the United State Geological Survey (USGS) (12045500 Elwha River at McDonald bridge near Port Angeles, WA) and estimated suspended and bedload sediment discharge (tonnes per day) (Ritchie et al. 2018). Estimates for naturally spawning Chinook salmon spawners (total escapement estimate minus hatchery take) and the estimated number of Chinook 0+ outmigrating subyearlings was used to generate a Chinook age-0/subyearling per spawner estimate for each year.

We developed a flow index for stream discharge that includes the number of days above 56.6 m3·s−1 between October 1st and December 31st. We estimated that 56.6 m3·s−1 is approximately the bankfull discharge level where bedload will be mobilized (Ritchie et al. 2018), and assumed October 1st to December 31st was the primary egg incubation and emergence period (Greene et al. 2005). We summed the number of days above 56.6 m3·s−1 and multiplied that by the average discharge greater than 56.6 m3·s−1 to give an indication of the overall duration and magnitude of potential events that could have affected egg-to-fry survival for the period of incubation.

$$Number\ of\ days > 56.6\ m3{\cdot}s-1 * average\ discharge > 56.6\ m3{\cdot}s-1 \qquad (2)$$

Eq. 2 assumes that the number of days and the amount of flow over the course of the entire incubation period would have the largest impact to egg-to-fry survival, a factor that can limit overall Chinook salmon productivity (Greene et al. 2005). We did not account for when the flows specifically occurred, aside from the overall seasonal period (i.e., early in incubation vs. when the eggs may have hardened or when the fry would emerge from the gravels).

We developed a sediment transport index by summing the average total amount of sediment transport (tonnes) during the egg incubation and emergence period (Ritchie et al. 2018). Processed data were not available after September 30, 2016, so we estimated sediment transport from October 1, 2016 to

December 31, 2016 using bedload data from bedload impact sensor plates located near rkm 4.9 available from the Bureau of Reclamation (Personal communication with Rob Hilldale, Research and Development Office, U.S. Department of the Interior, Bureau of Reclamation (BOR), PO Box 25007, Denver CO 80225-0007, 303-445-3135). Based on prior years, the bedload sediment sensors quantify approximately 44% of the total estimated bedload transport. In addition, the daily bedload sediment is roughly 25% of the total sediment load mobilized. The overall total sediment discharge estimate for the October 1, 2016 to December 31, 2016 period is estimated with Eq. 3:

$$(Daily\ measured\ sediment\ bedload\frac{\frac{tonnes}{day}}{0.44})/0.25 \qquad (3)$$

We compared prior year estimates to measured sediment discharge, resulting in an r^2 of 0.89.

The flow-sediment index was calculated as the product of two values. The first is the sum of all daily discharge values (D_d) > 56 m3·s−1 during egg incubation (October 1st to December 31st) and the second is the sum of all sediment (S_d) values during the same period.

$$flowSedIndex = \sum_{d\,=\,Oct\ 1st}^{Jan\ 1} \begin{cases} D_d, & D_d > 56\ m3 \cdot s - 1 \\ 0, & D_d \leq 56\ m3 \cdot s - 1 \end{cases} \times \sum_{d\,=\,Oct\ 1st}^{Jan\ 1} S_d$$

(4)

We fit a linear model to the log-log relationship between the flow/sediment index and Chinook salmon subyearlings/spawner. We assumed that log Chinook salmon subyearlings/spawner was linearly related to the log flow-sediment index. Visual inspection of the relationship on the log-log scale suggested that the assumption of linearity was appropriate and that the variance was stable across the range of the flow-sediment index.

1.6 Adult-to-adult Chinook salmon productivity

We estimated the total number of adult fish produced by Chinook salmon spawning naturally in the Elwha River from 2004–2015 using a combination of abundance, hatchery mark, age structure, and harvest information. For each return year, we estimated the number of naturally produced Chinook salmon by multiplying the abundance of adults returning to the river by (1 – hatchery mark rate). Within each year, we pooled all collection sources of hatchery mark rate data because the difference between sources was very small (< 2% summed across all years, see Table 3). Within each return year, natural-origin adult returns were then allocated to spawning cohorts using age data from scales collected from 2007 to 2019 (median = 449 individuals per year, range = 157–898). Because we sampled so few unmarked, natural-origin salmon (≤ 55 each year, see Table 3), we assumed no difference in the age structure between hatchery-origin and natural-origin fish. This allowed us to increase our age structure sample size, and implicitly prioritized capturing age variation among years rather than age variation between hatchery-origin and natural-origin salmon.

For each spawning cohort, the number of adult recruits returning to the river were further expanded by estimates of fishery mortality. For fishing years 2007–2016, total exploitation rates of Elwha River Chinook salmon were estimated by the Fishery Regulation Assessment Model (FRAM) validation run version 6.2 (Derek Dapp, personal communication WDFW, 1111 Washington St SE Olympia, WA 98501, 360-688-6380). During this period, the majority of Elwha harvest mortality occurred in northern (Alaska, B.C) pre-terminal ocean fisheries that might encounter Chinook salmon during the ocean-phase of their life cycle (i.e., not on a spawning migration). Thus, for each spawning cohort, we used the median total exploitation rate experienced by age-3, age-4, and age-5 fish to account for harvest in estimates of adult recruitment. We report productivity, for both return to the river and after harvest, as the ratio of adult recruits to the spawners that produced them. A value of 1.0 indicates replacement. We note that these productivity estimates encompassed the period before and a small portion during (but not after) dam removal.

1.7 Spatial distribution of spawning Chinook salmon and steelhead

We conducted redd counts to determine the distribution of spawning Chinook salmon and steelhead. Chinook salmon and steelhead spawning nests or “redds” were identified by disturbed areas in the streambed where gravels were overturned and there was a clear depression and associated tailspill (Gallagher et al. 2007). Each individual redd was geolocated (latitude and longitude) using a Garmin GPS (model GPSmap 60CSx).

Chinook salmon redd counts

We conducted annual one- to five-day duration peak redd counts in the mainstem Elwha River, its larger floodplain channels, and several major tributaries in mid-September from 2012 to 2018. Survey timing was based on the estimated historical date of peak spawning activity for Elwha River Chinook salmon, approximately September 15th–September 25th (personal communication with Randy Cooper, WDFW, 375 Hudson St. Port Townsend, WA 98368. 360-302-3030). The Elwha River was divided into three sections. The Lower Elwha (LE) is defined as the area downstream of the former Elwha Dam (rkm 0.0-7.9). The Middle Elwha (ME) is the reach immediately upstream of the former Elwha Dam, including the former Aldwell Reservoir, upstream to the former Glines Canyon Dam (rkm 7.9-21.7). The Upper Elwha (UE) is the reach upstream of the former Glines Canyon Dam, including the former Mills Reservoir, Cat and Boulder creeks, upstream to Chicago Camp (rkm 21.7-61.6). The LE and ME were surveyed in all years, while the UE was surveyed in 2016–2018. Supplemental surveys were conducted in the UE beginning in 2014 and 2015; however, these only included the former Mills Reservoir area from the former Glines Canyon Dam (rkm 22) upstream to the entrance of Rica Canyon (rkm 25.7). We did not survey any of the major canyon areas of the Elwha River during peak surveys with the exception of Rica Canyon in 2014 and 2015. These include the canyons above the former Glines Canyon Dam, including Rica Canyon (rkm 25.2), Grand Canyon (rkm 31.2), and Carlson Canyon (rkm 52.6) (Fig. 1). Additionally, no comprehensive surveys have occurred to date in larger upriver tributaries with the exception of Long Creek in 2018.

Both river discharge and turbidity levels where highest in 2012, which limited surveys to above the Elwha Dam site where turbidity levels were much lower. In 2013, water clarity of the river improved enough to allow surveys below the former Elwha Dam and 2014 conditions allowed for a full survey from the mouth to just above the former Glines Canyon Dam. Since 2015, turbidity has not been a factor during surveys in any reach.

Steelhead redd counts

We conducted weekly to bi-weekly redd counts from February through June/early-July to determine the location and timing of adult steelhead spawning (Gallagher et al. 2007). Most redd counts occurred in tributaries because their water clarity was unaffected by dam removal and their small size made them easy to survey. Surveys were completed in four Upper Elwha tributaries (estimated percent of potential steelhead spawning habitat surveyed) including: Cat Creek (100%), Long Creek (90%), Hurricane Creek (100%) and Boulder Creek (100%) and six Middle Elwha tributaries: Little River (50%), Indian Creek (25%), Griff (100%), Madison (100%), Campground (Sanders) (100%), and Hughes Creeks (100%). Surveys of the mainstem channel were conducted as conditions allowed, but the frequency was severely limited by reduced water clarity that often made it impossible to visually identify and count redds.

Snorkel surveys

We conducted annual snorkel surveys in Little River (2013) and the mainstem Elwha River (2016–2020). The objective was to enumerate adult Chinook salmon, summer steelhead, and the presence/absence of juvenile salmonids in the sample areas. Snorkel counts were conducted in August, September, or October, depending on the year, though in most years surveys occurred from early- to mid-September to coincide with the peak spawn timing of Chinook and ensure the majority of adult summer steelhead had entered freshwater (Table 1). The survey in 2013 was conducted only in Little River, a tributary in the middle Elwha River, because it was the only easily accessible stream with adequate visibility for underwater surveys.

From 2016–2020 we conducted snorkel surveys in the mainstem Elwha. The length of stream surveyed varied by year depending on stream flows, visibility, and access to the backcountry wilderness. Generally, surveyors covered more extensive sections of the mainstem Elwha River as sediment levels stabilized following dam removal and stream visibility became increasingly sufficient to observe, distinguish, and enumerate adult steelhead.

Once in the water, divers moved downstream and would enumerate fish in each habitat unit and then relay those numbers to a bank recorder. Generally, the process consisted of two divers swimming downstream side-by-side. However, the upper Elwha River became low and clear enough in 2019 that one experienced diver covered the vast majority of habitat. Multiple divers were used further downstream where the river became larger and more difficult to cover with a single diver. Summer steelhead were distinguished from resident rainbow trout by their relatively large size, silvery coloration, presence of a strong sea line, and few spots below the lateral line. Divers also classified each adult steelhead as hatchery, wild, or unknown, depending on the presence of an adipose fin, which is clipped on the majority of hatchery summer steelhead in Washington State. For 2013 and from 2016–2018 we conducted multiple snorkel counts to estimate the relative abundance of adult summer steelhead, which is the total number of steelhead observed each year.

Results

2.1 Returning adult Chinook salmon and steelhead population size estimates

Prior to dam removal (1986–2010), the number of returning adult Chinook salmon to the Elwha River averaged 2,827 (S.D. 1,778) (Fig. 2a). During dam removal (2011 to 2015), the number of adult Chinook salmon returning to the Elwha River averaged 3,444 (S.D. 1,125). Post dam removal adult Chinook salmon returning to the Elwha River averaged 4,734 (S.D. 2,409). In-river Chinook salmon spawners during those periods averaged 1,393 (S.D. 1,218), 1,930 (S.D. 747), and 3,523 (S.D. 1,949), respectively (Fig. 2a). The proportion of total returning adult Chinook salmon that were taken for hatchery breeding purposes pre dam removal was 53% (S.D. 15%), compared to 45% (S.D. 6%) during dam removal and 31% (S.D. 8%) post dam removal.

The estimated number of returning adult winter steelhead to the Elwha River from 2013 to 2020 ranged between 385 and 1,985. In 2020, the number of returning adult winter steelhead was estimated at 1,985. Returning adult winter steelhead increased from 2013 to 2015, with a decrease in 2016, followed by increasing numbers (Fig. 2b). A relatively small proportion of fish were taken for hatchery purposes, so the abundance of naturally spawning steelhead closely follows the pattern of total abundance (Fig. 2b). The utilization of SONAR for enumerating Chinook salmon and steelhead adult returns allowed us to quantify several sources of error in estimating abundance. For both species, filling data gaps when the SONAR is not in-river was typically the largest source of uncertainty, with a CV of 3.3% (S.D. 1.7%). This is followed by observation error (CV 2.6%, S.D. 1.4%), species composition identification (CV 2.4% S.D. 1.4%), and expansion from sub-sampling (CV 1.9%, S.D. 1.7%).

2.2 Proportion of natural and hatchery-origin Chinook salmon and winter steelhead spawners

Across return years 2009–2020, the median proportion of hatchery-origin Chinook salmon was 96.0% (range = 90.3–98.0%, Table 3). The hatchery mark rate in return years 2016–2020, when some naturally spawned salmon might have been produced upstream of the Elwha Dam site, was no different than 2009–2015, based on a mixed effects model ($p > 0.10$).

Combined across return years 2014–2018, the proportion of hatchery winter steelhead captured during net sampling was 85% below the former dams (below former Elwha Dam site) and 25% above the former dams (above former Elwha Dam) (Table 4). In 2019, the calculated range of proportion of hatchery origin (pHOS) of winter steelhead for the whole basin was estimated to be ~38% (Peters et al. 2020). pHOS for steelhead in 2019 was 55% (40 of 73) below the former dams and 0% (0 of 24) above the former dams (Table 4).

2.3 Abundance of subyearling and smolt outmigrants

The average Chinook salmon subyearling (age 0+) and yearling (age 1+) hatchery releases prior to dam removal (pre 2011) was 2,596,545 (S.D. 801,861), in comparison to an average release of 1,953,609 (S.D. 808,897) during and after dam removal. The number of natural-origin outmigrating 0+ Chinook salmon from the Elwha River averaged 43,828 (S.D. 47,932), 46,973 (S.D. 39,798), and 323,764 (S.D. 407,976), before, during, and after dam removal, respectively (Fig. 3a). There was a dramatic increase in the estimated number of natural-origin outmigrating 0+ Chinook salmon in 2019 and 2020 (Fig. 3a) to over 500,000 0+ Chinook salmon in 2019 and near 1 M in 2020 (Fig. 3a). The 2016, 2017, and 2020 estimated 1+ Chinook salmon outmigrants were 1-2 orders of magnitude less than the subyearling outmigrants, the only years trap efficiency was sufficient to allow estimates of 1+ outmigrants (Table 5). The average steelhead smolt hatchery releases during and after dam removal of steelhead was approximately 122,596 (S.D. 53,514). The average natural origin estimates of outmigrating steelhead smolts during and after dam removal was 8,884 (+/-5,380) (Fig. 3b).

Between 2013 and 2020, outmigrating 0+ Chinook salmon from Indian Creek, a tributary located at rkm 12.1 not impacted by the sediment supply changes from the dam removal, ranged between 1,188 and 129,759 and averaged 53,396 (Fig. 3c). Between 2013 and 2020, steelhead smolts from Indian Creek averaged 1,523 with a low of 146 in 2014 and a high of 2,550 in 2019 (Fig. 3d). There has been an increasing trend in the number of steelhead smolts from Indian Creek since 2014 (Fig. 3d).

2.4 Examination of Chinook salmon age-0/subyearling per spawner vs. flow and sediment events during the egg incubation phase

Examination of the discharge, sediment, and subyearling Chinook migrants per spawner data from 2011 to 2018 reveals a correlation between the flow/sediment index and Chinook subyearlings per spawner (Fig. 4). The number of Chinook age-0/subyearling per spawner decreases with an increase in the flow-sediment index where the intercept and slope were 5.73 and -0.436 respectively. During and after dam removal, the years 2014, 2015, and 2017 had the highest flow-sediment index, and the lowest estimated Chinook salmon freshwater productivity. These data suggest an inverse relationship between the flow-sediment index and freshwater productivity.

2.5 Smolt-to-adult and adult-to-adult Chinook salmon productivity

Smolt-to-adult return rates (SAR) varied by Chinook salmon origin (natural vs. hatchery) (Fig. 5). Overall, SAR of natural-origin Chinook salmon was consistently greater than hatchery-origin Chinook salmon in the Elwha River. Prior to dam removal (brood years 2005–2010), hatchery-origin Chinook salmon SAR rates averaged 0.11% (SD +/-0.098%) while natural origin Chinook salmon SAR rates averaged 0.54% (SD +/- 0.59%). During dam removal (brood years 2011–2015), SAR rates for hatchery Chinook salmon slightly increased (average = 0.21%, SD +/- 0.12%) but not for natural origin Chinook salmon (average = 0.53%, SD +/- 0.40%).

Adult-to-adult productivity of Chinook salmon spawning naturally in the Elwha River was well below the replacement value of 1.0 each year 2004–2016 (Table 6). Return-to-the-river estimates were ≤ 0.50 in all years and ≤ 0.15 in nine of 13 years. Accounting for harvest increased productivity estimates somewhat, but not enough to exceed replacement in any year.

2.6 Spatial distribution of spawning Chinook salmon and steelhead

Chinook salmon immediately utilized the Middle Elwha River since the removal of the Elwha dam (rkm 7.9) in April of 2012 (Fig. 6). Since dam removal, the density of Chinook salmon redds in the Middle Elwha has been similar or greater than the densities below the former Elwha Dam. Chinook salmon redds have been consistently observed above the former Glines Canyon Dam (rkm 21.6) since 2016, after the blockage was removed at the site in 2015. Since 2015, there has been an increasing number of Chinook salmon redds, while the overall extent of redd distribution (difference between furthest upstream and downstream) has ranged between 45 and 55 km upstream. Former Mills Reservoir (rkm 22 to 25) has seen an increase in the number of Chinook salmon redds from 2016 to 2018. The location of the 90th percentile redds, organized from downstream to upstream, also expanded to above the former Glines Canyon Dam site after the blockage was removed in 2015. The overall distribution of Chinook salmon redds from 2015 to 2018 above the former Glines Canyon dam site is heavily skewed towards the former Mills Reservoir area, with relatively few overall Chinook salmon redds above rkm 25 (Fig. 6).

Steelhead utilization of tributaries in the Middle and Upper Elwha have also increased since the Elwha River dam removals (Fig. 7). Little River has had the most documented steelhead spawning activity since dam removal began in 2011. Indian Creek, located directly to the west of Little River, has also had consistent steelhead spawning since 2011, while other tributaries such as Hughes Creek have increased over that same period (Fig. 7). Barrier removal of the blockage at former Glines Canyon Dam resulted in the utilization of tributaries that drain into and above former Mills Reservoir (Fig. 7). Overall, for both Chinook salmon and steelhead, the spatial distribution of redds shifted from the Lower Elwha prior to dam removal to the Middle Elwha during and after dam removal.

2.6 Steelhead life history diversity

The number of observed adult summer run steelhead has increased since 2013 (Table 7). The number of observed summer steelhead were respectively one and six in 2013 and 2016 in a relatively small amount of area surveyed across the Elwha River (5 to 18 km respectively). The number observed increased in 2017 to 74 during the month of September, and 216 in 2018 when a much large portion of the river system was surveyed during an extensive snorkel survey (63 km total extent) (Table 7). Approximately 90% of the steelhead observed in 2018 were located between rkm 35 and 58, which is comparable to the 2017 snorkel survey (Table 7). In 2019, the number of summer run steelhead directly observed through snorkel surveys in the Elwha River was 341, followed by a decrease to 114 in 2020 (Table 7).

Discussion

Damming rivers causes fundamental changes to the aquatic ecosystem including shifts in ecological communities and altered watershed baseline conditions (Bellmore et al. 2019). Dam removal may reverse those changes, but because removal of large dams is a relatively new conservation action, many questions remain about the possible physical and ecological outcomes (Bellmore et al. 2019). The removal of the Elwha River dams is unique because of the large magnitude and short duration of change to the physical environment, combined with the relatively intact state of the majority of the watershed upstream of the former dam locations. As a result, influences on the Elwha River ecosystem include a short-term major disturbance in the form of a large-scale increase and subsequent reduction in sediment supply, the creation and alteration of geomorphic features and aquatic habitats (e.g., estuarine river delta), and access to a large expanse of previously inaccessible intact aquatic habitats for fish to recolonize. The physical effects of dam removal is coupled with other salmon management actions in the Elwha River basin including hatchery production and a fishing moratorium implemented in 2011 that will continue through at least June 2021 (Peters et al. 2014). The combined effects of dam removal, hatchery management, habitat restoration prior to dam removal (Pess et al. 2012*a*), and the fishing moratorium have induced an array of large-scale physical and ecological changes in the Elwha River ecosystem.

3.1 Dam removal, a change in sediment supply, and its impacts to Chinook salmon and steelhead

Downstream sediment movement from the former reservoirs, corresponding geomorphic and aquatic habitat changes, and salmon response to the magnitude and rate of reservoir sediment erosion was one of the largest unknowns associated with the removal of the Elwha River dams. The rate of dam removal was designed to be fast enough to affect only several generations of salmon, but slow enough that reservoir sediment erosion and redistribution kept pace with dam removal and maintained conditions suitable to meet residential and commercial water needs provided by the Elwha River (Randle et al. 2015). Removal of the Elwha Dam and drawdown of the former Aldwell Reservoir began in September 2011 and was completed by April 2012. Former Mills Reservoir was lowered according to planned increments in the first year (September 2011 to October 2012), followed by one year of no removal due to technical issues (Magirl et al. 2015; Warrick et al. 2015). Although Glines Canyon Dam deconstruction was finalized in October 2014, additional demolition was required through October 2016 to clear boulders and rockfall impeding fish passage downstream of the former dam.

The magnitude of sediment effects in each year was determined by the supply of accessible sediments in the former reservoirs, the magnitude of flows relative to mobilization thresholds, and the timing of flows relative to the salmon life cycle. A large quantity of sediment was accessible in the former reservoirs immediately after dam removal was initiated, but higher magnitude flows did not occur for several years. Suspended sediment concentrations were consistently high during the Chinook salmon egg-to-fry incubation period from October through December of 2012, largely due to the considerable increase in sediment supply as 3 Mt of stored sediment were mobilized (Ritchie et al. 2018). This was in combination with bed material movement, which was initiated en masse from former Mills Reservoir, aggrading the streambed in the Middle Elwha by over 1.0 m and the Lower Elwha by 0.5 m after October of 2012 (Ritchie et al. 2018). However, high discharge events did not occur until 2014 and 2015, when several discharge events that were above the two year recurrence interval (RI) and two near or over the 10-year RI caused further aggradation and degradation (+/- 0.3 m, Ritchie et al. 2018). Over 3 Mt and over 1.5 Mt was mobilized in 2014 and 2015 respectively. The years 2011 and 2013 did not have the same large discharge events, with only 151 and 865 thousand metric tonnes (Kt) mobilized respectively. Both flow and sediment discharge was relatively low in 2018, correlating to one of the highest juvenile Chinook salmon fry migrants per spawner estimate during and post dam removal.

The massive change in sediment supply during dam removal affected outmigrating salmonid smolts, as well as the ability to enumerate outmigrating smolts. This impact was most likely due to changes in streambed scour and fill associated with changes to the sediment supply, since fine sediment deposition in mainstem spawning riffles for Chinook salmon appeared limited through 2014 (Peters et al. 2017). Salmonid reproductive success, measured as egg-to-fry survivorship, depends in part on egg burial depths exceeding the depth of streambed scour during the incubation period (Montgomery et al. 1996; DeVries 1997). Salmonid egg burial depths in the streambed can range from 0.03 m to 0.5 m depending upon the species, size of the female, substrate size, and multiple other factors (DeVries 1997). The likelihood of scour affecting salmon redds typically increases as the sediment supply increases beyond the normal variation (Tripp and Poulin 1986). During the dam removal years, aggradation and degradation in the mainstem Elwha River approached or exceeded these depths, suggesting significant impacts to survival during egg incubation.

Our ability to integrate changes in physical habitat, such as flow and sediment, during a specific period in life was critical to understanding the survival of naturally spawning Chinook salmon. Our combined index of flow and sediment discharge captured the annual variability of physical impacts during the Chinook salmon egg-to-fry incubation stage and provided a strong indicator of disturbance to the streambed. This was important because annual flow and sediment discharge were not synchronous during and immediately after dam removal. The asynchronous nature of peak flows and sediment supply in the Elwha River basin from 2011 to approximately 2015 is common to Puget Sound rivers that have had varying land use and flow impacts. The progressive loss of channel capacity in the Skokomish River, for example, was due to a combination of increased sedimentation from one portion of the sub-basin, coupled with reduced downstream flows in another portion of the sub-basin (Collins et al. 2019). The result was an unusual effect of downstream channel capacity decrease and increased flooding where these impacts spatially coalesced (Collins et al. 2019). Thus, our ability to integrate changes in physical habitat, such as flow and sediment, during the egg-to-fry life stage of Chinook salmon was critical to understanding the survival of the fish that spawned naturally in the Elwha River.

Outmigrating steelhead smolts did not follow a similar correlation to the change in sediment supply as Chinook salmon. There are several potential reasons for this. First, steelhead spawn in spring rather than late summer through early fall, and their emergence occurs in summer, both of which are after the peak flow events. Second, their spawning locations differed from Chinook salmon to some degree. For instance, while steelhead also spawned in the mainstem, they frequently spawned in clear water tributaries. Thus, the timing and location of their spawning and emergence reduced their vulnerability to the sediment impacts. Accordingly, as annual sediment loads stabilize to background levels (Ritchie et al. 2018) and conditions in the mainstem become more favorable for spawning and egg incubation, we hypothesize future survival will increase and become more similar to what we observed for Chinook salmon in 2018.

3.2 The role of hatchery Chinook salmon and steelhead

Major dam removal projects present several benefits, risks, and challenges to recovery of salmon and steelhead populations. For example, managers face decisions with complex trade-offs, including whether to use hatcheries or rely on natural origin fish for recolonization, the source of potential hatchery brood, and the colonization strategy, or method by which salmon will reach the newly accessible habitat (Anderson et al. 2014). In the case of the Elwha River, the long-term goal is self-sustaining natural reproduction that can support fisheries without the need for hatchery supplementation (Ward et al. 2008; Peters et al. 2014).

Hatcheries on the Elwha River are being used to reduce the risk of population extinction and to increase the abundance of Chinook salmon and steelhead source populations that represent a unique component of regional genetic diversity (Ward et al. 2008; Peters et al. 2014). Within the Puget Sound Chinook salmon Evolutionary Significant Unit (ESU), where genetic homogenization of Chinook salmon has been widespread, Elwha Chinook salmon are unique in that they are only similar to the neighboring Dungeness population but different from the other 20 extant populations (Ruckelshaus et al. 2006). Prior to dam removal, hatchery managers intentionally avoided releasing non-native Chinook salmon into the Elwha River to preserve their unique genetic lineage (Brannon and Hershberger 1984). The current winter steelhead hatchery program is more recent (first releases in 2011) but is also derived from the native gene pool; a previous winter steelhead hatchery program using non-native origin steelhead was phased out in 2012. For both hatchery programs, the intent was to provide demographic insurance during dam removal and lower the risk of extinction following the release of large quantities of sediment from the former reservoirs. Additionally, for both species, the recolonization strategy has largely relied on natural colonization, as the vast majority of Chinook salmon and steelhead spawning above the Elwha Dam site have volunteered to those locations without translocation (see Tables 1 and 2).

As stated previously, the long-term goal for the Elwha Chinook salmon and steelhead populations is self-sustaining natural reproduction without hatchery supplementation. Currently, the Chinook salmon population is demographically dominated by hatchery-origin fish (≥ 90% in all years, Table 3), and natural reproduction is well below replacement (Table 3). Thus, the adult abundance fluctuations we have seen since dam removal for Chinook salmon in the Elwha River are, in large part, due to hatchery production and survival of hatchery-reared juveniles. A sustained increase in natural origin adult abundance would signal less demographic reliance on hatchery production and suggest hatchery releases could be reduced while maintaining abundance. However, considering the long duration of hatchery production, and the associated potential domestication selection for traits advantageous to the hatchery environment and loss of fitness in the wild (Christie et al. 2014), some level of re-adaptation to the natural environment may be necessary for population growth. Under this hypothesis, the naturally spawning population must have a level of reproductive isolation from the hatchery to observe any such "re-wilding," and reduced hatchery production could help achieve this goal. Whether the population retains suitable genetic material for re-wilding and the degree of reproductive isolation needed to achieve it are open questions.

The role of hatchery operations for winter steelhead in the Elwha River differs from Chinook salmon. The proportion of hatchery-origin spawners is less, and their distribution is different from natural-origin spawners. The majority of identified adults that have returned above the dams are natural origin but are genetically similar to the below dam population which includes the native broodstock program (Fraik et al. 2021). Lastly, there has been a re-awakening of a summer steelhead population (Nichols et al. 2019). Each of these factors point towards recovery.

3.3 Dam removal, an increase in the amount of available salmon and steelhead habitat, and population expansion

Since the removal of the Elwha Dam (rkm 7.9) in April of 2012, Chinook salmon have utilized the Middle and Upper Elwha River, increasing in number upstream of the former barriers and total spatial extent. Expansion of adult Chinook salmon into newly opened habitats is a typical result of barrier removals (Kiffney et al. 2009; Pess et al. 2014; Anderson et al. 2015). Chinook salmon population stray rates range from less than 5% to up to 34%, averaging ~15% (Westley et al. 2013; Keefer and Caudill 2014; Pearsons and O'Connor 2020), so some colonizers may have originated from other river systems. Close proximity to a source population tends to increase the rate of recolonization (Pess et al. 2014; Pearsons and O'Connor 2020), and in this case, prior to dam removal, both Chinook salmon and steelhead spawned in the lower river below the Elwha Dam, and a large number of hatchery-origin Chinook salmon returned annually to the lower river. Furthermore, the expansion of distribution by adult Chinook salmon can allow for increases in population productivity (recruits per spawner) and population growth rates (Anderson et al. 2014; Pess et al. 2014). For example, the estimated numbers of recruits per spawner were two times greater for spawning pink salmon in the Fraser River above the former Hell's Gate rockfall than below it during the peak time of recolonization (Pess et al. 2014). However, the uneven distribution of Chinook salmon above the former Glines Canyon dam site, which is heavily skewed towards the former Mills Reservoir area, may impact population productivity and population growth rates.

Winter and summer steelhead have also shown positive trends in abundance and expansion in the Elwha River during and after dam removal. Overall, winter steelhead estimates have increased from the hundreds to >1,000 in a matter of several years. Hatchery-origin steelhead have made a significant contribution to the overall increased abundance of winter steelhead, but our samples of adults upstream of the former dam sites suggests it is being driven by natural origin fish, with increased expansion into reconnected tributaries since 2015. Steelhead stray rates from other nearby donor populations range from less than 5% to 14% (Keefer and Caudill 2014; Pess et al. 2014; Pearsons and O'Connor 2020), while winter steelhead recipient stray rates are typically greater than donor stray rates (~29%) (Pearsons and O'Connor 2020). As with Chinook salmon, the combination of factors make steelhead conducive to population expansion by natural origin spawners (Pess et al. 2014; Pearsons and O'Connor 2020).

Resident rainbow trout upstream of the former barriers may also have contributed to population expansion. Resident rainbow trout can be a source to anadromous populations, particularly when anadromous adult abundances are low (Losee et al. 2020), and populations isolated above barriers often retain both the genetic (Clemento et al. 2008) and physiological (Holecek et al. 2012) traits of anadromy. Resident rainbow trout upstream of Glines Canyon Dam were producing migrants that were seawater tolerant and apparently capable of an anadromous life history as late as the early 1990's (Hiss and Wunderlich 1994). Residents can also mate with (McMillan et al. 2007) and contribute genes to their anadromous counterparts (Christie et al. 2011). Considering the abundance of resident rainbow trout above the dams, dam removal may have facilitated more interactions between the two life histories and thereby increased the number of breeders and genetic variation (Weigel 2013).

3.4 Can life history diversity increase with dam removal?

Increased life history diversity was a predicted response to the removal of the Elwha River dams (Brenkman et al. 2008; Pess et al. 2008), and adaptive management guidelines recognized the importance of life history diversification to the recovery of Chinook salmon and steelhead in the basin (Peters et al. 2014). Given the considerable longitudinal differences in habitat characteristics in short, coastal rivers such as the Elwha River (e.g., temperature, gradient, floodplain valley width), colonization of upstream habitats may present new environmental conditions. Diversification of habitat niche utilization during colonization can increase life history diversity, and in turn, benefit abundance and productivity. In Puget Sound, snowmelt river conditions favor early adult spawning and stream-type juvenile rearing strategies in Chinook salmon, but occupancy of these headwater habitats is under-represented in the region due to dams, restricting life history diversity (Beechie et al. 2006).

Specific life history types of Chinook salmon and steelhead in the Elwha River where thought to be part of those populations historically, including spring Chinook salmon and summer steelhead, due to the environmental conditions and geomorphic characteristics of the Elwha River basin (Beechie et al. 2006; Brenkman et al. 2008; Pess et al. 2008). The cold-water stream temperature regime above the dams had been thought to be conducive to slower growth rate and overall size of juvenile Chinook salmon, creating a growth trajectory favoring the stream-type life history characterized by one year of freshwater rearing prior to outmigration (Beechie et al. 2006; Pess et al. 2008). Similarly, summer steelhead were hypothesized to predominate in the upper Elwha River basin due to its series of canyons interspersed between alluvial valleys, creating habitats conducive to that life history (Brenkman et al. 2008).

Summer steelhead have been documented over the last four years, increasing in numbers from 2015 to 2019 (Table 7). The “reawakening” of the summer steelhead life history strategy in the Elwha River, particularly since 2017, is a positive sign that the ability of fish from the basin to express this life history strategy is a response to dam removal and re-connectivity of the watershed. Configuration of the Elwha River watershed and potential genetic disposition of resident rainbow trout could both play a role in this life history re-expression since dam removal. As we have already stated, the Elwha River is a series of alternating alluvial and canyon reaches, and it has generally low stream temperatures for the majority of the basin across the year, both of which favor expression of the summer steelhead life history. Preliminary genetics work completed suggest that these fish are most likely originating from the resident rainbow trout above both dams, owing to the harboring of alleles for early run timing in the up-river population (Nichols et al. 2019).

3.5 The role of a terminal fishing moratorium in Chinook salmon and steelhead abundance

The Elwha River has been under a recreational and commercial fishing closure since 2011 to eliminate harvest impacts and allow for the rebuilding of salmonid runs before and after dam removal. Moratoriums and banning specific fisheries for a period can affect salmon populations in many ways. For example, a ban on a Norwegian coastal drift net fishery resulted in a change in the age structure of returning adult Norwegian Atlantic salmon (*Salmo salar*) as well as other Atlantic salmon populations in Russia (Jensen et al. 1999). Closure of the Newfoundland commercial Atlantic salmon fishery for one year resulted in a variable response to 25 rivers throughout Newfoundland, with some spawning escapements increasing by a factor of two, while others showed lower than average returns post closure (Dempson et al. 2004). Additionally, steelhead on the Kamchatka Peninsula were dramatically reduced due to illegal fishing in the early 1990s, which was correlated with an increased proportion of residents, a pattern that reversed when illegal fishing was ended (Savvaitova et al. 1997; Savvaitova et al. 2002).

Attempts to re-establish self-sustaining populations through barrier removals can also be hindered by fisheries (Pess et al. 2012*a*; Anderson et al. 2014; Bellmore et al. 2019). The harvest moratorium in the Elwha River was used as a means to increase abundance in the short term, reduce risk of population extinction during dam removal, and increase the number of potential colonizers. It has resulted in an average offshore exploitation rate of 15% (+/-7%) for Elwha River Chinook salmon (FRAM validation run 6.2, D. Dapp, Washington Department of Fish and Wildlife, unpublished data). In contrast, Chinook salmon exploitation rates for Puget Sound during the same period averaged 31% (+/-5%) (FRAM validation run 6.2, D. Dapp, Washington Department of Fish and Wildlife, unpublished data). Assuming Elwha River Chinook salmon would have been harvested at a similar rate, the moratorium has resulted in 3,754 (+/-1,668) additional spawners, which equates to roughly one additional year of adult Chinook salmon returns over that time frame. We do not know the Elwha River steelhead exploitation rates prior to the moratorium, however, using the average steelhead harvest rate in Puget Sound for the same period 7% (S.D. 6%) (Cram, Kendall et al. 2018), which results in 493 (+/-35) additional spawners since 2011.

3.6 Can we determine success yet?

Recolonization of larger watersheds can take up to 20 years or more (DOI 1996; Milner et al. 2008; Pess et al. 2012*a*), while smaller watersheds can establish self-sustaining salmon populations in five years or less (Bryant et al. 1999; Glen 2002). It is too early to characterize the response of Chinook salmon and steelhead populations to the Elwha River dam removals and associated management actions since there has not yet been one complete generation since dam removal was completed. Thus, determining if there is a self-sustaining spawning population of Chinook salmon and steelhead, and which factors have most contributed to any changes seen to date, is premature. However, in the short period since dam removal we found several promising results that point towards eventual success.

For example, increasing trends in abundance for adult Chinook salmon and steelhead are a positive sign, even though the vast majority of Chinook salmon are hatchery origin. Given our estimates of hatchery mark rates, at this point, the abundance of adult Chinook salmon is largely driven by the number of fish released from the hatchery, and their post-release survival. However, the increase currently documented was not seen in the 20 years prior to dam removal, nor has such an increase occurred recently in any other Puget Sound or Washington Coast watershed during this period. In addition, the increase in natural-origin Chinook salmon outmigrants and natural-origin steelhead adults suggest the river habitat conditions are improving and fish are increasingly colonizing more habitat as the sediment load becomes more normative.

The preceding changes combined with expansion of Chinook salmon and steelhead adults into upstream habitats that are protected within Olympic National Park, a forested wilderness without roads, will allow the populations to occupy more natural in-river and riparian conditions relative to the Lower Elwha River. Intact aquatic habitat conditions can play an important role in the survival, productivity, and overall abundance of salmonids (Pess et al. 2002; Magnusson and Hilborn 2003). However, it is also important to remember that expansion into areas upstream of former barriers can lead to relatively higher productivity rates, irrespective of habitat conditions (Pess et al. 2012*a*).

One of the most important attributes associated with successful salmon colonization in newly opened habitats is the link between compatible life history adaptations and geographic, hydrologic, and ecological characteristics (Pess et al. 2014). In the Elwha River, the “re-awakening” of the summer steelhead life history strategy resulted in large-scale increases in returning summer steelhead adults in a short time period. Observations of less than ten to hundreds in a matter of several years suggest that the linkage for summer steelhead between life history, genetic disposition, and physical habitat characteristics is conducive to the establishment of a self-sustaining summer steelhead population. While initial post dam removal fish monitoring in the Elwha River has already provided encouraging results, continued monitoring over the ensuing decades will be necessary to inform whether these types of large-scale restoration actions can lead to the establishment of self-sustaining salmon populations.

We suggest rather than focusing on one set of specific actions for salmon population recovery (i.e., dam removal) it is important to understand and recognize that cumulative, simultaneous restorative actions (cumulative recovery actions) will be necessary to reverse the trend of declining salmon and steelhead populations. The Elwha River points to an integrated set of actions that include habitat restoration, harvest moratorium, and hatchery production designed help jumpstart population recovery for Chinook salmon and steelhead. The Elwha River dam removal has benefited Chinook salmon and steelhead populations with increases in habitat amount and types. Harvest restrictions have also benefited Chinook salmon and steelhead and allowed for increases in population abundance and expansion. Hatchery production has helped to preserve and increase the overall abundance of Elwha Chinook salmon and winter steelhead, particularly during dam removal. Summer steelhead, due to their source population likely being in the resident rainbow trout population above the former dams (Prince et al. 2017, Nichols et al. 2019; Fraik et al. 2021), are increasing in abundance in the absence of hatchery intervention. We hypothesize that none of these factors, alone and in isolation, would lead to the changes we have documented. Thus, just as multiple, cumulative impacts contributed to the depleted salmon populations and degraded habitat conditions prior to dam removal, reversing those effects and recovering abundant and diverse salmon populations and high quality habitat will require multiple, and synchronized cumulative large-scale recovery actions.

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Data availability statement

Supplementary data are available with the article (PID: DOI/compact identifier/accession number), and hyperlink.

References

Anderson, J.H. and Topping, P.C. 2018. Juvenile life history diversity and productivity of Chinook salmon in the Green River, Washington. N. Am. J. Fish. Manage. **38**(1): 180–193.

Anderson, J.H., Pess, G.R., Carmichael, R.W., Ford, M.J., Cooney, T.D., Baldwin, C.M., and McClure, M.M. 2014. Planning Pacific salmon and steelhead reintroductions aimed at long-term viability and recovery. N. Am. J. Fish. Manage. **34**(1): 72–93.

Anderson, J.H., Faulds, P.L., Denton, K.D., Koehler, M.E., Atlas, W.I., and Quinn, T.P. 2015. Dispersal and newly accessible habitat. Can. J. Fish. Aquat. Sci. **72**: 454–465.

Beechie, T., Buhle, E., Ruckelshaus, M., Fullerton, A., and Holsinger, L. 2006. Hydrologic regime and the conservation of salmon life history diversity. Biol. Conserv. **130**(4): 560–572.

Bellmore, J.R., Duda, J.J., Craig, L.S., Greene, S.L., Torgersen, C.E., Collins, M.J., and Vittum, K. 2016. Status and trends of dam removal research in the United States. WIREs Water. doi:10.1002/wat2.1164

Bellmore, J.R., Pess, G.R., Duda, J.J., O'Connor, J.E., East, A.E., Foley, M.M., Wilcox, A.C., Major, J.J., Shafroth, P.B., Morley, S.A., and Magirl, C.S. 2019. Conceptualizing ecological responses to dam removal: If you remove it, what's to come? BioScience **69**(1): 26–39.

Brannon, E.L. and Hershberger, W.K. 1984. Elwha River fall Chinook salmon. *In* Proceedings of the Olympic wild fish conference. *Edited by* J.M. Walton and D.B. Houston. Peninsula College: Port Angeles, WA. pp. 169-172.

Brenkman, S.J., Pess, G.R., Torgersen, C.E., Kloehn, K.K., Duda, J.J., and Corbett, S.C. 2008. Predicting recolonization patterns and interactions between potamodromous and anadromous salmonids in response to dam removal in the Elwha River, Washington State, USA. Northwest Sci. **82**(sp1): 91–106.

Brenkman, S.J., Peters, R.J., Tabor, R.A., Geffre, J.J., and Sutton, K.T. 2019. Rapid Recolonization and Life History Responses of Bull Trout Following Dam Removal in Washington's Elwha River. N. Am. J. Fish. Manage. **39**(3): 560–573.

Bryant, M.D., Frenette, B.J., and McCurdy, S.J. 1999. Colonization of a watershed by anadromous salmonids following the installation of a fish ladder in Margaret Creek, Southeast Alaska. N. Am. J. Fish. Manage. **19**(4): 1129–1136.

Christie,M.R., R.A French,R.A., Marine, M.L. and Blouin,M.S. 2014. How much does interbreeding contribute to the reduced fitness of hatchery-born steelhead (*Oncorhynchus mykiss*) in the wild?

Christie, M.R., Marine, M.L., and Blouin, M.S. 2011. Who are the missing parents? Grandparentage analysis identifies multiple sources of gene flow into a wild population. Mol. Ecol. **20**(6): 1263–1276. J. Hered **105**:111-119. doi:10.1093/jhered/est076

Clemento, A. J., Anderson E.C., Boughton, D. Girman, D., and Garza, J.C. 2008. Population genetic structure and ancestry of *Oncorhynchus mykiss* populations above and below dams in south-central California. Conserv. Genet. **10**: 1321–1336.

Collins, B.D., Dickerson-Lange, S.E., Schanz, S., and Harrington, S. 2019. Differentiating the effects of logging, river engineering, and hydropower dams on flooding in the Skokomish River, Washington, USA. Geomorphology **332**: 138–156.

Cram, J., Kendall, N., Marshall, A., Buehrens, T., Seamons, T., Leland, B., Ryding, K., and Neatherlin, E. 2018. Steelhead At Risk Report: Assessment of Washington’s Steelhead Populations. WDFW FPT 19-03.

Dempson, J.B., O'Connell, M.F., and Schwarz, C.J. 2004. Spatial and temporal trends in abundance of Atlantic salmon, Salmo salar, in Newfoundland with emphasis on impacts of the 1992 closure of the commercial fishery. Fish. Manag. Ecol. **11**(6): 387–402.

Department of the Interior (DOI). 1996. Elwha River ecosystem restoration implementation, final environmental impact statement. NPS D-271A. Department of the Interior, National Park Service, Olympic National Park, Port Angeles, WA.

DeVries, P. 1997. Riverine salmonid egg burial depths: review of published data and implications for scour studies. Can. J. Fish. Aquat. Sci. **54**(8): 1685–1698.

Duda, J.J., Brenkman, S.J., and Crain, P. 2018. Ch. 4: Pacific salmonids. *In* Natural resource condition assessment: Olympic National Park. *Edited by* R. McCaffery and K. Jenkins. Natural Resource Report NPS/OLYM/NRR—2018/1826. National Park Service, Fort Collins. pp. 123–167.

Enzenhofer, H.J. and Cronkite, G. 2005. A simple adjustable pole mount for deploying DIDSON and split-beam transducers. Can. Tech. Rep. Fish. Aquat. Sci. **2570**: iv + 14 p.

Foley, M.M., Warrick, J.A., Ritchie, A., Stevens, A.W., Shafroth, P.B., Duda, J.J., Beirne, M.M., Paradis, R., Gelfenbaum, G., McCoy, R., and Cubley, E.S. 2017. Coastal habitat and biological community response to dam removal on the Elwha River. Ecol. Monogr. **87**(4): 552–577.

Fraik, A.K., McMillan, J.R., Liermann, M., Bennett, T., McHenry, M.L., McKinney, G.J., Wells, A.H., Winans, G., Kelley, J.L., Pess, G.R., and Nichols, K.M. 2021. The Impacts of Dam Construction and Removal on the Genetics of Recovering Steelhead (Oncorhynchus mykiss) Populations across the Elwha River Watershed. Genes **12**(1): 89.

Gallagher, S.P., Hahn, P.K., and Johnson, D.H. 2007. Redd counts. *In* Salmonid field protocols handbook: techniques for assessing status and trends in salmon and trout populations. *Edited by* D.H. Johnson, B.M. Shrier, J.S. O'Neal, J.A. Knutzen, X. Augerot, T.A. O'Neil and T.N. Pearsons. American Fisheries Society, Bethesda, Maryland. pp. 197–234.

Glen D. 2002. Recovery of salmon and trout following habitat enhancement works: review of case studies 1995–2002. *In* Proceedings of the 13th international salmonid habitat enhancement workshop, Westport, County Mayo, Ireland. *Edited by* M. O'Grady. Central Fisheries Board, Dublin. pp 93–112.

Greene, C.M., Jensen, D.W., Pess, G.R., Steel, E.A., and Beamer, E. 2005. Effects of environmental conditions during stream, estuary, and ocean residency on Chinook salmon return rates in the Skagit River, Washington. Trans. Am. Fish. Soc. **134**(6): 1562–1581.

Hare, J.A., Kocik, J.F., and Link, J.S. 2019. Atlantic Salmon Recovery Informing and Informed by Ecosystem-Based Fisheries Management. Fisheries, **44**(9): 403–411.

Hiss, J.M. and Wunderlich, R.C. 1994. Salmonid availability and migration in the middle Elwha River system. Miscellaneous Report. Western Washington Fishery Resource Office, U.S. Fish and Wildlife Service, Olympia, Washington.

Holecek, D.E., Scarnecchia, D.L., and Miller, S.E. 2012. Smoltification in an impounded, adfluvial redband trout population upstream from an impassable dam: does it persist? Trans. Am. Fish. Soc. **141**(1): 68–75.

Holmes, J.A., Cronkite, G.W., Enzenhofer, H.J., and Mulligan, T.J. 2006. Accuracy and precision of fish-count data from a "dual-frequency identification sonar" (DIDSON) imaging system. J. Mar. Sci. **63**(3): 543–555.

Jensen, A.J., Zubchenko, A.V., Heggberget, T.G., Hvidsten, N.A., Johnsen, B.O., Kuzmin, O., Loenko, A.A., Lund, R.A., Martynov, V.G., Næsje, T.F., and Sharov, A.F. 1999. Cessation of the Norwegian drift net fishery: changes observed in Norwegian and Russian populations of Atlantic salmon. ICES J. Mar. Sci. **56**(1): 84–95.

Keefer, M.L. and Caudill, C.C. 2014. Homing and straying by anadromous salmonids: a review of mechanisms and rates. Rev. Fish Biol. Fish. **24**(1): 333–368.

Kiffney, P.M., Pess, G.R., Anderson, J.H., Faulds, P., Burton, K., and Riley, S.C. 2009. Changes in fish communities following recolonization of the Cedar River, WA, USA by Pacific salmon after 103 years of local extirpation. River Res Appl. **25**(4): 438–452.

Liermann, M., Pess, G., McHenry, M., McMillan, J., Elofson, M., Bennett, T., and Moses, R. 2017. Relocation and recolonization of Coho Salmon in two tributaries to the Elwha River: implications for management and monitoring. Trans. Am. Fish. Soc. **146**(5): 955–966.

Lilja, J., Ridley, T., Cronkite, G.M., Enzenhofer, H.J., and Holmes, J.A. 2008. Optimizing sampling effort within a systematic design for estimating abundant escapement of sockeye salmon (Oncorhynchus nerka) in their natal river. Fish. Res. **90**(1-3): 118–127.

Losee, J.P., Claiborne, A.M., Madel, G.M., Kungle, M., and Campbell, L. 2020. Is marine survival for Puget Sound's wild steelhead really that bad? A Nisqually River case study evaluating the estimates of productivity and survival of *Oncorhynchus mykiss*. Trans. Am. Fish. Soc. **150**(2): 160–174. https://doi.org/10.1002/tafs.10275

Magirl, C.S., Hilldale, R.C., Curran, C.A., Duda, J.J., Straub, T.D., Domanski, M., and Foreman, J.R. 2015. Large-scale dam removal on the Elwha River, Washington, USA: Fluvial sediment load. Geomorphology, **246**: 669–686.

Magnusson, A. and Hilborn, R. 2003. Estuarine influence on survival rates of coho (Oncorhynchus kisutch) and Chinook salmon (Oncorhynchus tshawytscha) released from hatcheries on the US Pacific coast. Estuaries, **26**(4): 1094–1103.

McMillan, J.R., Katz, S.L., and Pess, G.R. 2007. Observational evidence of spatial and temporal structure in a sympatric anadromous (winter steelhead) and resident rainbow trout mating system on the Olympic Peninsula, Washington. Trans. Am. Fish. Soc. **136**(3): 736–748.

Milner, A.M., Fastie, C.L., Chapin, F.S., Engstrom, D.R., and Sharman, L.C. 2007. Interactions and linkages among ecosystems during landscape evolution. BioScience, **57**(3): 237–247.

Milner, A.M., Robertson, A.L., Monaghan, K.A., Veal, A.J., and Flory, E.A. 2008. Colonization and development of an Alaskan stream community over 28 years. Front. Ecol. Environ. **6**(8): 413–419.

Montgomery, D.R., Buffington, J.M., Peterson, N.P., Schuett-Hames, D., and Quinn, T.P. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Can. J. Fish. Aquat. Sci. **53**(5): 1061–1070.

Nichols K., Fraik, A., Pess, G., Bennett, T., Denton, K., Corbett, S., McMillan, J., and McHenry, M. 2019. Recolonization following dam removal: Observations on genetic and life history variation in *Oncorhynchus mykiss* in the Elwha River, Washington, USA. International Conference on Integrative Salmonid Biology Conference in Edinburgh, Scotland, November 2019.

O'Connor, J.E., Duda, J.J., and Grant, G.E. 2015. 1000 dams down and counting. Science, **348**(6234): 496–497.

Pearsons, T.N. and O'Connor, R.R. 2020. Stray rates of natural-origin Chinook salmon and steelhead in the upper Columbia River watershed. Trans. Am. Fish. Soc. **149**(2): 147–158. doi: 10.1002/tafs.10220.

Pess, G.R., Montgomery, D.R., Steel, E.A., Bilby, R.E., Feist, B.E., and Greenberg, H.M. 2002. Landscape characteristics, land use, and coho salmon (Oncorhynchus kisutch) abundance, Snohomish River, Wash., USA. Can. J. Fish. Aquat. Sci. **59**(4): 613–623.

Pess, G.R., McHenry, M.L., Beechie, T.J., and Davies, J. 2008. Biological impacts of the Elwha River dams and potential salmonid responses to dam removal. Northwest Sci. **82**(sp1): 72–91.

Pess, G.R., Hilborn, R., Kloehn, K., and Quinn, T.P. 2012***a***. The influence of population dynamics and environmental conditions on pink salmon (Oncorhynchus gorbuscha) recolonization after barrier removal in the Fraser River, British Columbia, Canada. Can. J. Fish. Aquat. Sci. **69**(5): 970–982.

Pess, G.R., Liermann, M.C., McHenry, M.L., Peters, R.J. and Bennett, T.R. 2012***b***. Juvenile salmon response to the placement of engineered log jams (ELJs) in the Elwha River, Washington State, USA. River. Res. and Appl. **28**(7): 872-881.

Pess, G.R., Quinn, T.P., Gephard, S.R., and Saunders, R. 2014. Re-colonization of Atlantic and Pacific rivers by anadromous fishes: linkages between life history and the benefits of barrier removal. Rev. Fish Biol. Fish. **24**(3): 881–900.

Peters, R.J., Duda, J.J., Pess, G.R., Zimmerman, M., Crain, P., Hughes, Z., Wilson, A., Liermann, M.C., Morley, S.A., McMillan, J., and Denton, K. 2014. Guidelines for monitoring and adaptively managing restoration of Chinook salmon (Oncorhynchus tshawytscha) and steelhead (O. mykiss) on the Elwha River. U.S. Fish and Wildlife Service, 111 p.

Peters, R.J., Liermann, M., McHenry, M.L., Bakke, P., and Pess, G.R. 2017. Changes in streambed composition in salmonid spawning habitat of the Elwha River during dam removal. J Am Water Resour As. **53**(4): 871–885.

Peters, R.J., Denton, K., and Liermann, M. 2020. Proportion of Hatchery Origin Winter Steelhead and Broodstock Collection in the Elwha River: 2019. U.S. Fish and Wildlife Report # 4837-1336 to the Lower Elwha Klallam Tribe.

Plummer, M. 2003. March. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proc. 3rd Int. Work. Distrib. Stat. Comput. **124**(125.10): 1–10.

Prince, D.J., O'Rourke, S.M., Thompson, T.Q., Ali, O.A., Lyman, H.S., Saglam, I.K., Hotaling, T.J., Spidle, A.P., and Miller, M.R. 2017. The evolutionary basis of premature migration in Pacific salmon highlights the utility of genomics for informing conservation. Sci. Adv. **3**(8): e1603198.

Pringle, C.M., Freeman, M.C., and Freeman, B.J. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the new world: tropical-temperate comparisons: the massive scope of large dams and other hydrologic modifications in the temperate New World has resulted in distinct regional trends of biotic impoverishment. While neotropical rivers have fewer dams and limited data upon which to make regional generalizations, they are ecologically vulnerable to increasing hydropower development and biotic patterns are emerging. BioScience, **50**(9): 807–823.

Quinn, T.P., Bond, M.H., Brenkman, S.J., Paradis, R., and Peters, R.J. 2017. Re-awakening dormant life history variation: stable isotopes indicate anadromy in bull trout following dam removal on the Elwha River, Washington. Environ. Biol. Fishes. **100**(12): 1659–1671.

Randle, T.J., Bountry, J.A., Ritchie, A., and Wille, K. 2015. Large-scale dam removal on the Elwha River, Washington, USA: Erosion of reservoir sediment. Geomorphology, **246**: 709–728.

Ritchie, A.C., Warrick, J.A., East, A.E., Magirl, C.S., Stevens, A.W., Bountry, J.A., Randle, T.J., Curran, C.A., Hilldale, R.C., Duda, J.J., and Gelfenbaum, G.R. 2018. Morphodynamic evolution following sediment release from the world's largest dam removal. Sci. Rep. **8**: 13279.

Ruckelshaus, M.H., Currens, K.P., Graeber, W.H., Fuerstenberg, R.R., Rawson, K., Sands, N.J., and Scott, J.B. 2006. Independent populations of Chinook salmon in Puget Sound. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-78.

Savvaitova, K.A., Kuzishchin, K.V., Maksimov, S.V., and Pavlov, D.S. 1997. Population structure of mikizha, Salmo mykiss in the Utkholok River (western Kamchatka). J. Ichthyol. **37**(3): 216–225.

Savvaitova, K.A., Tutukov, M.A., Kuzishchin, K.V., and Pavlov. D.S. 2002. Changes in the population structure of mikizha Parasalmo mykiss from the Utkholok River, Kamchatka, during the fluctuation in its abundance. J. Ichthyol. **42**(3): 238–242.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. Nature, **465**(7298): 609.

Shaffer, J.A., Juanes, F., Quinn, T.P., Parks, D., McBride, T., Michel, J., Naumann, C., Hocking, M., and Byrnes, C. 2017. Nearshore fish community responses to large scale dam removal: implications for watershed restoration and fish management. Aquat. Sci. **79**(3): 643–660.

Team, R.C. 2015. R: A language and environment for statistical computing.

Thompson, T.Q., Bellinger, M.R., O'Rourke, S.M., Prince, D.J., Stevenson, A.E., Rodrigues, A.T., Sloat, M.R., Speller, C.F., Yang, D.Y., Butler, V.L., and Banks, M.A. 2019. Anthropogenic habitat alteration leads to rapid loss of adaptive variation and restoration potential in wild salmon populations. Proc. Natl. Acad. Sci. **116**(1): 177–186.

Tripp, D.B. and Poulin, V.A. 1986. The effects of logging and mass wasting on salmonid spawning habitat in streams on the Queen Charlotte Islands. Ministry of Forests and Lands, Research Branch, Land Management Report 50, Victoria, B.C.

Tullos, D.D., Collins, M.J., Bellmore, J.R., Bountry, J.A., Connolly, P.J., Shafroth, P.B., and Wilcox, A.C. 2016. Synthesis of common management concerns associated with dam removal. J. Am. Water Resour. Assoc. **52**(5): 1179–1206.

Waples, R.S., Pess, G.R., and Beechie, T. 2008. Evolutionary history of Pacific salmon in dynamic environments. Evol. Appl. **1**(2): 189-206.

Ward, L., Crain, P., Freymond, B., McHenry, M., Morrill, D., Pess, G., Peters, R., Shaffer, J.A., Winter, B., and Wunderlich, B. 2008. Elwha River Fish Restoration Plan–Developed pursuant to the Elwha River Ecosystem and Fisheries Restoration Act, Public Law 102-495. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-90.

Warrick, J.A., Bountry, J.A., East, A.E., Magirl, C.S., Randle, T.J., Gelfenbaum, G., Ritchie, A.C., Pess, G.R., Leung, V., and Duda, J.J. 2015. Large-scale dam removal on the Elwha River, Washington, USA: Source-to-sink sediment budget and synthesis. Geomorphology, **246**: 729–750.

Weigel, D.E. 2013. Colonization of steelhead (Oncorhynchus mykiss) after barrier removal in a tributary to the Methow River, Washington. Ph.D. thesis, University of Idaho.

Westley, P.A., Quinn, T.P., and Dittman, A.H. 2013. Rates of straying by hatchery-produced Pacific salmon (Oncorhynchus spp.) and steelhead (Oncorhynchus mykiss) differ among species, life history types, and populations. Can. J. Fish. Aquat. Sci. **70**(5): 735–746.

Winter, B.D. and Crain, P. 2008. Making the case for ecosystem restoration by dam removal in the Elwha River, Washington. Northwest Sci. **82**(sp1): 13–29.

Xie, Y., Gray, A.P., Martens, F.J., Boffey, J.L., and Cave, J.D. 2005. Use of Dual-Frequency Identification Sonar to Verify Salmon Flux and to Examine Fish Behaviour in the Fraser River. Pacific Salmon Comm. Tech. Rep. No. 16.

Zimmerman, M.S., Kinsel, C., Beamer, E., Connor, E.J., and Pflug, D.E. 2015. Abundance, survival, and life history strategies of juvenile Chinook salmon in the Skagit River, Washington. Trans. Am. Fish. Soc. **144**(3): 627–641.

Tables

Table 1. Chinook salmon relocation by sex from the hatchery facilities in the Lower Elwha River to areas upstream the former Elwha Dam site. Blanks indicate no relocation, jacks are excluded from the counts below.

Year	Indian Creek		Little River		Elwha River rkm 16.5		Elwha River rkm 20.5		Elwha River rkm 22.0	
	M	F	M	F	M	F	M	F	M	F
2011									7	3
2012	179	0								
2013			117	0						
2014										
2015										
2016										
2017										
2018							877	113		
2019					181	395				
2020										

Table 2. Steelhead relocation from the Lower Elwha River to Indian Creek and Little River above the former lower Elwha Dam location.

Year	**Indian Creek**		**Little River**	
	Natural	Hatchery	Natural	Hatchery
2012	11	0	35	0
2013			53	35
2014			1	58
2015				
2016	3	32		
2017				
2018				
2019				
2020				

Table 3. Hatchery mark rates of Elwha Chinook salmon from three sample collection sources. The weir and stream survey samples represent Chinook salmon that spawned naturally in the river.

Return year	**Hatchery broodstock**		**Weir**		**Stream survey**		**Percent marked**
	Marked	**Unmarked**	**Marked**	**Unmarked**	**Marked**	**Unmarked**	
2009	271	5	NA	NA	21	1	98.0%
2010	218	12	3	4	38	0	94.2%
2011	533	21	405	9	24	0	97.0%
2012	5	0	87	10	1	0	90.3%
2013	537	27	275	14	79	2	95.4%
2014	481	18	NA	NA	272	12	96.2%
2015	456	28	NA	NA	337	27	93.5%
2016	278	8	NA	NA	245	15	95.8%
2017	555	11	NA	NA	484	29	96.3%
2018	307	3	NA	NA	420	12	98.0%
2019	236	1	NA	NA	352	20	96.6%
2020	234	2	NA	NA	141	25	93.3%

Table 4. Number and proportion of marked and unmarked winter steelhead in the Elwha River from 2014 to 2019.

Years	River section	Hatchery origin	Natural origin	Proportion hatchery origin
2014–2018	Downstream of Elwha Dam	235	42	0.85
2014–2018	Upstream of Elwha Dam	6	18	0.25
2019	Downstream of Elwha Dam	40	44	0.55
2019	Upstream of Elwha Dam	0	24	0.00

Table 5. Elwha River smolt trap catch data and abundance estimates for yearling Chinook salmon from 2014 to 2020.

Year	**Raw catch**	**Trap efficiency**	**Abundance estimate**
2014	71	NA	NA
2015	25	NA	NA
2016	86	0.076	1374 (960-3672)
2017	47	0.134	593 (389-1098)
2018	21	NA	NA
2019	4	NA	NA
2020	142	0.023	4301 (4031-7248)

Table 6. Adult-to-adult productivity of Chinook salmon spawning naturally in the Elwha River watershed. Fishery mortality data were only available through 2016 whereas abundance, hatchery mark rate and age structure data were available through 2019, explaining the shorter pre-harvest time series.

Return year	Spawners	Total recruits		Productivity	
		Return to river	Pre-harvest	Return to river	Pre-harvest
2004	2075	64.4	77.3	0.03	0.04
2005	835	83.6	102.0	0.10	0.12
2006	693	15.7	19.1	0.02	0.03
2007	380	45.8	57.2	0.12	0.15
2008	470	121.6	151.9	0.26	0.32
2009	678	341.9	406.4	0.50	0.60
2010	569	190.9	215.0	0.34	0.38
2011	852	240.3	261.7	0.28	0.31
2012	1655	127.9		0.08	
2013	2426	47.3		0.02	
2014	2509	155.6		0.06	
2015	2552	343.2		0.13	
2016	2019	116.1[A]		0.06[A]	

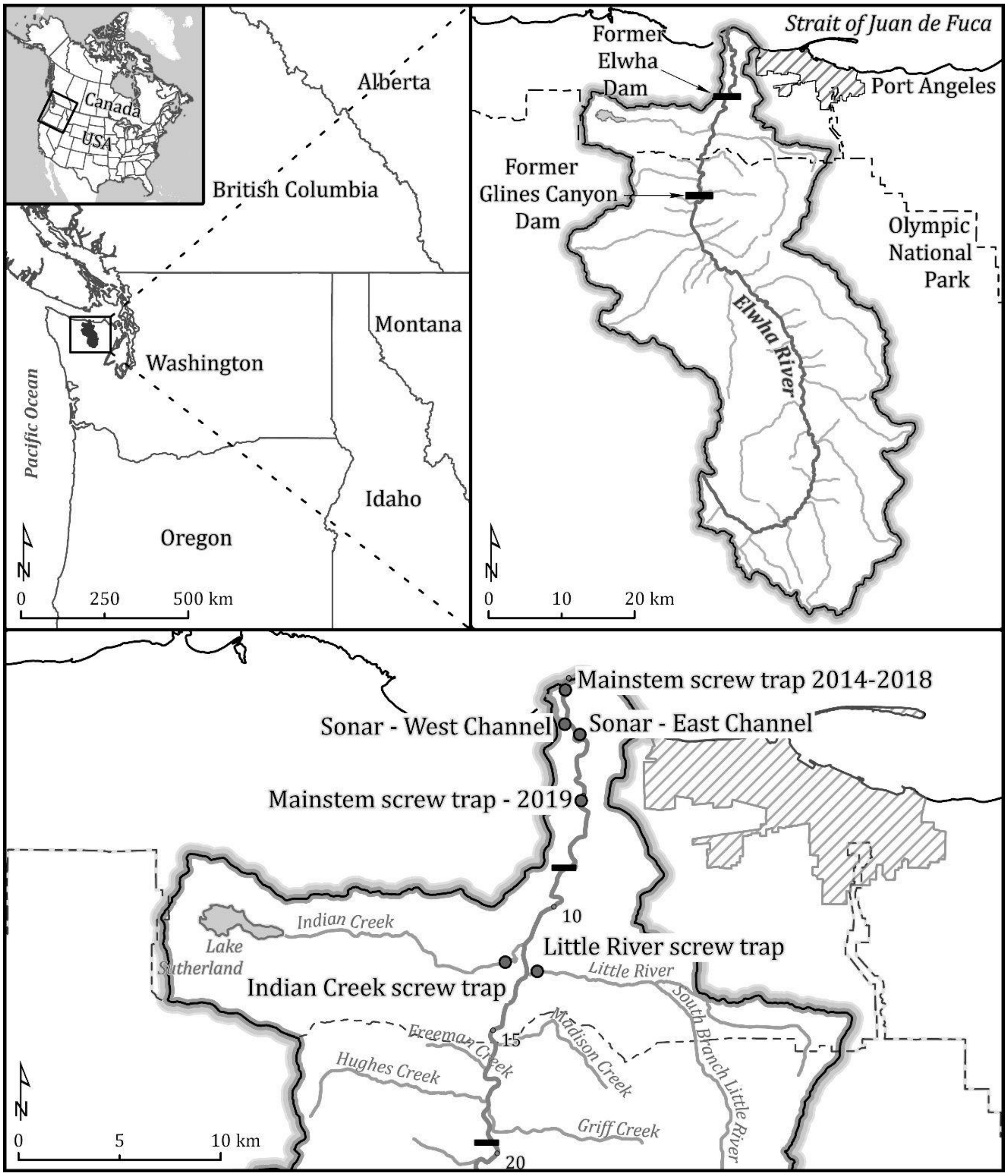
[A] Incomplete cohort, does not include age-5 returns.

Table 7. Number of adult summer steelhead counted through snorkel observations in the Elwha River from 2013 to 2020.

Year	Rkm location	Total rkm surveyed	Snorkel survey month	Adult summer steelhead observed
2013	[*]0.0–5.0	5	October	1
2016	20.0–25.0	5	August	1
2016	40.0–53.0	13	August	5
2017	35.0–58.0	23	September	74
2018	0.0–63.0	63	September	216
2019	0.0–63.0	63	September	341
2020	0.0–63.0	63	September	114

[*]Snorkel survey was conducted in Little River, a tributary of the Elwha River

1114 **Figures**



1115

1116 **Fig. 1. The Elwha River basin.** Upper left is regional map of Elwha River, upper right is the entire Elwha
1117 River watershed. Lower map includes location of SONAR units and smolt screw traps.

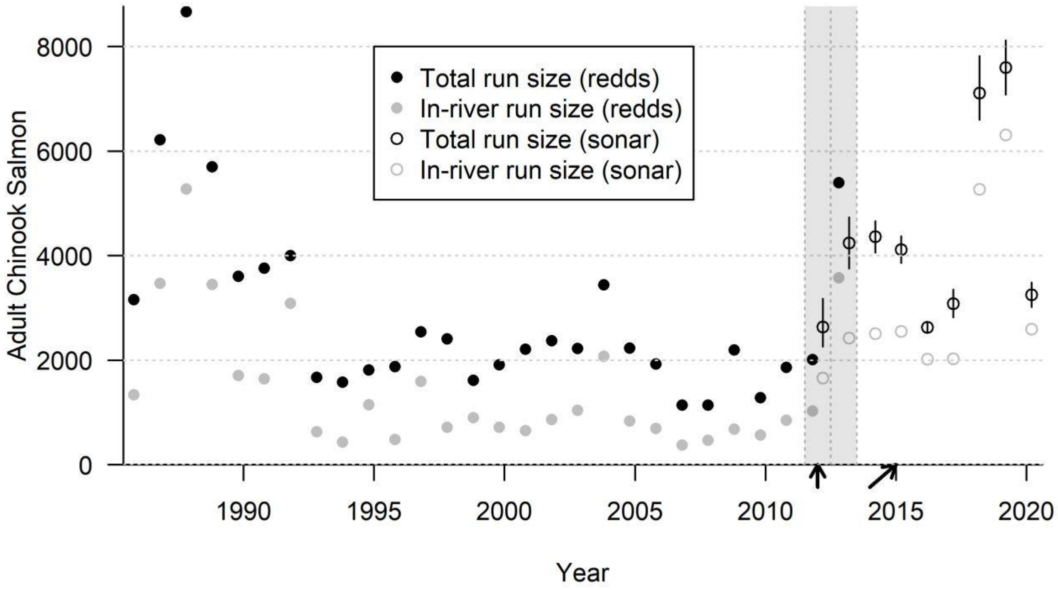


Fig. 2a. Chinook salmon adult abundance in the Elwha River from 1986 to 2020. Shaded areas denote estimates from Chinook salmon redd surveys and SONAR. Dark solid lines denote 95% confidence intervals. Arrows (straight and angled) denote the removal of the Elwha and Glines Canyon dams. Removals for hatchery broodstock account for the difference between total run size and in-river run size.

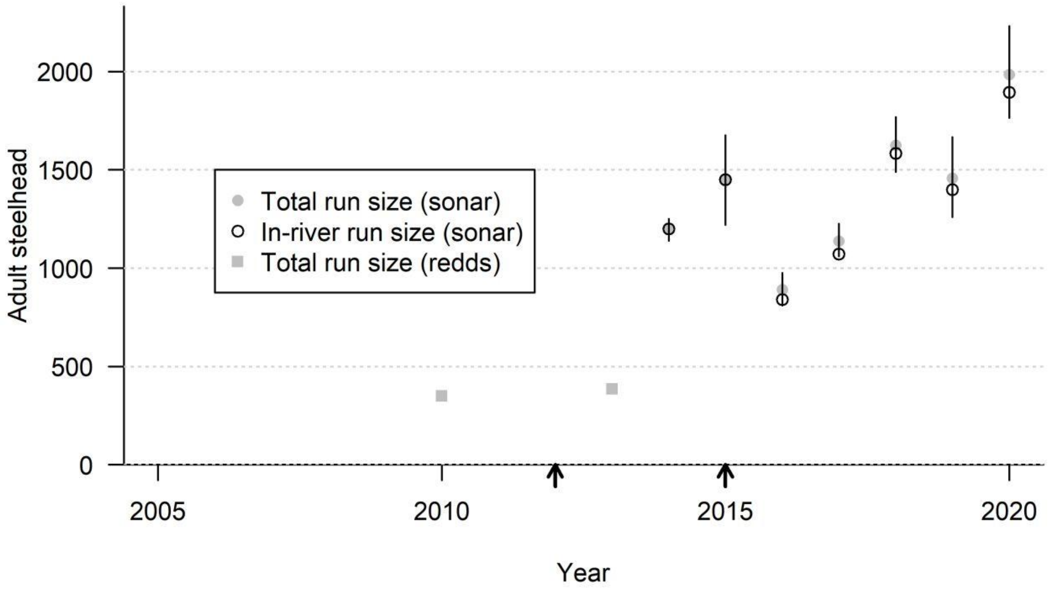


Fig. 2b. Winter steelhead adult abundance in the Elwha River from 2010 to 2020. Dark solid lines denote 95% confidence intervals. Arrows denote the removal of the Elwha and Glines Canyon dams.

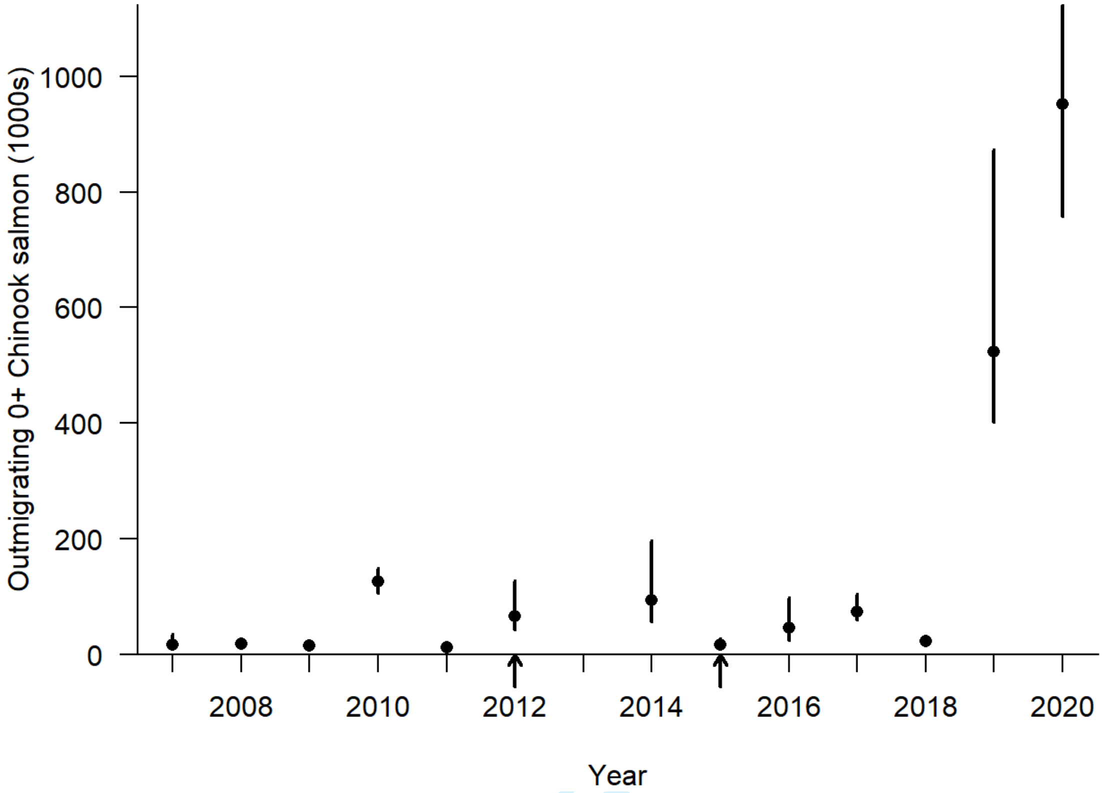


Fig. 3a. Abundance of outmigrating subyearling juvenile Chinook salmon from the Elwha River - 2007 to 2020, as estimated at the screw trap in the mainstem Elwha River (rkm 0.3 and 3.3 in 2014 and 4.0 in 2019). The filled circles and vertical bars represent the median estimate and 95% credible interval. Arrows denote the removal of the Elwha and Glines Canyon dams.

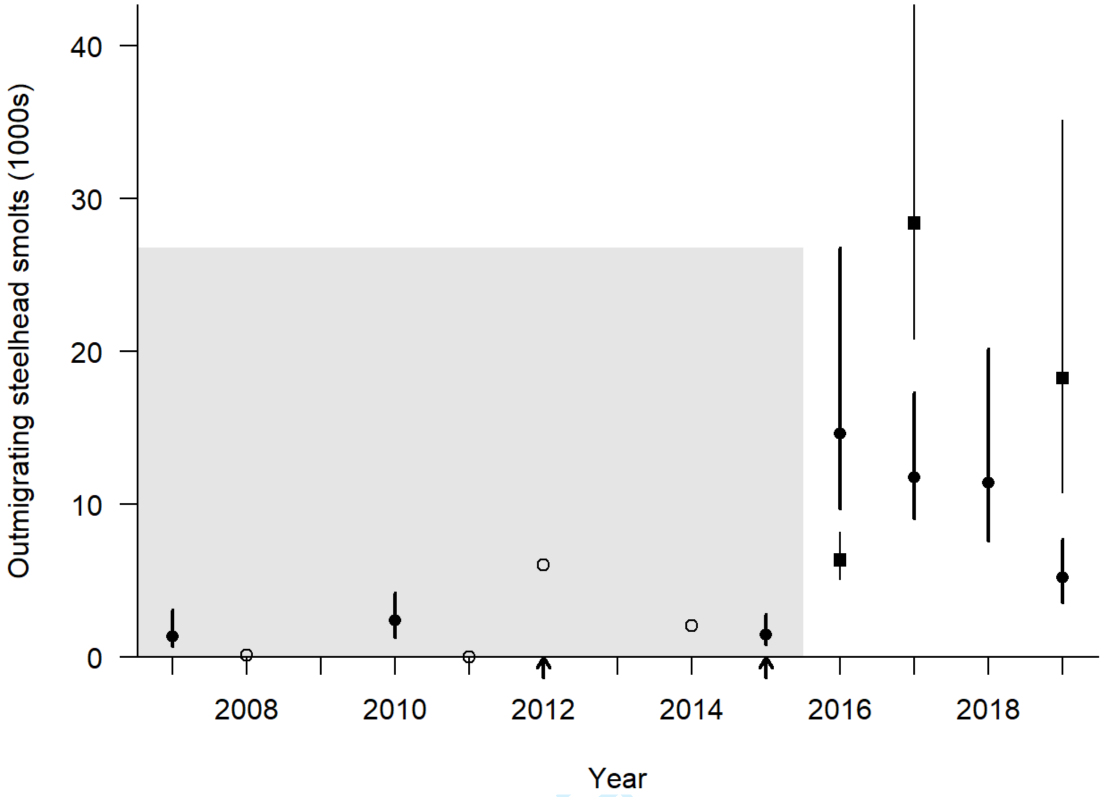


Fig. 3b. Abundance of outmigrating steelhead smolts from the Elwha River - 2007 to 2019, as estimated at the screw trap in the mainstem Elwha River (rkm 0.3 and 3.3 in 2014 and 4.0 in 2019). The filled circles and vertical bars represent the median estimate and 95% credible interval. The open circles without credible intervals represent years in which the catch was less than 10. The black filled rectangles represent the separate estimates based on the independent large-bodied fish efficiency estimates. The gray region represents years in which the outmigrant estimates are believed to be under-estimated. Arrows denote the removal of the Elwha and Glines Canyon dams.

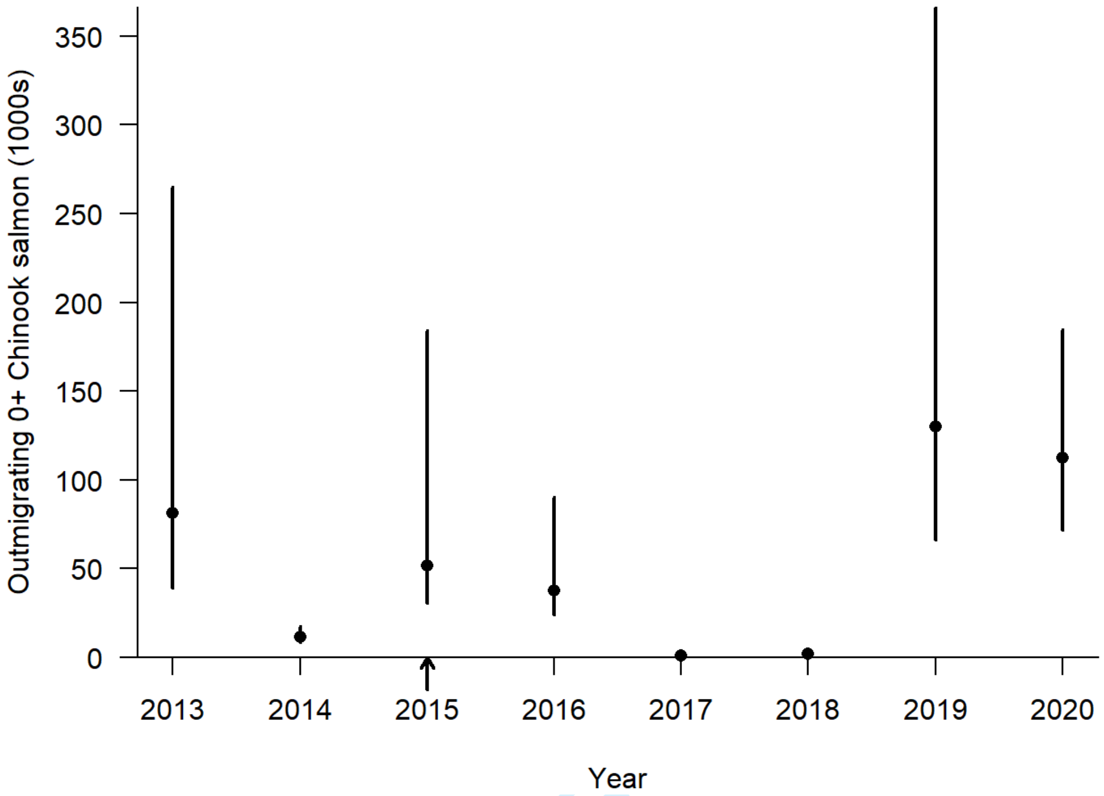


Fig. 3c. Abundance of outmigrating subyearling juvenile Chinook salmon from Indian Creek - 2013 to 2020 estimated from screw trap (rkm 0.7). The filled circles and vertical bars represent the median estimate and 95% credible interval. Arrow denotes the removal of the Glines Canyon dam.

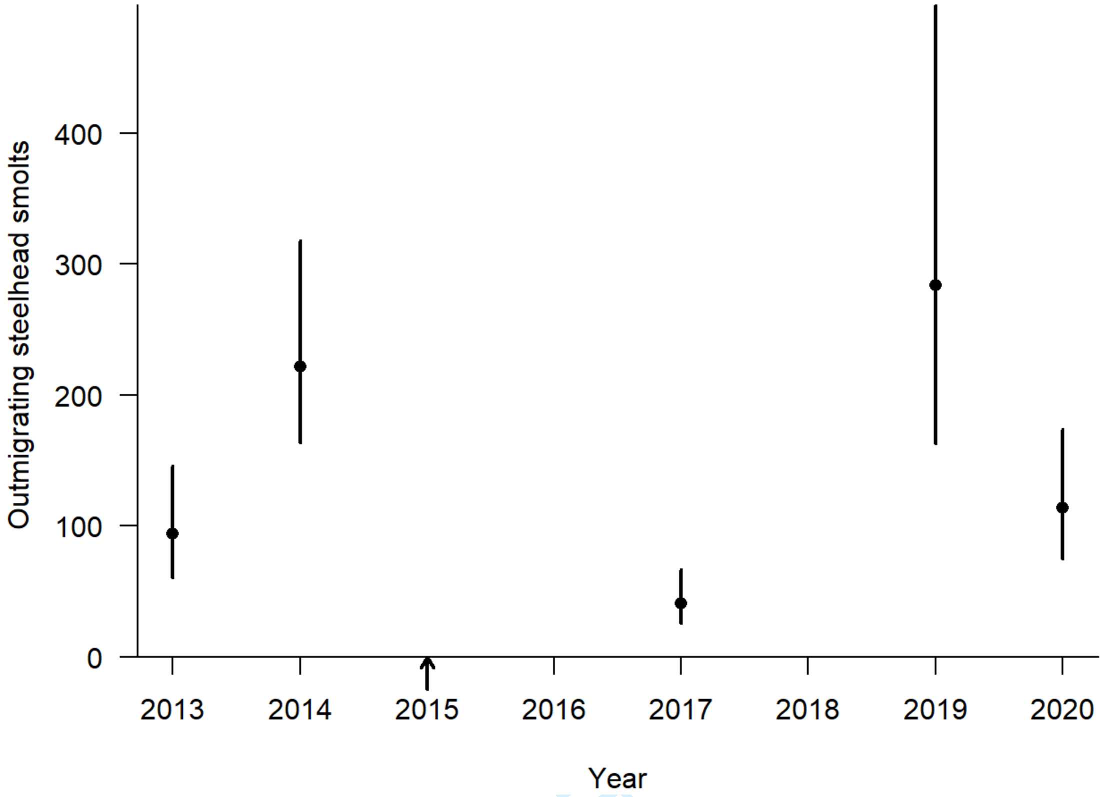


Fig. 3d. Abundance of outmigrating steelhead smolts from Indian Creek - 2013 to 2020 estimated from screw trap (rkm 0.7). The filled circles and vertical bars represent the median estimate and 95% credible interval. Arrow denotes the removal of the Glines Canyon dam.

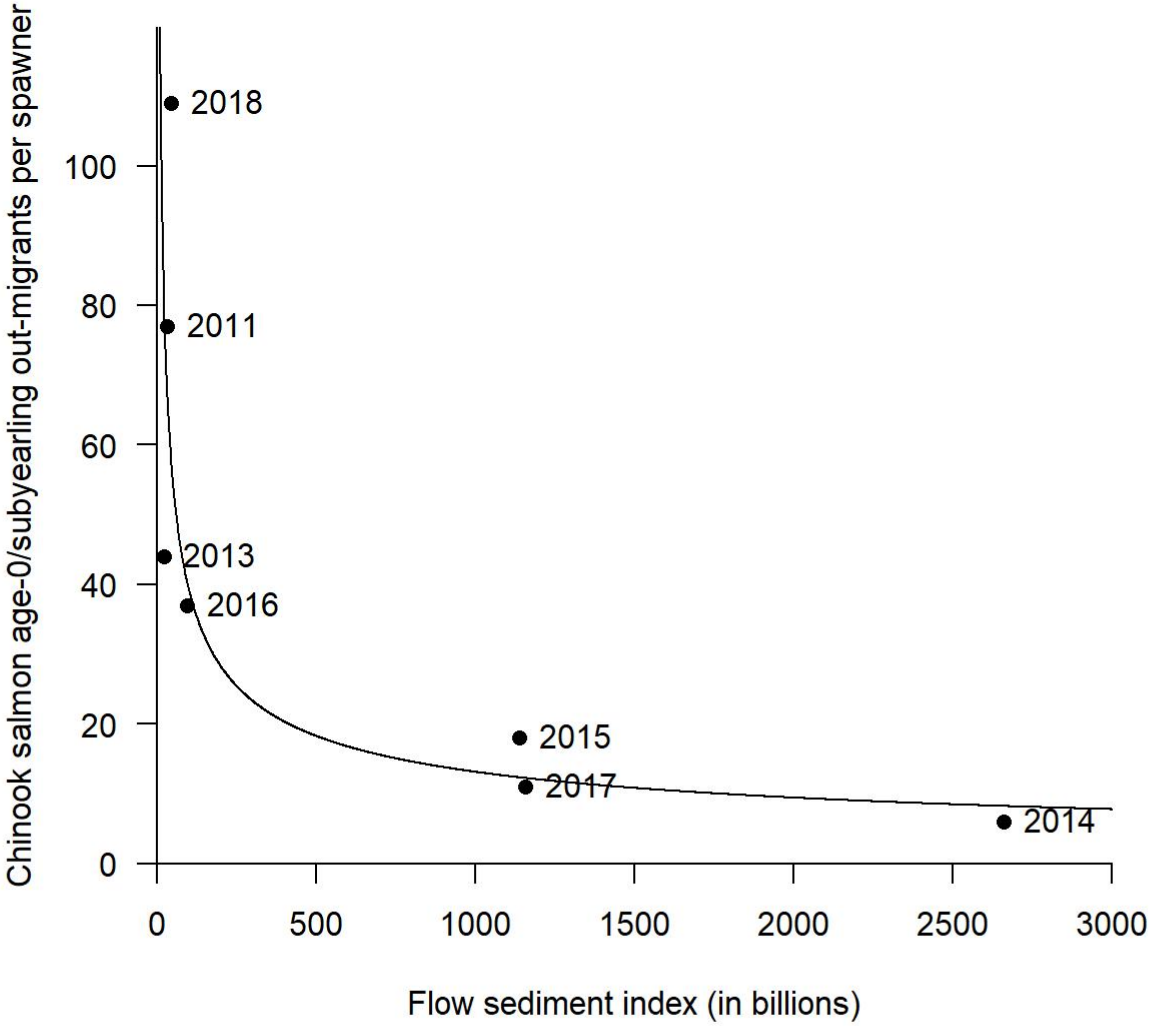


Fig. 4. The relationship between the number of days where flow is above bankfull discharge (56.6 cms) multiplied by the total sediment volume (tonnes) during incubation (September to December) vs. the number of subyearling juvenile Chinook salmon per spawner - 2011 to 2018.

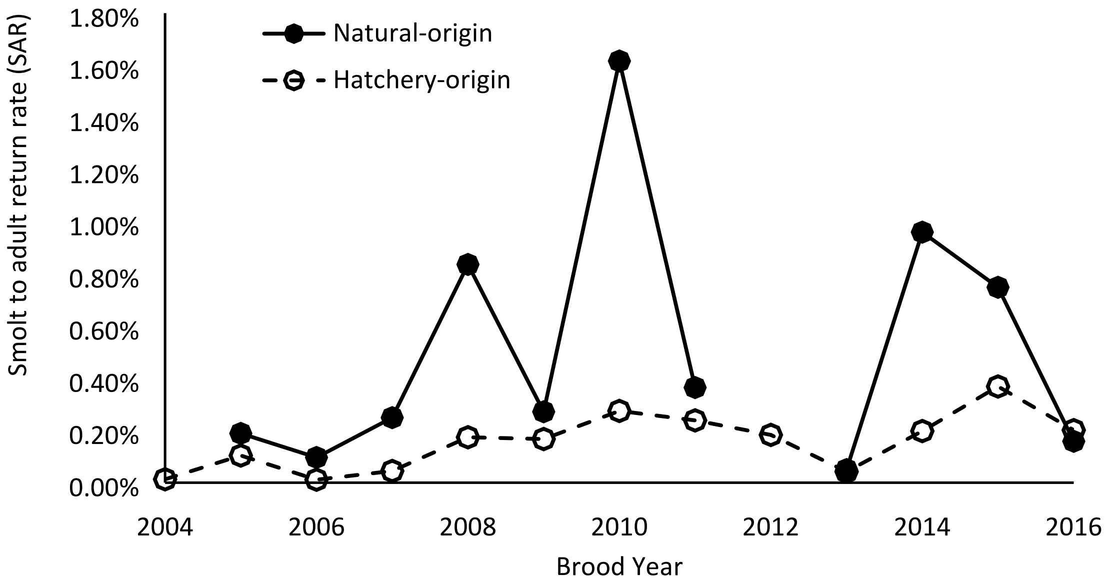


Fig. 5. Smolt-to-adult return (SAR) rate from brood year 2004 to 2016 for hatchery and natural origin Chinook salmon in the Elwha River. The filled circles and solid line represent natural origin Chinook salmon. The open circles and dashed line represent hatchery origin Chinook salmon. Brood year 2016 represents an incomplete cohort (age-5 adults not yet included). For each brood year (BY), hatchery-origin juveniles include subyearling (BY + 1) and yearling (BY + 2) releases.

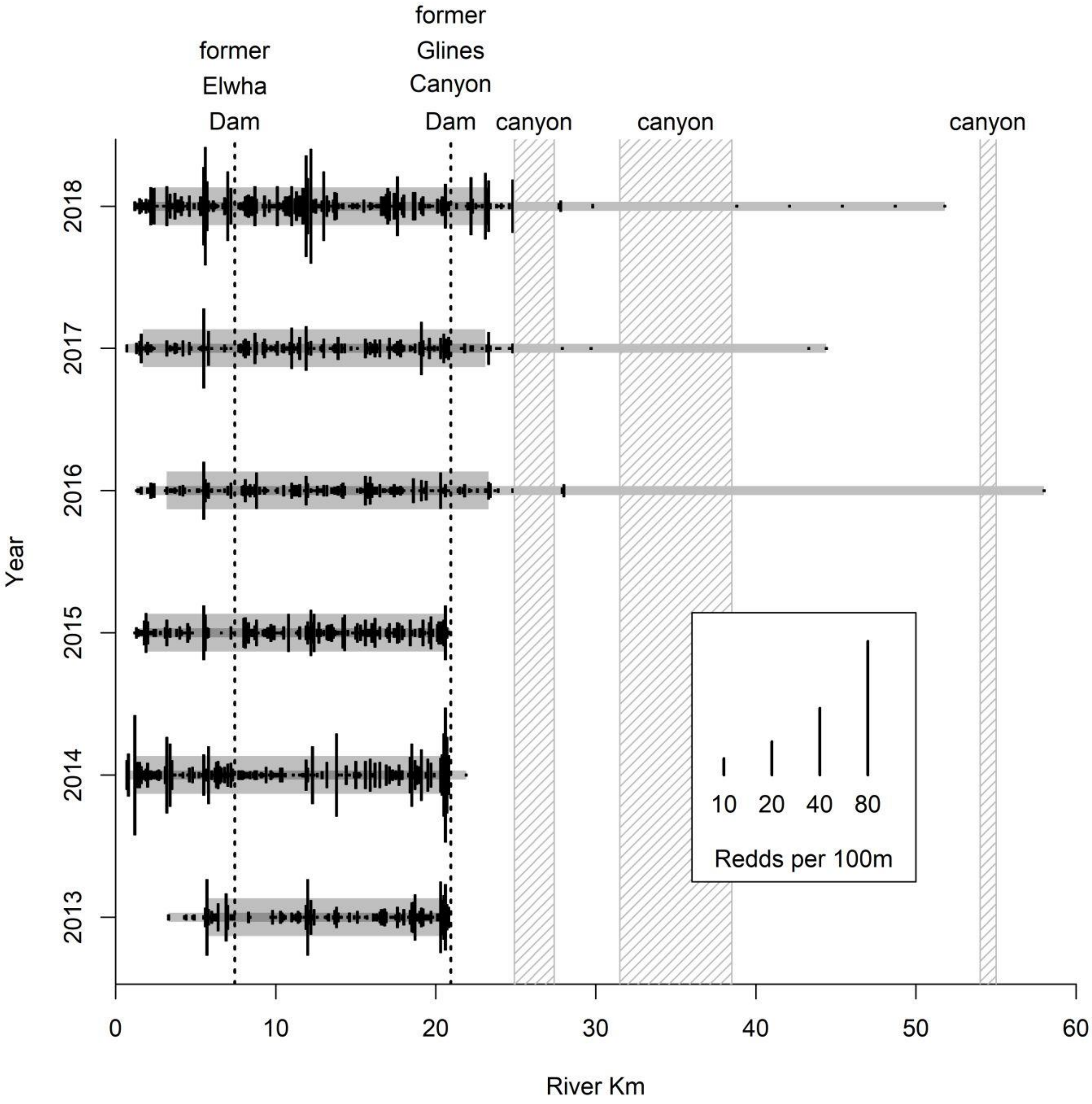


Fig. 6. Chinook salmon spawning distribution by year and rkm 2013 to 2018. Solid black lines denote Chinook salmon redd density/100 m. Narrow grey lines denote the total extent of Chinook salmon redd distribution. Thicker grey line denotes the central 90% of Chinook salmon redd distribution.

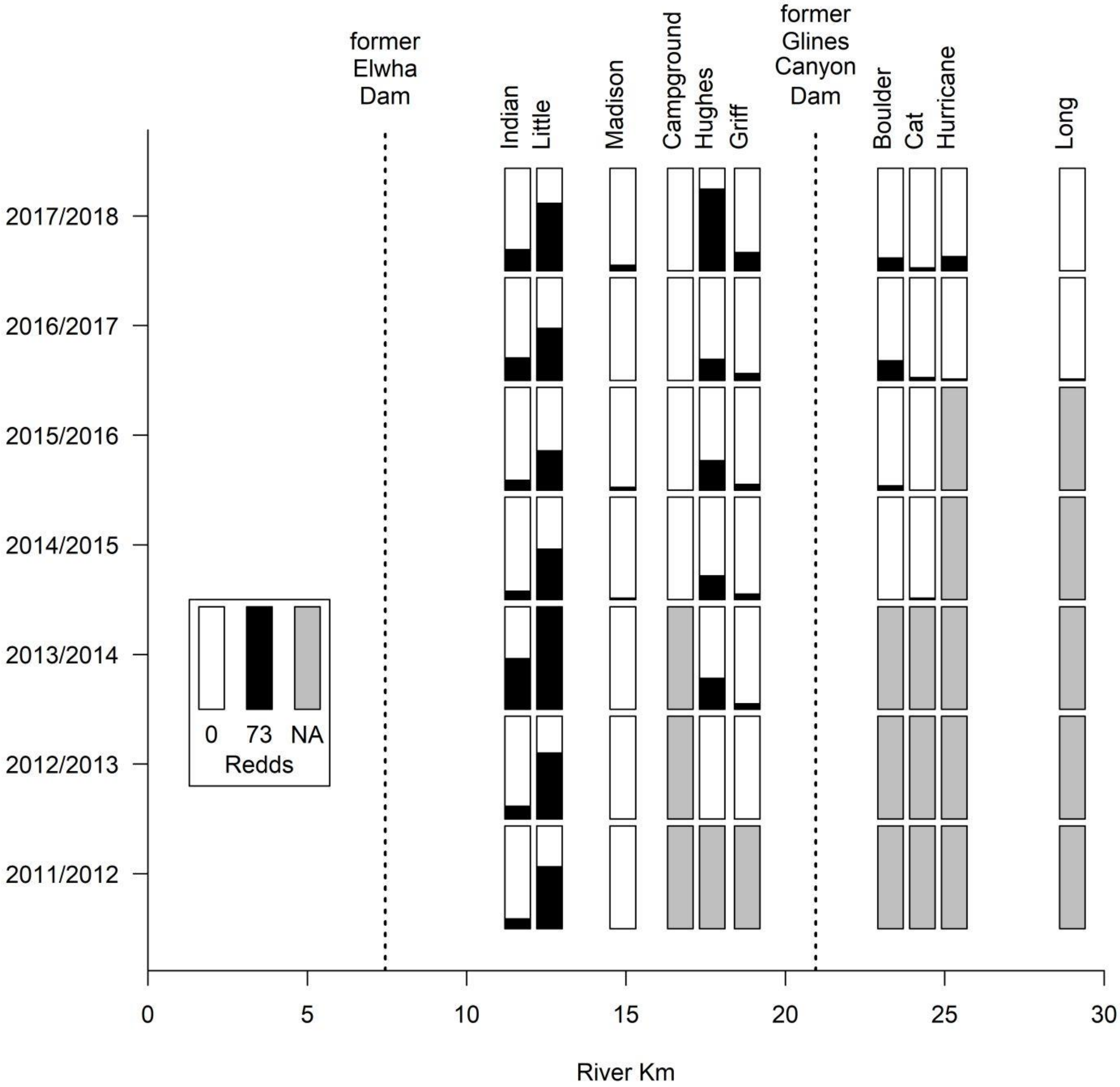


Fig. 7. The number of steelhead redds in surveyed tributaries in the Middle and Upper Elwha River – 2011 to 2018. “NA” indicates no survey conducted.

Appendix A.

Each SONAR was attached to a pole mount (Enzenhofer and Cronkite 2005) that was mounted on a reinforced ladder. The SONAR and ladder were positioned just under the surface of the water with a downward angle of approximately 4-6 degrees. The goal of this placement was to ensonify the bottom of the river across the entire width of the channel in addition to clearly identify the far bank. We constructed a picket weir approximately 3 m downstream of the DIDSON that extended from the bank to 3 m beyond the SONAR. This weir directed fish to an area of the channel more effectively covered by the sonar beams, producing greatly improved imagery and minimizing the possibility of fish passing directly underneath the beam and avoiding detection. The Hunt's Road Channel (HRC) was connected to line power, which ensured a constant power supply. The Old Mainstem (OMS) site was powered by a 24-volt, 200-amp hour battery bank that was continually charged by an array of solar panels. A weir was also constructed at the OMS site to direct upstream passage of adult fish.

All DIDSON data was processed using DIDSON proprietary software (V5.25.26). Files were background subtracted, using the default parameters, to remove rocks and make it easier to discern moving objects, such as migrating fish. Subsequently, each file was transformed into an echogram using the default parameters, with the exception that all 96 beams were included rather than only the center beam. This dramatically increases the probability that any fish entering the ensonified area will be detected in the echogram.

An echogram is a graph of the data with distance from the SONAR head on the y-axis and time on the x-axis. If no targets are present, the echogram will be blank. If a fish swims through the ensonified area, the echogram will have a series of targets connected along the x-axis, whose overall length correlates with the length of time it took the fish to pass through the ensonified area. The string of targets along the x-axis may trend up or down along the y-axis if the fish was swimming diagonally away or towards the sonar head during its passage. To count fish passage events, target echograms were simultaneously reviewed along with the raw video file. This enabled the reviewer to quickly scan through an echogram until a target pattern that could potentially represent a fish was encountered. The raw video imagery was then reviewed to ensure identified targets were indeed fish.

The procedure for processing ARIS data was the same (background subtraction, echogram formation, manual review of likely targets), except ARIS data is processed with its own software, ARISFish (v.1.5). After determining that a pattern on the echogram was indeed a fish, we noted several variables, including the date, time, direction (upstream or downstream), distance from SONAR head, and length (mm).

We used a simulation-based approach to validate the expansion of raw SONAR counts to a population estimate and replicated this simulation procedure a large number of times (10,000). Data were organized into 6-hour strata, four per day. We initialized the values in each cell (360 to 600 rows depending on the season and year representing each of the six-hour strata and 10,000 columns, representing the iterations) to the net passage based on the raw counts from the files. During each of the three or four steps in the adjustment procedure described below, we were able to generate updated estimates of escapement, and at varying temporal scales (six-hour estimates, daily estimates, and annual estimates). To determine the coefficient of variation for the final escapement, the standard deviation of all 10,000 estimates was divided by the mean of all 10,000 estimates.

A.1 20-minute expansion

For Chinook salmon we used a 20-minute count expansion due to the number of Chinook passing the SONARs. Counting 20 minutes of each hour is on the upper end of recommended sub-sampling regimes (Lilja et al. 2008). Due to relatively low fish passage during steelhead season, the full hour was counted for each file. In order to expand our 20-minute counts and encompass the uncertainty inherent in the process, we typically counted the full 60 minutes of 15 six-hour strata of Chinook data each year. We regressed these 60-minute counts against those predicted from the first 20 minutes of the same six-hour strata to create a vector of residuals. Each raw 20-minute count was then adjusted by multiplying by three and adding a randomly sampled value from the residual vector.

A.2 Species composition

We conducted tangle net surveys for Chinook salmon on a weekly or bi-weekly basis during the course of the SONAR operations to capture live adult salmonids at multiple sites in the lower two km of the Elwha River. We used the tangle net data to determine the beginning and end of the Chinook and steelhead runs, to differentiate species of salmonids passing by the SONAR sites during the course of the run, and to determine a minimum size threshold for SONAR target inclusion in the final escapement calculation. Captured fish were measured for fork length and qualitatively categorized as “new” if they appeared to have been in the river for less than two weeks, “holding” if they appeared to have been in the river for more than two weeks, or “spawned out” if they appeared to have finished or initiated spawning. In an effort to only include actively migrating fish in the date-specific data set, only fish categorized as “new” or “holding” were included in the species composition adjustment. The tangle net was designed to snare fish from the jaw not the gills in order to reduce encounter effects. The tangle net was approximately 20 m long and 3 m deep with a 10 cm mesh of 6# monofilament. We also used the in-stream netting data to determine a minimal threshold for SONAR measured targets to be included in the final escapement estimation by comparing the lengths of Chinook and non-Chinook salmonids, which were mostly bull trout during the steelhead run and pink and coho salmon towards the end of the Chinook run.

In-river netting provided the necessary data to adjust the expanded counts to account for the number of Chinook and steelhead moving passed the SONAR sites. We summed fish between adjacent sampling events to arrive at daily totals for fish caught and Chinook and steelhead caught. We simulated the proportion of Chinook or steelhead on given iteration and day as:

$$p_{i,j,k} = Binomial\left(\frac{N_{i,j,k}^{chinook\ or\ steelhead}}{N_{i,j,k}^{total}}, N_{i,j,k}^{total}\right)/N_{i,j,k}^{total} \qquad \text{(A1)}$$

where $_i$ represents the iteration (1–10,000), $_j$ indexes the 6-hour chunk and $_k$ indexes the channel. The total number of fish, $N\_(_{i,j,k})^{total}$, and total number of Chinook or steelhead $N\_(_{i,j,k})^{Chinook\ or\ steelhead}$ were available on a daily basis, so the four six-hour strata from each day were assumed to have the same species composition. We then adjusted each of the expanded counts for the proportion that were Chinook or steelhead as a random draw from a binomial distribution:

$$X_{i,j,k}^{chinook\ or\ steelhead} \sim Binomial\left(p_{i,j,k}, X_{i,j,k}^{total}\right) \qquad \text{(A2)}$$

Thus, this two-step sampling is accounting for both uncertainty in the proportion of Chinook salmon and steelhead (first step) and random sampling variation (second step).

A.3 Observer error

It is generally recommended to account for the possibility of observer error in SONAR counts (Holmes et al. 2006). We quantified observation error by comparing counts for 10 to 15 six-hour strata between the primary technician and a more experienced “expert” counter. Similar to the expansion procedure, six-hour total passage counts by the expert counter were considered to be a measure of “actual” passage and were compared to the technicians “predicted” counts. A regression line was fit to the expert versus technician data, with a forced intercept of 0 and then a vector of observer error residuals was generated. Each cell of the expanded Chinook matrix was then adjusted by multiplying it by the coefficient from the regression trendline and adding a random residual.

A.4 Filling missing data gaps

We used a generalized additive modeling (GAM) approach to fill in missing counts or values, because this approach also allowed us to include uncertainty estimates (gamin the ‘mgcv’ package in R). We fit a smoothing spline over time (days), which allowed both a flexible shape of return timing, and uncertainty to increase as the spline became further away from data. For example, if a five-day data gap exists, the uncertainty is highest on the mid-point (day three) of the gap, and the uncertainty associated with passage during the gap would increase as the length of the gap increases. For each iteration of the simulation, we first fit the GAM to fill in the data gaps, then for each six-hour chunk generated random values (using the mean and corresponding standard error from the GAM). Because our approach does not include autocorrelation in missing values, but assumes each six-hour chunk to be independent, it represents upper bounds of uncertainty estimates.

Appendix B.

B.1 A history of screw trap operations for Chinook salmon and steelhead fry/smolt outmigration estimates

During the pre-project and dam-removal periods, mainstem trapping operations were initiated in mid to late February and continued until late June. These dates were predicated by flow and tidal conditions in the early portion of the season and interactions with releases of up to 3.5 million of 0+ Chinook salmon smolts from the WDFW hatchery in the later season. Dates of trap operation were extended for mainstem trapping efforts during the post-dam-removal period. During the pre-dam-removal period, the end of trap operations was determined by catch rates and the mainstem trap catches tended to drop toward zero by mid to later June, likely because the total natural production of salmon in the Elwha was historically low. In other Puget Sound drainages, Chinook outmigration is typically bimodal, with earlier peaks dominated by small recently emerged migrants and later peaks dominated by larger parr migrants that rear in freshwater for several to many weeks (Zimmerman et al. 2015; Anderson and Topping 2018). As Chinook salmon have now colonized areas above the dams, we have documented the re-expression of that bimodal outmigration pattern and have extended the trapping period.

During the pre-dam removal period, the mainstem 2.4 m screw trap was fished continuously (24 hours/day) except when flows exceeded ~2000 cfs (~56 m3·s−1). During the dam-removal period (2011-2014), sediment and debris entrained in the river made trapping effectively difficult to impossible. Conditions were so poor in 2013 that trapping operations were discontinued as sediment and small organic debris overwhelmed the trap box. The changes in fishing conditions forced changes in both trap size and mainstem location during the dam removal period. River conditions have steadily improved since 2015 and a larger 2.4 m screw trap has been utilized in the lower river.

This original site was temporarily abandoned during the 2013–2014 seasons because of sediment aggradation associated with dam removal and operations were moved upstream to rkm 4.4. By the early winter of 2015, the lower river site had evacuated enough sediment to support trapping operations with the smaller 1.5 m screw trap. Changes in stream channel morphology during the dam removal period have not only affected the mainstem fishing site, but also the size of trap used. During the pre-dam-removal period (2006–2011), river conditions were quite stable and LEKT utilized a 2.4 m rotary screw trap at rkm 0.3. However, as dam removal progressed into 2013, the pool at rkm 0.3 rapidly filled and was reduced from greater than 3.0 m to less than 1.0 m in depth. This forced a reduction in the size of trap to a 1.5 m screw trap that could physically operate, as the river was not deep enough to support the larger trap. Since the 2016 season, enough sediment had evacuated the lower river fishing site to support the operation of the larger 2.4 m screw trap.

Establishment of tributary smolt monitoring sites on Little River occurred in 2012 and in Indian Creek in 2013. For Little River, we used the bridge crossing at rkm 0.2. For Indian Creek, we used the bridge crossing located at rkm 0.6. On Little River for the 2012–2015 period, we used a standard 1.5 m diameter screw trap that floats in a pool approximately 1.5 m deep. In 2016, we retrofitted the Little River trap with a 1.2 m screw to reduce drag during low flow periods. In 2018, LEKT commenced trapping operations in the mainstem in mid-February and ceased trapping efforts in mid-August when daily catches declined to very low levels. A significant number of fishing days were lost because of the combination of high flows, damage by debris, and hatchery releases.

B.2 Field methods

Determining the origin (hatchery vs. natural) of most Elwha salmon species is facilitated by unique marks applied at the two hatcheries, although only a small percentage of the hatchery Chinook salmon are adipose clipped or marked with a detectable CWT. The WDFW hatchery has two age classes of hatchery Chinook releases on the Elwha: one in early April of 1+ Chinook, and another in June of 0+ Chinook. We typically ceased fishing for a period of several days immediately following any hatchery release. However, residual hatchery fish can remain in the system for several weeks and are inevitably captured in the trap. The hatchery 1+ Chinook salmon are generally larger than natural 1+ Chinook salmon and their origin is determined by size and timing. The smaller 0+ Chinook salmon are difficult to determine origin as they are of very similar size and appearance to naturally produced Chinook salmon. This has led to some uncertainty in determining the origin of Chinook salmon in past years. Elwha hatchery Chinook salmon are thermally marked in the hatchery and that results in a unique growth pattern which can be determined following dissection and laboratory analysis. In 2017, we collected otoliths from Chinook salmon (N = 50) over a several week period following resumption of fishing two weeks after the release of hatchery 0+ Chinook salmon. Those fish were sent to the WFDW laboratory to determine origin. That of marked hatchery-origin fish proportion was applied to the total 0+ Chinook salmon catch during the period following 0+ Chinook salmon hatchery releases and subtracted from the total estimate to yield the abundance of naturally produced juvenile Chinook salmon.

B.3 Data analysis

Total passage past the trap (T_i) was assumed to follow a negative binomial distribution.

$$T_i \sim negbinom(mean_i days_i, disp_i) \qquad \text{(B1)}$$

$$log(disp) \sim normal(0,100) \qquad \text{(B2)}$$

Where the mean daily passage is a temporal random walk with the variance of the jump size proportional to the number of days the trap was fished before it was checked (days). This allows the mean to change from day to day but only incrementally.

$$log(mean_i) \sim normal\left(log(mean_{i-1}), rwSD_i days_i^{-1/2}\right) \qquad \text{(B3)}$$

$$rwSD_i \sim normal(0,100) \qquad \text{(B4)}$$

The observed catch (*C*$_i$) was modeled as a binomial distribution where a period-specific proportion (p_i) of total passage past the reader (*T*$_i$) was captured.

$$rwSD_i \sim normal(0,100) \qquad \text{(B5)}$$

The proportion captured by the trap (i.e., the efficiency, p_i), was estimated from efficiency trials where large groups of marked fish (M_j) were released above the trap and the number of marked fish recaptured at the trap (R_j) was recorded.

$$R_j \sim binomial(p_j, M_j) \qquad \text{(B6)}$$

$$p_j \sim beta(1,1) \qquad \text{(B7)}$$

The models were implemented in the JAGS software (Plummer 2003) and the R language (R Core Team 2015) was used for all synthesis. Chains were run until the models appeared to converge. Visual inspection of the trace plots and the *Rhat* statistic were used to assess convergence and determine the appropriate number of simulations. Model fit was also examined using plots of the data with estimated quantities overlaid.