

Nearshore fish community responses to large scale dam removal: implications for watershed restoration and fish management

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Abstract The nearshore is a critical zone for northeast Pacific Ocean fish communities, including ecologically and culturally important salmon species. The largest dam removal in the world was recently completed on the Elwha River, with the goal of restoring fisheries and ecosystems to the watershed. The nearshore Elwha fish community was monitored monthly from January 2008 to November 2015 before, during and after dam removal. As of September 2015, approximately 2.6 million m³ of sediment material had increased the area of the Elwha delta to over 150 ha. Newly formed nearshore habitats were quickly colonized by fish communities during the dam removal period but the communities were similar in total species richness and Shannon diversity before and after dam removal, and were similar to a nearby reference site (Salt Creek estuary). Select fish species, including ESA-listed Pacific salmon and

trout *Oncorhynchus* spp., and eulachon *Thaleichthys pacificus*, and non-native, American shad (*Alosa sapidissima*), appeared quickly in these new habitats. Hatchery releases of Chinook, *O. tshawytscha*, coho, *O. kisutch*, and steelhead, *O. mykiss* (over 3 million total fish annually to the lower river), dominated the Elwha estuary catch from April through August of each year before, during, and after dam removal. Chum salmon catch rate, size, and duration of estuary occupancy declined during and after dam removal. Overall catches of chum salmon fry prior to, during, and after dam removal were significantly negatively correlated with Chinook salmon catches but significantly, and positively, correlated with coho salmon. When assessed at the Elwha estuary separately, chum abundance was significantly positively correlated with Chinook, coho, and steelhead abundance. These patterns indicate overlap, and likely interaction between these respective groups of hatchery and wild fish. Continued hatchery releases may therefore further challenge chum salmon recovery and should be considered when planning for watershed recovery.

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Introduction

The nearshore of the North Pacific Ocean is critical habitat for numerous species of Pacific salmon (*Oncorhynchus* spp.) and forage fish as they grow, rest, and migrate between spawning and rearing areas (Healey 1982; Simenstad 1982; Thorpe 1994; Quinn 2005). Many populations of these species, including Chinook (*O. tshawytscha*), coho (*O. kisutch*), and chum salmon (*O. keta*), steelhead (*O. mykiss*), and forage fish including surf smelt, *Hypomesus*

pretiosus, eulachon, *Thaleichthys pacificus*, and sand lance, *Ammodytes hexapterus*, are in steep decline across parts of the northeast Pacific (NOAA 2010, 2015, 2016). To reverse these population trends, the United States has spent billions of dollars restoring fish habitat along the Pacific coast over the last decade, including approximately US \$30 million a year through the Washington State Salmon Recovery Office (Washington State 2013). Hatcheries are also a complex element of salmon management that can complicate watershed recovery efforts, though little work has been done assessing hatchery impacts to nearshore ecosystems (see Naish et al. 2008 for an overview).

Located on the north Olympic Peninsula, in Washington State, the Elwha River dam removal project is the largest dam removal project completed to date in the United States with the specific, federally mandated intent of restoring native fisheries and ecosystems of the Elwha River watershed (DoI 2005) (Fig. 1). The estimated project cost is US \$325 million (Olympic National Park 2015). The Elwha River system has populations of

all salmonid species native to the region but they were greatly diminished by the dam installations (Pess et al. 2008; Ward et al. 2008).

Chum and pink salmon are important components of northeast Pacific watershed ecosystems as drivers of nutrient cycling. While both species are the most abundant salmon in many watersheds, chum salmon are much larger, do not have an alternating year life cycle (Quinn 2005), and so are especially important from the standpoint of nutrient cycling. The biomass of returning chum salmon predicted the extent of marine nutrient subsidy to species of mosses, herbs, shrubs, trees and insects in riparian areas of coastal British Columbia (Hocking and Reimchen 2009). Further work has also shown that marine nutrients derived from chum and pink salmon transform riparian plant community structure and diversity (Hocking and Reynolds 2011; Hurteau et al. 2016). Adult chum and pink salmon can also provide an important cross-boundary nutrient source to coastal streams, including the production of juvenile coho salmon (Nelson and Reynolds 2014).

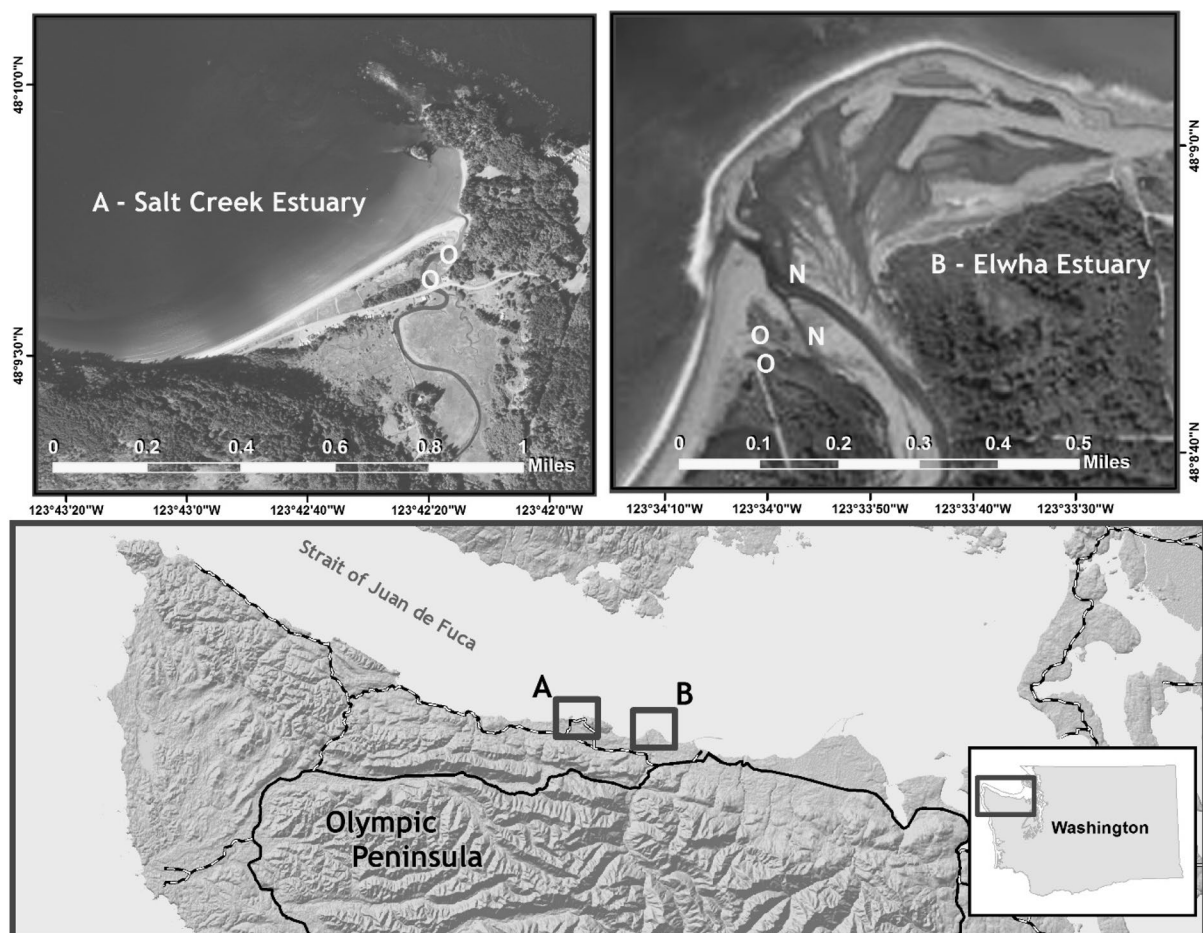


Fig. 1 Elwha River and Salt Creek study sample sites. Map by Terry Johnson, WDFW. *O* original sites sampled 2008-present; *N* New sites created from delivery of dam removal sediment and sampled from 2013-present

Prior to dam installations early in the twentieth century, chum salmon were the second most abundant salmon species in the Elwha River (Ward et al. 2008) but before dam removal began in 2011 they had declined to ca. 1% of historic levels (ca. 200 vs. 18,000 in the past; Ward et al. 2008). Juvenile chum salmon migrate downstream in their first year of life after at most a short period of residence in the stream, and occupy estuarine waters for several weeks or more (Healey 1982; Simenstad et al. 1982; Salo 1991). In contrast, pink salmon tend to make little use of estuaries and move quickly offshore (Quinn 2005). Due to their important role in supporting ecosystem function, the high potential for their population recovery in the relatively pristine watershed, and strong dependence on the Elwha nearshore, chum salmon are important for the Elwha recovery project.

There are two hatcheries on the lower Elwha River within 3 km of the estuary that, combined, annually released over three million juvenile Chinook and coho salmon and steelhead during the period when juvenile chum salmon are present (Shaffer et al. 2009; Quinn et al. 2013, 2014). Peters (1996) did not observe any predation by hatchery-produced salmonids on chum salmon in the Elwha River system but recommended that releases be delayed to avoid overlap with chum salmon. Therefore, such possible interactions merit further investigation.

After over two decades of planning, Elwha River dam removals began in September 2011, and were completed by September 2014. The nearshore fish community's response to this sediment delivery to the nearshore lower river and estuary has not been quantified. Our study documents the changes in nearshore habitat due to Elwha Dam removal and the subsequent response of the nearshore fish community, with a focus on juvenile chum salmon. Comparing periods before, during, and one year after dam removal, we investigated whether changes in fish use of the Elwha nearshore, as defined by basic ecological metrics of fish abundance, species composition, diversity, and richness, occurred. We also assessed whether juvenile chum salmon utilization of the estuary changed, and considered what interactions, if any, may have occurred between chum and other salmon species observed in the Elwha estuary. Finally, we assessed the relationship between hatchery practices in the Elwha system and the fish community of the Elwha nearshore. In total this study provides first insights into how nearshore fish communities respond during and in the early years after a large-scale dam removal that involves large sediment delivery to the estuary. This will provide important information for future large-scale dam removals and can guide Elwha nearshore restoration and fisheries management.

Methods

To provide a context for the extent of ecological change in the Elwha River estuary, we mapped the area of the shoreline, delta, and lower river before, during, and after dam removal. A time-series of lower river channel and shoreline positions were digitized from geo-referenced digital ortho-photograph mosaics (WDNR 2011; Randle et al. 2015) for the pre-dam removal (1936–2011), dam removal (2011–2014), and post dam removal periods (2014–2015) using ARC-GIS 10 (ESRI 2010). Control baselines were established in the lower river at the approximate upper limit of tidal influence and on the east and west limits of the active delta. The areal extent (ha) of the delta was then systematically measured over time by digitizing a series of line and polygon shape files in ARC-GIS in relation to the established baselines. Root Mean Square Error (RMSE) for mapped line and polygon positions was on the order of 1–2 m.

We quantified the nearshore Elwha fish community using standardized beach seining techniques (PSWQA 1996) every month from January 2008 to November 2015 using a modified 'Before, After, Control, Impact (BACI)' design (Smith et al. 1993). Pre, during, and post dam removal sampling were the "before vs during vs. after" comparison. Sampling in the nearshore of the Elwha River and a nearby, unaffected stream (Salt Creek) were the 'control vs impact' component. It should be noted that there are a number of differences between the two rivers of this study. The basin area of the Elwha River is 824 km² whereas Salt Creek is smaller (121 km²) and the Elwha River system is also steeper and glacially-fed whereas Salt Creek is a lower gradient, rain-dominated watershed (Smith 1999; McHenry et al. 2004). Furthermore, Salt Creek has no hatchery in the watershed. Notwithstanding these differences, the Salt Creek nearshore is proximate and thus subject to similar climate influences, is similarly accessible to marine and euryhaline fish species, and has many of the same freshwater fish species. Salt Creek therefore provides a useful comparison to assess variation (rather than a true 'control') with respect to the nearshore community.

Two locations were sampled each at the Elwha River and at Salt Creek estuaries each month (Fig. 1) on a single day each month during neap tide and daylight hours. Due to unavoidable constraints, the Salt Creek estuary was not sampled during March, April, July–Sept of 2008, and neither site was sampled from July 2009 through January 2010. Two additional sample locations were added along the newly formed Elwha estuary after the large amount of sediment delivered along the Elwha River mouth caused it to grow dramatically, beginning in March 2013. The original sample locations were labeled Elwha 'original estuary

sites,' and the new sample locations, Elwha 'new estuary sites' (Fig. 1).

All fish captured were identified and up to 25 of each were measured to the nearest mm (total length for all non-salmonids, and both total and fork length for salmonids), and then all were released alive on site. All collections were conducted according to guidelines set out by the Canadian Council for Animal Care and protocols approved by the University of Victoria Animal Care Committee, and with permits from the Washington Department of Fish and Wildlife, and NOAA-Fisheries.

For analysis, data were divided into two rivers (Elwha River and Salt Creek), three sample locations (Elwha original, Elwha new, and Salt Creek, each with two seining sites), and three dam removal phases: pre-dam removal (Jan 2008–31 July 2011), dam removal (Aug 2011–30 Aug 2014), and post dam removal (Sept 2014–1 Nov 2015). Four response variables were tested in this analysis: (1) community species richness (number of species collected), (2) community diversity (Shannon-Weiner index), (3) chum salmon abundance and, (4) chum salmon body size.

Elements of the pre-dam removal fish use data have been published as baseline data by the co-authors, and are provided in their entirety for use in this study to define fish use response to dam removal (Shaffer et al. 2009, 2012; Quinn et al. 2013, 2014). Data were nested by sample location and month, and therefore length, abundance, and richness data were analyzed using generalized linear mixed effect models with a Poisson distribution using the package lme4 in R (R core team 2013, Bates et al. 2015). Abundance data were highly skewed and thus were log transformed to improve model performance. A Gaussian distribution was used for species diversity data. The dependent variables (species richness, diversity, juvenile chum salmon abundance, and body size) were related to the predictive variables (month, location, other salmon species and size, and dam removal phase during the December to June period when chum salmon migrate) through this analysis. Candidate models with different fixed effects were competed through model dredging and averaging of top models with $\Delta AIC < 4$ was performed using the package MuMIn in R (Wagenmakers and Farrell 2004; Bolker et al. 2009; Barton 2012). The random effects were month and sample location for community analysis, and sample location for chum salmon analysis. To better define dam removal effect on chum salmon, additional models were run for chum abundance and length for (December–March) and late (April–June) periods for the Elwha River data. The random effect for this set of models was 'month'. Table 1 provides a summary of questions addressed by the models, and results of full models are provided in Appendix Table 8.

We obtained hatchery data from the resource management information system of the Regional Mark Processing

Table 1 Mixed effects models used for data analysis

Hypothesis	Model Parameters	Response Variable	Random effect
Fish community species richness is related to dam removal, site, site*dam removal interactions	Dam removal phase, site, interaction of site*dam removal phase	Species richness	Sample location, Month
Fish community species diversity is related to dam removal, site, site* dam removal interactions	Dam removal phase, site, interaction of site*dam removal phase	Species diversity	Sample location, Month
Juvenile chum salmon abundance is related to dam removal, site, site* dam removal interactions, and other species	Dam removal phase, site, interaction of site*dam removal phase, Chinook, coho, and steelhead abundance	Chum abundance (both sites)	Sample location
Juvenile chum abundance is related to dam removal, early/late outmigration season, other species, and dam removal* season interactions	Dam removal phase, other salmon species, and chum outmigration season defined as early (December through March) and late (April thru June), interaction of dam removal phase*season	Chum abundance Elwha only	Month
Juvenile chum salmon length is related to dam removal, site, interaction of dam removal*site	Dam removal phase, site, interaction of site*dam removal phase	Chum length (both sites)	Sample location
Juvenile chum salmon length at the Elwha is related to dam removal, site, and interaction of dam removal* outmigration (early/late) season	Dam removal phase, other salmon species, and chum outmigration season defined as early (December through March) and late (April through June), interaction of dam removal phase*season	Chum length Elwha only	Month

Center (RMPC) a subsidiary of the Pacific States Marine Fisheries Commission: <http://www.rmpec.org/> and detected a positive correlation between hatchery releases of Chinook salmon, coho salmon, and steelhead trout with our catches of these species for the months of release over the seven years of the study ($R^2=0.63$, $p<0.05$). We used catches of these three species in our seining data and modeled the relationship between chum abundance and to Chinook, steelhead, and coho salmon catches as an indicator of hatchery influence. The numbers of fish released were not used because the timing of releases varies so much with respect to our sampling that they seemed less representative than our catches.

One of the hatcheries also released, in five of the seven years of our study, chum salmon fry. The chum salmon releases were small and opportunistic, based largely on the interception of spawning adults for brood stock (Patrick Crain, Olympic National Park, pers. comm., Appendix Table 8). These releases did not correlate with our monthly catches ($R^2=0.29$; $p>0.50$; $n=5$) and were always $<1\%$ of the total number of hatchery fish released. They were also likely a very small fraction of the total number of chum salmon, though there was no enumeration of the wild population. Consequently, we did not consider the chum hatchery releases in any more quantitative detail.

Results

Habitat mapping

Over the 80 years prior to dam removal the lower Elwha River and estuary were dynamic, reflecting ongoing disruption of hydrodynamic processes through lower river diking and sediment starvation from in river dams (Fig. 2, Appendix Table 6). Overall the lower river and estuary ranged from 115 to 122 ha (mean=119.3) before dam removal began. The area remained similar in 2011 (115.4 ha) and 2013 (116.8 ha) but increased to 142.8 ha in 2014 and 157.7 ha in 2015. The wetted area of the delta also increased to approximately 3 times the pre-dam removal size, from <4 ha in 1956 to >15 ha in 2015. The length of the main river channel varied greatly, initially doubling, and then returning to pre-dam removal lengths over the course of four years of dam and post dam removal (Appendix Table 6).

The largest change in aerial extent of the estuary occurred during 2013–2014, after the second year of the dam removal phase. By the end of the first year of post dam removal, scale and rate of changes in the Elwha delta and shoreline appeared to be decreasing (Table 3, Appendix Table 6). The sediment and associated wetted area appear to be shifting east with prevailing marine wave energy

rather than merely growing. The western shore of the delta expanded during the first months of dam removal but then contracted (Appendix Table 6).

Fish use of the Elwha nearshore

Species richness ranged from 1 to 13 over the seasons and years at the Elwha River and Salt Creek locations. The Elwha River was dominated seasonally by Chinook salmon, coho salmon, sculpins (primarily *Leptocottus armatus*, and *Oligocottus snyderi*), and surf smelt, whereas Salt Creek was dominated seasonally by three spine stickleback (*Gasterosteus aculeatus*), shiner perch (*Cymatogaster aggregata*), sculpins, and coho and chum salmon (Tables 2, 3). Both species richness and species diversity varied with dam removal phase and location. Species richness was only significantly different during the dam removal phase, when it was higher at the Elwha River than Salt Creek, but not after dam removal. Species diversity was significantly different after dam removal [Table 4, $p<0.001$; $t>2.0$; Figs. 3 and 4, Appendix Table 9], and significantly higher at the Elwha River than Salt Creek [Table 4, $p<0.001$; $t>2.0$; Figs. 3 and 4, Appendix Table 9]. Diversity was also affected by the interaction of the two factors (Table 4, $p<0.001$; $t>2.0$; Figs. 3, 4, Appendix Table 9). Species diversity and richness indices were not significantly different between original and new estuary locations within the Elwha estuary during the dam removal and post dam removal phases (Figs. 3, 4, Appendix Table 9).

In general, the species percent composition stayed constant at both rivers over the entire dam removal project. However, there were a few changes in species of fish observed in the Elwha River estuary that were not observed at the comparative site, nor detected by the community analysis. Three species, bull trout (*Salvelinus confluentus*), eulachon, and redbside shiner (*Richardsonius balteatus*) were observed consistently in the Elwha west estuary, but not at Salt Creek, within weeks of initiating dam removal, through dam removal, and post dam removal (Tables). Eulachon were observed during winter months, primarily in the new habitat and most were gravid, or spent. Bull trout were observed in all months except early fall, and in new and original sampling locations of the Elwha. In addition, a non-native species, American shad (*Alosa sapidissima*) was observed for the first time in the Elwha nearshore during the second year of dam removal (2013) through the first year of post dam removal. Prior to dam removal this species was only observed at Salt Creek. Finally, adult chum salmon were observed in the original Elwha River estuary for the first time in November 2015, and were spawning there in 2016 (JAS, personal observations).

Juvenile salmon were the dominant component of the lower Elwha River and estuary community (but not Salt

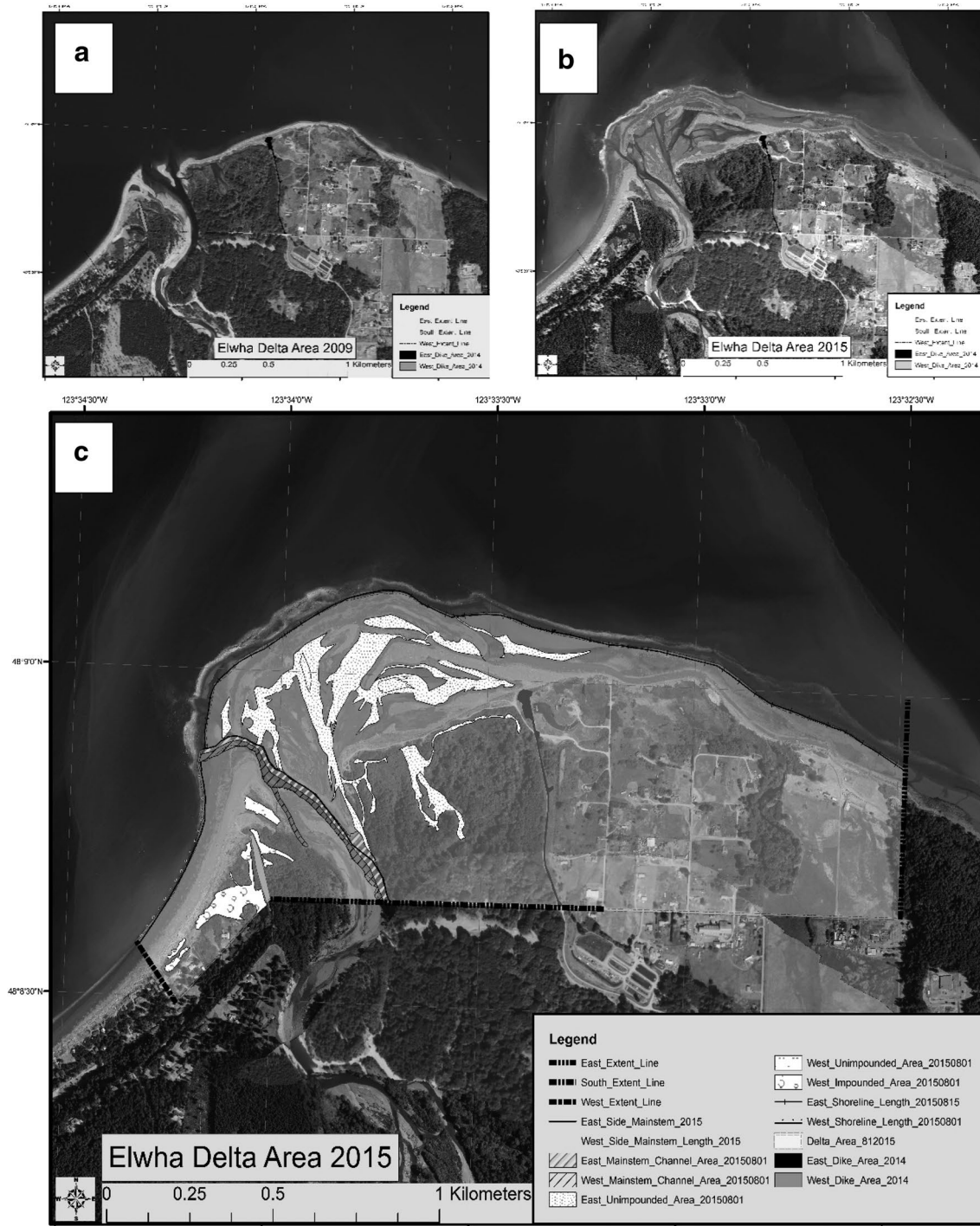


Fig. 2 Sediment distribution and example of mapping of aerial extent of the Elwha River delta, shoreline and lower river, and wetted area coverages 1956–2015. **A** 2009, **B** 2015. **C** Summary extent of classes mapped in [Appendix](#)

Creek) from January through August in all years. Salmon species percent composition of the Elwha catches reflected both hatchery release species and proportions throughout this study. Chinook and coho salmon abundance in the Elwha estuary decreased during dam removals and increased after dam removals concluded (Tables 2, 3)

but the results were influenced by hatchery releases during all three phases of the project. For all years, Chinook was the dominant salmon species in the Elwha nearshore and annually ranged from 20 to 90% of the salmon present, followed by coho salmon (4–60% of all salmon in the Elwha nearshore annually). Chinook, coho, and steelhead

Table 2 Total abundance and percent juvenile fish species composition Elwha River estuary 2008–2015

Elwha											
Year	Original estuary							New estuary			
	2008	2009	2010	2011	2012	2013	2014	2015	2013	2014	2015
Total Fish	5300	2192	19527	4647	3157	2668	11957	4384	1712	3008	1385
Chinook salmon <i>Oncorhynchus tshawytscha</i>	36%	30%	71%	8%	5%	3%	2%	13%	6%	26%	24%
Coho salmon <i>O. kisutch</i>	6%	14%	6%	10%	16%	6%	2%	7%	4%	7%	1%
Chum salmon <i>O. keta</i>	2%	7%	1%	1%	4%	1%	1%	1%	3%	2%	2%
Cutthroat trout <i>O. clarkii</i>	1%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
Steelhead trout <i>O. mykiss</i>	0%	0%	0%	0%	1%	0%	0%	1%	0%	0%	0%
Unid trout <i>Oncorhynchus spp</i>	1%	0%	0%	0%	1%	0%	0%	0%	0%	0%	0%
Bull trout <i>Salvelinus confluentus</i>	0%	0%	0%	0%	0%	0%	0%	1%	0%	0%	0%
Surf smelt (juv&adult)											
<i>Hypomesus pretiosus</i>	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
3-Spine stickleback											
<i>Gasterosteus aculeatus</i>	39%	39%	5%	23%	47%	74%	91%	70%	65%	3%	3%
Starry flounder <i>Platichthys stellatus</i>	3%	1%	0%	1%	1%	0%	0%	0%	6%	4%	19%
Staghorn sculpin <i>Leptocottus armatus</i>	9%	8%	2%	5%	6%	2%	0%	0%	6%	43%	27%
Prickly sculpin <i>Cottus asper</i>	1%	0%	0%	3%	11%	9%	1%	2%	9%	3%	20%
Redside shiner <i>Richardsonius balteatus</i>	0%	0%	0%	0%	3%	1%	2%	2%	0%	0%	0%
Eulachon <i>Thaleichthys pacificus</i>	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	10%

Red line indicates dam removal. Black line indicates the end of dam removal. Italic are new species to appear after dam removal

Table 3 Percent dominant fish species sampled in the Salt Creek estuary 2008–2015. 2008 was not sampled March–June, July–Sept

	2008	2009	2010	2011	2012	2013	2014	2015
Total fish	2256	2018	4678	7523	12,655	11,173	8019	2879
Chinook salmon <i>O. tshawytscha</i>	0%	0%	0%	0%	0%	0%	0%	0%
Coho salmon <i>O. kisutch</i>	0%	35%	7%	5%	20%	5%	2%	1%
Chum salmon <i>O. keta</i>	4%	2%	1%	0%	1%	0%	1%	3%
Cutthroat trout <i>O. clarkii</i>	0%	1%	0%	0%	0%	0%	0%	0%
Starry flounder <i>P. stellatus</i>	2%	1%	2%	0%	0%	0%	1%	0%
3-Spine stickleback <i>G. aculeatus</i>	0%	10%	4%	0%	0%	3%	3%	27%
Shiner perch <i>C. aggregata</i>	66%	29%	63%	72%	65%	72%	73%	42%
Staghorn sculpin <i>L. armatus</i>	25%	21%	16%	12%	8%	15%	17%	24%
Surf smelt <i>H. pretiosus</i>	0%	0%	0%	8%	0%	0%	0%	0%

proportions mirrored those of annual hatchery releases in the system (Appendix Table 6). In contrast, coho and chum were the only salmon observed consistently at Salt Creek over the course of the study.

Percent abundance of both juvenile Chinook and chum salmon dropped in the Elwha original sites during dam removal. Chinook salmon catches, however, increased at the Elwha new sites after dam removal. In contrast, Elwha coho salmon percent composition changed little during dam removal, at 16% or less of all salmon in new site catches. The relative contribution of juvenile chum salmon to overall percent composition of fish species stayed fairly constant, and low relative to the mean percent composition of other salmon species over the study period at both new and original sites of the Elwha River and Salt Creek estuary sites (Tables 2, 3).

All juvenile chum salmon in this study were caught from December through June. During this period, month was the strongest predictor for chum abundance, with maximum catches in March. In addition, other species of salmon, site, dam removal, and the interactions of site and dam removal project phase had significant effects in February–June ($p < 0.001$, Fig. 5A, B; Table 4). Prior to, during, and after dam removal, chum salmon appeared in the Elwha nearshore by March, two months earlier than at Salt Creek. During dam removal, chum salmon were first observed at the Elwha during the same months as pre-dam removal, but fish were present in the Elwha estuary for a shorter time period. During and after dam removal, juvenile chum were not observed in either the Elwha original or new locations after March (Fig. 5A).

Table 4 Top mixed-effects models that predict Elwha nearshore (1) fish community species richness, (2) community diversity, (3) chum salmon abundance, and chum salmon body size

Model	Δ (AIC)	Wi	Best model better than this model by factor of
Species richness			
DR, (1 SL), (1 Month)	0.00	0.64	1.00
DRS, Site, (1 SL), (1 Month)	2.00	0.24	2.71
DRS, Site, Site:DRS, (1 SL), (1 Month)	3.20	0.13	4.95
Species diversity			
DRS, site, Site:DRS, (1 SL), (1 Month)	0.00	0.46	1.00
DRS, (1 SL), (1 Month)	0.50	0.36	1.28
Site, DRS, (1 SL), (1 Month)	1.60	0.21	2.22
Site, (1 SL), (1 Month)	2.48	0.13	3.45
DRS, Site, Site:DRS, (1 SL)	4.50	0.05	9.47
Chum abundance both sites, individual interactive species			
Chinook, Coho, Steelhead, Month, DRS, Site, Site:DRS, (1 SL)	0.00	0.37	1.00
Chum abundance Elwha only			
Chinook, Coho, DRS, Season, Steelhead, DRS:Season, 1 Month	0.00	0.85	0.99
Coho, DRS, Season, Steelhead, DRS:Season, 1 Month	3.90	0.12	6.99
Chum fork length (both sites)			
Month, DRS, Site, Site:DRS, (1 SL)	0.00	0.83	1.01
Month, DRS, Site, Site:DRS, Site:Month, (1 SL)	3.17	0.17	4.94
Chum fork length Elwha only			
Season, DRS, (1 Month)	0.00	0.58	1.00
Season, SL, DRS, (1 Month)	0.78	0.39	1.48

Models are ranked using AIC. Top contributing models (Δ AIC < 4) for each analysis (*by italic*) are listed. Δ AIC change in AIC score from top model, *Wi* AIC model weight. The models are ordered by decreasing weight. *Site* Elwha/Salt Creek, *DRS* Dam Removal Stage, *SL* Sample location (Original/New). *Season* chum outmigration period (early = Dec through March, late = April through June). Random effects are noted as 1|effect and are, for community indices through = month, and sample location. Random effect for chum abundance = sample location. Random effect for chum length and abundance, Elwha only, = month. Interactive terms are cojoined with ':'. Coefficients, Standard Errors, and p-values are listed in Appendix Table 9

Juvenile chum salmon abundance was significantly related to dam removal phase, and the interaction of dam removal and site, as well as other species of salmon. Overall, juvenile chum catches in both estuaries were significantly, negatively correlated to Chinook catches, and significantly positively correlated with coho before, during, and after dam removal ($p < 0.001$; Table 4, Appendix Table 9). Assessing Elwha estuary alone, chum abundance was significantly, and positively correlated to Chinook, coho, and steelhead, and was also significantly lower at the Elwha after dam removal ($p < 0.001$, Fig. 6; Table 5 Appendix Table 9). In addition, catches from April through June ('late season') were significantly lower during and after dam removal than before dam removal ($p < 0.001$ and $p < 0.005$, respectively).

Juvenile chum salmon size was related to several factors. Prior to dam removals the Elwha River chum salmon were larger (and arrived earlier) in the nearshore than did those at Salt Creek ($p < 0.007$, Fig. 5B, Table 4). During

dam removals, Elwha chum salmon were smaller than those at Salt Creek ($p = 0.014$) but after dam removal, the Elwha River chum salmon were once again larger than those at Salt Creek ($p < 0.001$).

The two hatcheries released a total of 1.7–3.5 million Chinook, coho, and steelhead smolts annually over the course of this study. Most hatchery releases of Chinook, coho, and steelhead from 2008 to 2015 began in March and extended through June, and so overlapped with chum salmon migration (December through June; Appendix Table 7). When compared by month, average length of Chinook and coho salmon and steelhead were at least 50% larger than chum salmon for most of these releases. Assessing over the migration period, the Elwha River estuary chum salmon were significantly larger from April through June than earlier in the season (December through March). Chum salmon were therefore smaller than before dam removal, due in large part to their early exit from the estuary.

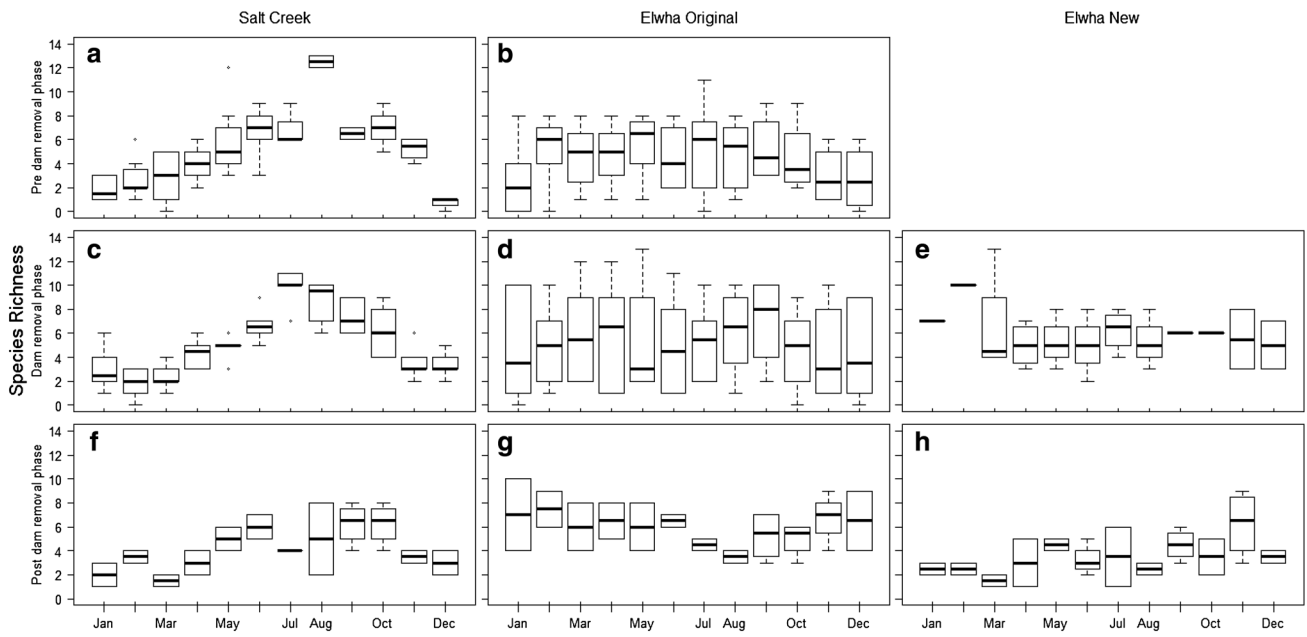


Fig. 3 Median, first and third quartiles, min and max values and outliers of species richness of the Elwha River and Salt Creek nearshore fish communities pre (2008–2011), during (2011–2014), and one year

post Elwha dam removal (2015). Elwha sampling sites include the original sites prior to dam removal and new sites created by sediment delivery during dam removal

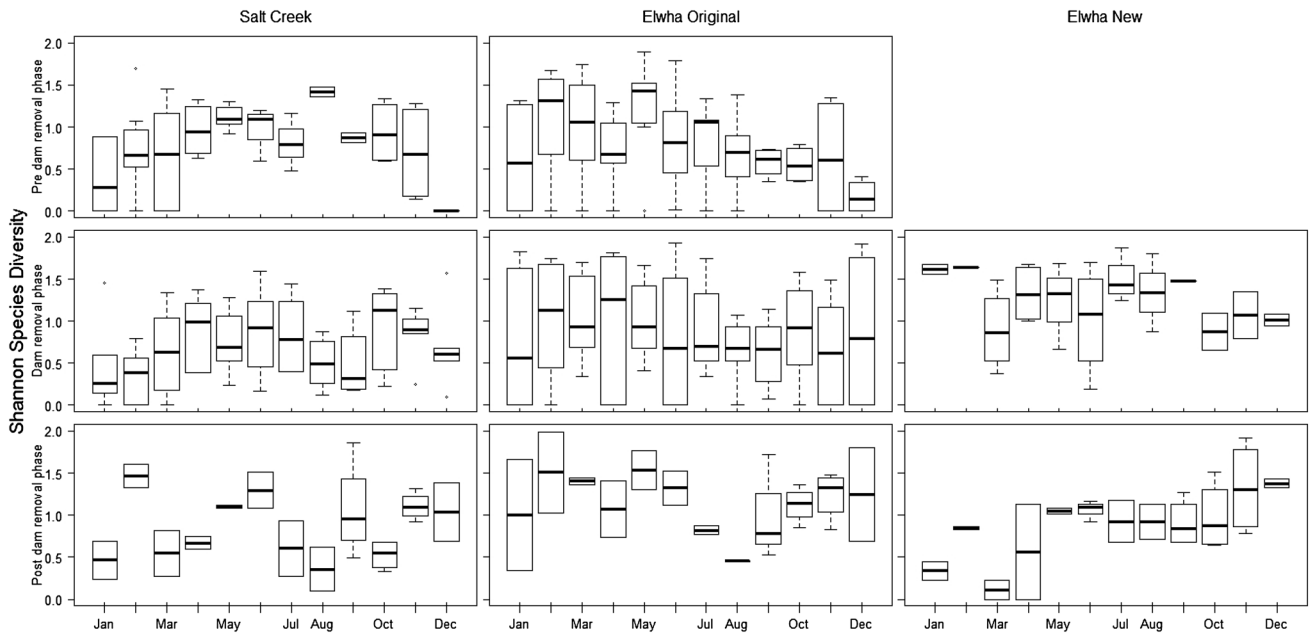


Fig. 4 Median, first and third quartiles, min and max values and outliers, Shannon index of species diversity of the Elwha River and Salt Creek nearshore fish communities pre (2008–2011), during (2011–2014), and one year post Elwha dam removal (2015). Rest of Legend as in Fig. 3

Discussion

This work provides a number of important insights into the nearshore ecological response to large scale dam removals, including changes in the habitat extent, fish

species use, interaction between species, and effects of processes (i.e. hatchery releases) distinct from the dam removal. Prior to dam removals the Elwha estuary was virtually non-existent. Though sediment deposition from dam removals increased the delta shorelines and estuary

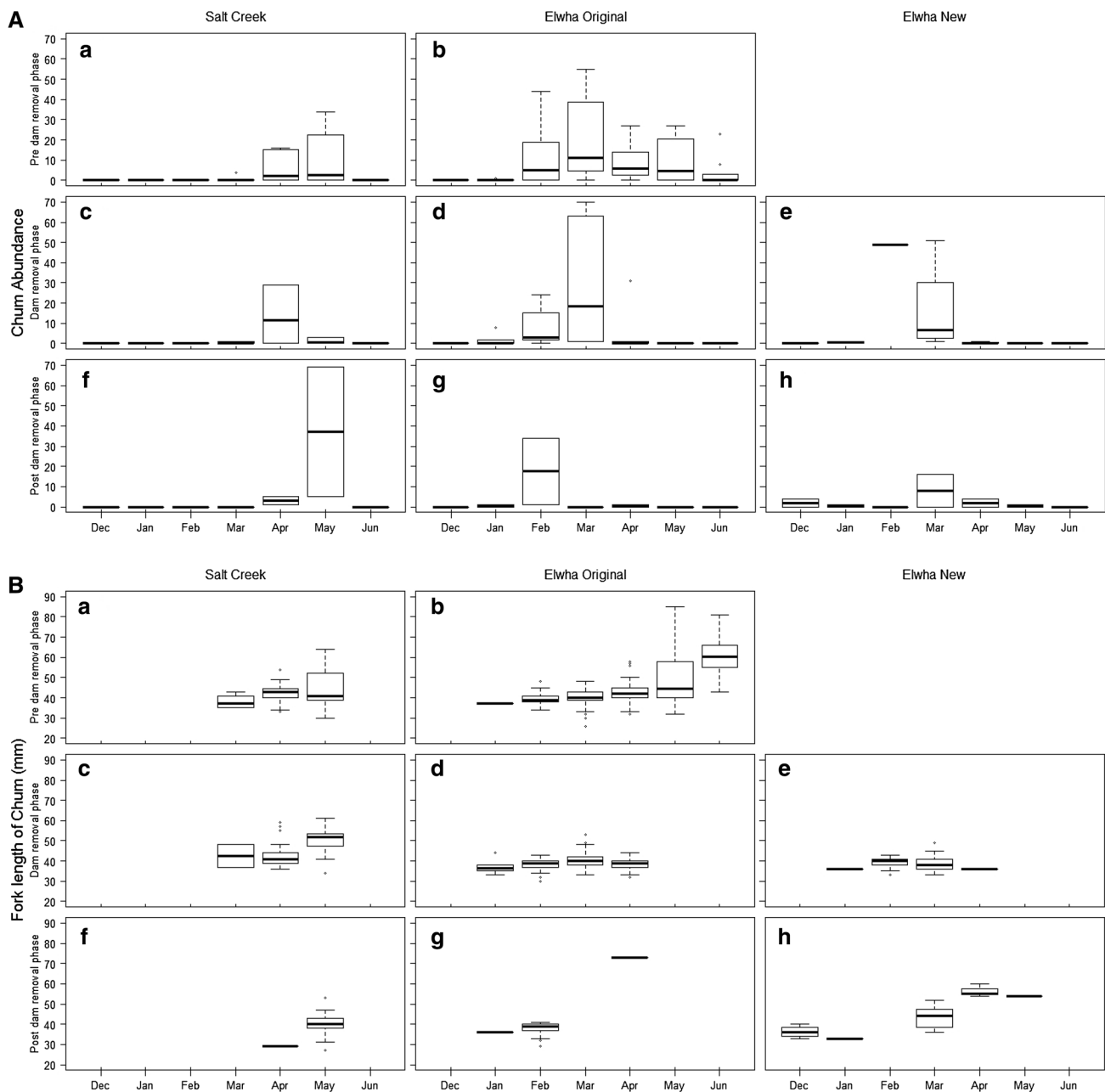


Fig. 5 **A** Median, first and third quartiles, min and max values and outliers of juvenile chum salmon catch from December to July in the Elwha River and Salt Creek nearshore during pre-dam removal (2008–2011), dam removal (2011–2014) and post dam removal (2015) phases. Rest of Legend as in Fig. 3. **B** Median, first and third quartiles, min and max values and outliers of juvenile chum salmon

length from December to July in the Elwha River and Salt Creek nearshore during pre-dam removal (2008–2011), dam removal (2011–2014) and post dam removal (2015) phases. Elwha sampling sites include the original sites prior to dam removal and new sites created by sediment delivery during dam removal

to approximately 150 ha, the estuary is still very small for the size of the river, and so all the more important for the function it provides to the nearshore of this region. A large proportion of the aerial extent of the new estuary and lower river habitat at the Elwha River mouth and shoreline was created within the first 15 months of dam removal, and was immediately used by fish along

the delta and shoreline. Fish community metrics (species richness and diversity) of the new areas were not significantly different than those of the original areas, indicating that the Elwha new and original nearshore is functioning similarly for fish across the lower river and delta before, during, and a year after dam removal.

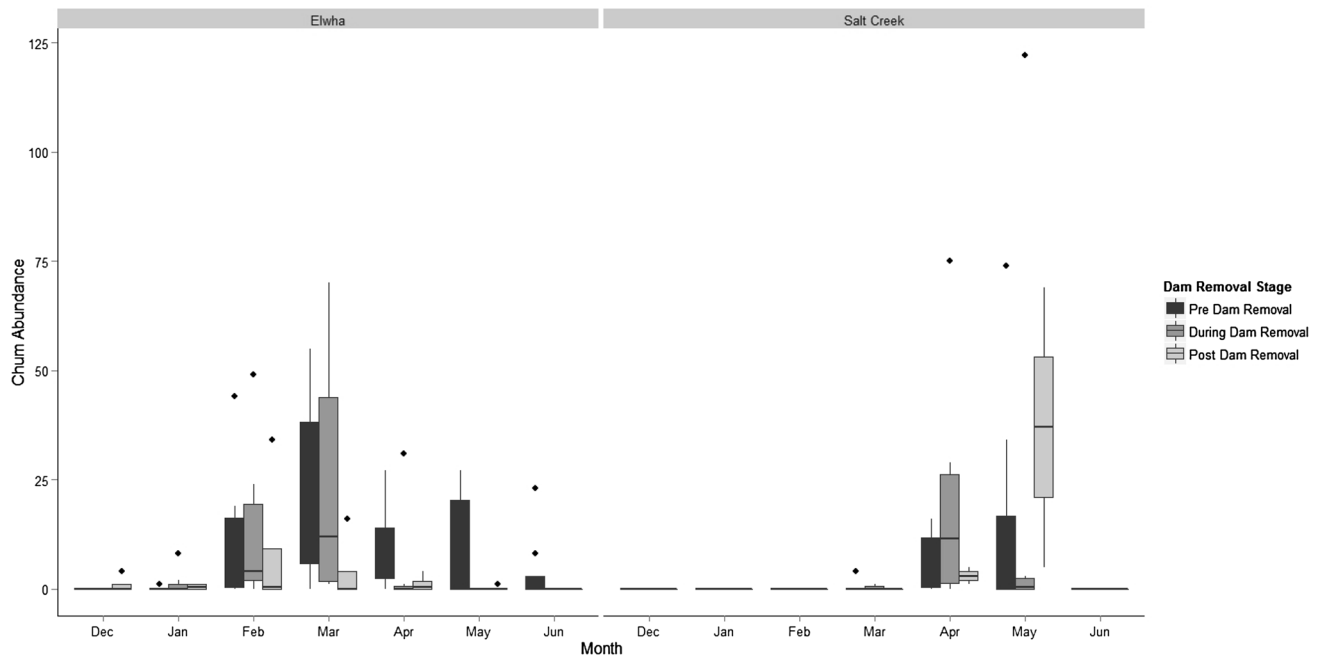


Fig. 6 Juvenile chum salmon abundance by month in the Elwha River (*left* side) and Salt Creek (*right* side) nearshore areas before, during and post Elwha dam removal

Table 5 Poisson regression model estimated average Chum abundances with upper and lower 95% CIs by site and dam removal phase

Percent change/difference from							
Dam removal phase	Site	Chum abundance (average number of fish)	95% CI		Previous dam removal phase	Pre-dam removal phase	Control site
			Lower	Upper			
Pre dam removal	Elwha	9.86	8.48	11.41			338%
Dam removal	Elwha	5.53	4.83	6.30	-44%	-44%	126%
Post dam removal	Elwha	2.11	1.62	2.70	-62%	-79%	36%
Pre dam removal	Salt Creek	2.91	2.39	3.53			
Dam removal	Salt Creek	4.39	3.61	5.31	51%	51%	
Post dam removal	Salt Creek	5.84	4.52	7.43	33%	101%	

Month was excluded from the model to get averages across all months. 95% CIs were computed using the mcprofile package in R (Gerhard 2014)

We are still early in the estuary restoration process. Ultimately the habitat stresses to the fish community of the Elwha delta due to large sediment loads from dam removal should be temporary, and river conditions for migrating salmon, including chum, should stabilize as the sediment delivery from dam removal decreases. The newly formed lower river and estuary habitat should continue to transition/stabilize into a 'normal' system, the vegetative communities should mature, and so provide additional habitat and prey resources for additional species as well as juvenile chum refuge, feeding, and transition to salt water, and

possibly spawning habitat for adults. In the long term the estuary will likely evolve to include detrital-based fauna, possibly increasing harpacticoid copepods that are important prey for juvenile salmon, including chum salmon (Sibert et al. 1977; Sibert 1979; Healey 1979).

The similar and variable fish species richness and diversity values during dam removal, and the first year of post dam removal phases at the Elwha River and Salt Creek nearshore sites are consistent with earlier studies that documented high seasonal and interannual variability in the nearshore fish community in the Elwha prior to dam

removal (Shaffer et al. 2012) and in other areas (Weitkamp et al. 2014). These results indicate that, as of one year after dam removal was completed, the juvenile fish community species diversity and richness of the Elwha estuary was resilient to the high volumes of sediment and hydrodynamic changes in the lower river and estuary. Month of the year was the dominant factor affecting which, how many, and the proportion of fish species utilizing the Elwha River and Salt Creek estuaries, consistent with other studies suggesting that seasonal variability is the dominant factor determining nearshore fish community structure in northeast Pacific systems (Miller et al. 1980; Fresh 2006; Shaffer et al. 2008, 2012). Specifically, the seaward migrations of salmonid fishes show a very strong seasonal component, linked to the basic life history of the species (Quinn 2005), and this was a dominant signal in the data.

The addition and persistence of new species, including bull trout, redband shiner, and eulachon to the lower Elwha River and estuary at the beginning of dam removal, and the first observation of adult spawning chum in the original estuary site one year after dam removal ended, were consistent with the physical changes documented by Draut and Ritchie (2015), East et al. (2015), and Foley et al. (2015). Specifically, the Elwha River mouth and tidally influenced areas have shifted north by over 100 m, and the original estuary area was, at the end of 2015, no longer tidally influenced. Thus, as the river mouth pushed north, new estuary areas were formed, and areas that were originally estuary are now freshwater and just at the head of tide. The increase in species richness and diversity during and after dam removal at Elwha reflects this increase in complexity of nearshore habitats created from sediment delivered after dam removal.

This increase in size and complexity of the lower river and additional estuary and freshwater habitats were reflected in changes in the Elwha fish community, which in turn have implications for recovery. Eulachon are a particularly important addition to this habitat. A US federally listed forage fish, eulachon spawn in natal rivers at the head of tide (Fisheries NOAA 2015), and are a priority for northeast Pacific restoration. Eulachon were documented in the Elwha River prior to dam removal (Shaffer et al. 2008) but were not observed in the estuary or lower river side channels prior to dam removal. Similarly, the presence of spawning chum salmon in the newly transformed lower river side channels (directly observed in the fall of 2016) indicates this area may be providing an important new function for restoring salmon spawning reaches in the lower river.

The fish community composition of the Elwha lower river and estuary appears to be defined by factors in addition to dam removal. When compared proportionally,

salmon abundance in the Elwha estuary mirrored salmon percent compositions released annually from the hatchery over the course of this study, irrespective of dam removals. For example, Chinook, coho, and steelhead were the dominant species released from the hatcheries and the dominant salmon in our catches, and seasonally dominated the fish community.

Our sampling also revealed interesting timing differences in juvenile salmon use of the nearshore. Prior to dam removal, Elwha River chum salmon arrived in the estuary approximately two months before they did in Salt Creek, and were the same size or slightly larger than Salt Creek chum salmon. Pacific salmon populations, including chum, often differ in the timing of adult return migration and spawning but the juveniles tend to migrate to sea at similar times in a given area (Tallman and Healey 1991). As described earlier, the Elwha River system is much larger and in many ways different than the Salt Creek basin so different adult timing would not be unexpected. However, the timing of juvenile migration would be expected to be similar, given the spatial proximity of the two systems and similar abundance of nearshore resources. The difference in timing may reflect the effects of the hatchery releases of other salmon species in on the Elwha River chum salmon population, resulting in a pressure for early timing of chum outmigration to avoid or minimize interactions with the other species. In addition, the high sediment loads during dam removal shifted water quality regime in the river (East et al. 2015; Foley et al. 2015), perhaps contributing to earlier and more rapid exit from the Elwha estuary and river system during dam removal.

It is also important to note that chum salmon size was related to dam removal phase. During dam removal, chum fry left the Elwha estuary sooner than other dam removals stages, and at a smaller size overall, but chum salmon in the Elwha estuary at any given month were not significantly smaller than in the same months during other phases of dam removal. One year after dam removal completed, the post dam removal size of juvenile chum salmon present in the Elwha appears to be increasing, suggesting that dam removal effects on chum size and abundance may be temporary.

The dominance of hatchery fish in the Elwha estuary fish community is likely attributed to the small size of the Elwha estuary relative to the river, the large numbers released from hatcheries relative to the wild populations, and the proximity of hatcheries to the estuary. Such preponderance of hatchery-origin salmonids is not unlike some other northeast Pacific estuaries, though many others are dominated by or exclusively occupied by wild populations (Weitkamp et al. 2014). Further, our results indicate that this dominance appears to be affecting fish

interactions in the Elwha estuary and lower river. Chinook, steelhead, and coho abundance in the Elwha estuary and lower river were largely defined by hatchery releases, and juvenile chum abundance was significantly and positively correlated to Chinook, steelhead, and coho abundance. The two months when juvenile chum salmon abundance was not significantly related to Chinook salmon abundance (April and May) were the months of and after the hatchery released chum fry, providing a pulse of chum to the estuary and masking, or possibly temporarily reducing changes in chum salmon abundance due to interactions. Collectively these observations indicate that hatcheries are playing an interactive role in fish use of the Elwha nearshore.

Collectively, the lower abundance and smaller size of Elwha estuary chum salmon relative to both the Salt Creek chum salmon and pre-dam removal phase Elwha estuary fish, and the earlier exit from the Elwha estuary during dam removal were likely all due in part to physical environmental stress, including likely trophic disruptions in the ecosystem.

Harpacticoid copepods are the principal food of chum salmon during the first critical weeks of estuarine life. Harpacticoids, in turn, depend on heterotrophic food sources, and primarily the bacterial flora associated with organic detritus. In general, estuaries receive pulsed inputs of detritus from several sources including vegetation from landward and downstream transport from the upland areas of the watershed. Chum residence in estuaries is thus related to a detritus-based, benthic derived food web (Sibert et al. 1977; Sibert 1979). Given the extremely small size and high energy nature of adjacent Elwha shoreline areas prior to and during dam removal, the detrital food web of the Elwha estuary was likely defined by the Elwha River. East et al. (2015), Foley et al. (2015) and others documented dramatic shifts in estuary water quality and configuration due to river sediment loads associated with dam removal. These shifts likely affected the harpacticoid/detrital systems in the estuary and lower river, and may also have temporarily decreased food resources, resulting in a shorter chum residence in the estuary (Healey 1979).

Modeling results also indicated that the timing and numbers of chum salmon in the Elwha estuary during dam removal were correlated with juvenile Chinook, steelhead, and coho abundance, all of which were driven by the large hatchery releases. Chinook salmon dominated the releases numerically, and occurred at the peak of the chum salmon migration. The interactions between juvenile chum and Chinook salmon might include competition for food (Cordell et al. 2011) and predation. Duffy et al. (2010) reported that Chinook salmon preyed

on fish up to 50% of their length. This is within the size ranges of Chinook smolts and chum fry we observed in the estuary but at the extreme ends of the distributions (i.e., large Chinook and small chum salmon). This could explain the significant negative relationship between the two species over both study sites. The coho salmon and steelhead are larger at release and so also potential predators on chum salmon (especially coho salmon: e.g. Parker 1971; Fresh and Schroder 1987) but tend to move through estuaries more rapidly than do chum and Chinook salmon. This could account for the significant positive relationship between chum and Chinook, coho, and steelhead at the Elwha estuary alone. Overall, our work indicates that the nature of ecological interactions between chum, Chinook, coho, and steelhead is complicated, and that here and in other restoration projects, the mix of species and the proportions of wild and hatchery origin populations may affect the behavior and ecology of the species involved.

The beneficial expansion of estuary and lower river habitat for juvenile chum salmon and other fishes discussed above could be offsetting the temporary detrimental effects of high sediment loads during the dam removal phases, further complicating the detection of causal connections between habitat alteration and fish population responses. However, hatchery releases will continue to affect the fish community of the Elwha estuary and lower river. More detailed study is therefore important to define ecosystem functions of the evolving estuary and interspecies interactions with hatchery management practices.

In summary, the fish communities of Elwha delta, shoreline, estuary and lower river were resilient, supporting a variety of fish species through the dam removal phase of the Elwha restoration project. Fish began using the newly formed estuary and lower river habitats as soon as the habitats became available, resulting in a somewhat higher species richness and diversity in the Elwha nearshore. This included non-native species, indicating that 'pioneering' by invasive species may be a concern. Chum salmon showed evidence of effects during the dam removal phase but this appeared to be temporary. There appears to be significant correlation between chum and other species of salmon in the nearshore, and in the Elwha estuary that may indicate interactions. Juvenile Pacific salmon dominated the fish community of the Elwha delta in the spring, and hatchery-produced fish were a large component of these populations. Consequently, behavioral and ecological interactions between wild and hatchery-origin cohorts of these species in the still-small estuary may influence the performance of species of concern such as the wild chum salmon that are important for watershed recovery.

Large scale dam removals are becoming an important tool for ecosystem recovery. This work provides conclusive evidence of nearshore fish community resilience, and rapid restoration associated with dam removal. To achieve full ecosystem recovery, it is important to integrate and prioritize the nearshore and estuary life histories of fish communities, and species interactions, in long term dam removal planning and adaptive management. It is also important to consider in detail and properly address hatchery management actions relative to nearshore ecosystem function.

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Appendix

See Tables 6, 7, 8 and 9.

Table 6 Change in areal extent of wetted habitat of the Elwha estuary and lower river due to dam removal sediment delivery prior to (pre 2011), during (2011–2014) and after dam removal (2015), and total area, hectares, of Elwha shoreline and delta habitats

Year	West River Estuary impounded Areas (ha)	West River Estuary Unimpounded Areas (ha)	East River Estuary Unimpounded Area (ha)	Total East and West Impounded, Unim- pounded Area (ha)	West\West River Wetted Area (ha)	West\East River Wetted Area (ha)	East\West Wet- ted Area (ha)	East\East Wet- ted Area (ha)	Total (ha) River		Total Area (hectares) shoreline and delta habitats
									Wetted Area	Wetted Area	
1939	0.00	2.49	4.69	7.18	0.37	0.42	1.85	1.91	4.54	120.18	
1956	0.00	1.05	2.50	3.55	0.95	1.27	1.40	1.67	5.29	121.30	
1965	2.23	0.00	6.73	8.97	0.46	0.52	0.00	0.00	0.98	121.80	
1974	1.66	0.41	2.95	5.02	1.58	2.07	0.00	0.00	3.65	119.98	
1981	1.45	0.23	2.76	4.45	1.09	1.26	1.45	0.60	4.39	115.90	
1990	1.49	0.00	4.12	5.62	1.88	1.66	0.00	0.00	3.54	116.85	
2003	1.74	0.34	3.62	5.70	3.10	2.92	0.00	0.00	6.02	122.30	
2006	1.58	0.26	2.71	4.55	3.82	1.85	0.00	0.00	5.67	120.63	
2009	1.49	0.89	2.74	5.12	3.23	1.57	0.00	0.00	4.80	114.72	
2011	1.92	0.55	2.63	5.10	2.08	2.03	0.00	0.00	4.11	115.42	
2013	1.98	0.80	3.52	6.30	3.39	2.29	0.00	0.00	5.69	116.81	
2014	2.32	3.795	18.38	24.50	4.895	4.17	0.00	0.00	2.81	142.80	
2015	1.74	0.57	11.75	14.06	1.47	1.35	0.00	0.00	2.81	157.63	

Numbers are generated by mapping of ortho-rectified aerial photographs using ArcGIS. Impounded area is west of dike along west shore of river

Table 7 Total number of hatchery-produced salmonids released into the Elwha River between January-June, 2008–2015

Species	2008	2009	2010	2011	2012	2013	2014	2015	Total
Chinook	2,145,350	1,279,946	3,248,747	1,437,386	1,737,669	1,607,746	2,841,045	2,857,337	17,155,226
Coho	323,813	444,514	218,720	506,402	444,275	291,779	77,327	294,612	2,601,442
Steelhead	35,710	98,889	302,798	229,687	161,038	119,623	104,082	231,549	1,283,376
Chum		24,763	52,686		59,851		105,770	49,122	292,192
Total	2,504,873	1,848,112	3,822,951	2,173,475	2,402,833	2,019,148	3,128,224	3,432,620	21,332,236

Data provided by Regional Mark Information System (RMIS) system: <http://www.rmipc.org>

Table 8 Comparison of percent composition of Pacific salmon in the Elwha River prior to dam construction, the percent composition of salmon released from hatcheries, and catch of juveniles in our study 2008–2015

Species	Prior to dams	After dams installed	Prior to, During and after dams removed 2008–2015	
	(from Ward et al. 2008) (%)	(Ward et al. 2008) (%)	Released from hatcheries (%)	Estuary (this study) (%)
Chinook	5	57	78	57
Coho	8	14	13	32
Chum	13	7	1	10
Pink	66	5	0	0
Sockeye	4	1	0	0
Steelhead	4	7	5	1
Bull trout	1	7	NA	0

Hatchery data from Regional Mark Information System (RMIS) system: <http://www.rmipc.org> NA bull trout are not released by the hatchery

Table 9 Fixed effects top model coefficients, standard error, and significance * = 0.05; ** = <0.01; *** = <0.001

Category	Model	(AIC)/ Coefficient	SE	p	Significance
Species richness	DR, (1 SL), (1 Month)	(1880.30)			
	DRS2	0.17	0.50	0.00	**
	DRS3	0.02	0.07	0.77	
	DRS, Site, (1 SL), (1 Month)	(1882.30)			
	DR S2	0.17	0.05	0.00	**
	DRS3	0.02	0.06	0.77	
	Site	0.00	0.19	0.97	
	DRS, site, Site:DRS, (1 SL), (1 Month)	(1883.90)			
	DRS2	0.23	0.07	0.00	**
	DRS3	0.11	0.08	0.21	
	Site	0.11	0.21	0.59	
	Site2:DRS2	-0.14	0.11	0.20	
Site2:DRS3	-0.22	0.13	0.11		
Species diversity	DRS, site, site:DRS, (1 SL), (1 Month)	(558.90)			
	DRS2	0.16	0.72	p < 0.05	*
	DRS3	0.20	0.09	P < 0.05	*
	Site2	-0.01	0.17	p > 0.05	
	Site2:DRS2	-0.25	0.10	p < 0.05	*
	Site2:DRS3	-0.11	0.13	p > 0.05	
	DRS, (1 SL), (1 Month)	(559.40)			
	DRS2	0.06	0.05	p > 0.05	
DRS3	0.15	0.07	p < 0.05	*	

Table 9 (continued)

Category	Model	(AIC)/ Coefficient	SE	p	Significance
	Site, DRS, (1 SL), (1 Month)	(560.50)			
	Site2	-0.16	0.15	p > 0.05	
	DRS2	0.05	0.05	p > 0.05	
	DRS3	0.15	0.07	p < 0.05	*
	Site, (1 SL), (1 Month)	(561.38)			
	Site	-0.18	0.16	p > 0.05	
	DRS, site, site:DRS, (1 SL)	(563.40)			
	DRS2	0.15	0.07	p < 0.05	*
	DRS3	0.19	0.09	p < 0.05	*
	Site2	-0.01	0.17	p > 0.05	
	Site2:DRS2	-0.26	0.11	p < 0.05	*
	Site2:DRS3	-0.11	0.13	p > 0.05	
Chum abundance (both sites all species)	Chinook, coho, Steelhead, Month, DRS, Site, Site:DRS, (1 SL)	(3429.9)			
	Chinook	-0.27	0.03	0.00	***
	coho	0.15	0.018	0.00	***
	Steelhead	0.11	0.06	0.07	
	Month	2.45	0.28	0.02	***
	DRS2	-0.36	0.08	0.00	*
	DRS3	1.00	0.15	0.00	***
	Site2	0.99	0.50	0.05	*
	DRS2:Site2	0.99	0.13	0.00	***
	DRS3:Site2	1.69	0.210	0.00	***
	Chinook, Coho, Steelhead, Month, DRS, 1 SL	(3514.2)			
	Chinook	-0.27	0.03	0.00	***
	Coho	0.013	0.018	0.00	***
	Steelhead	-0.056	0.0619	0.37	
	Month	2.11	0.338	0.03	*
	DRS2	0.05	0.06	0.42	
	DRS3	0.199	0.10	0.05	*
Chum abundance Elwha only all species	Chinook, Coho, Steelhead, Season, DRS, Season:DRS, (1 Month)	(1602.80)			
	Chinook	0.08	0.03	0.01	*
	Coho	0.10	0.03	0.00	***
	Steelhead	0.66	0.01	0.00	***
	DRS2	0.12	1.40	0.16	
	DRS3	-1.23	0.15	0.00	***
	Season	0.50	0.43	0.67	
	DRS2:Seasonlate	-2.20	0.30	0.00	***
	DRS3:Seassonlate	-1.99	0.47	0.00	***
	Coho, DRS, Season, Steelhead, DRS:Season	(1606.70)	0.00		
	Coho	0.14	0.02	0.00	***
	Steelhead	0.70	0.11	0.00	***
	DRS2	0.08	0.09	0.34	
	DRS3	-1.20	0.15	0.00	***
	Season	0.73	1.16	0.53	
	DRS2:Seasonlate	-2.31	0.23	0.00	***
	DRS3:Seassonlate	-2.03	0.46	0.00	***

Table 9 (continued)

Category	Model	(AIC)/ Coefficient	SE	p	Significance
Chum length (both sites)	Month, DRS, Site, Site:DRS, (1 SL)	(5158.43)	0.00		
	Month	0.3	0.00	0.00	***
	DRS2	0.30	0.03	0.00	***
	DRS3	-0.03	0.02	0.05	*
	Site2	-0.07	0.03	0.01	**
	Site2:DRS2	0.08	0.02	0.00	**
	Site2:DRS3	-0.18	0.04	0.00	***
	Month, DRS, Site, Site:DRS, Site:Month, (1 SL)	(5161.60)	3.17		
	Month	0.30	0.06	0.00	***
	DRS2	-0.03	0.02	0.07	
	DRS3	0.04	0.03	0.18	
	Site2	-0.09	0.03	0.01	**
	Site2:DRS2	0.07	0.29	0.01	*
	Site2:DRS3	-0.18	0.04	0.00	***
	Site2:Month (&NS)	0.03	0.05	0.5	
Chum length (Elwha only)	Season, DRS, (1 Month)	(3703.90)	0.00		
	SeasonLate	0.27	0.08	0.00	***
	DRS2	-0.03	0.02	0.06	
	DRS3	0.04	0.03	0.12	
	Season, SL, DRS, (1 Month)	(3704.68)	0.78		
	Season Late	0.27	0.008	0.01	***
	Sample location (SL)	0.03	0.02	0.26	
	DRS2	-0.03	0.02	0.03	*
DRS3	0.03	0.03	0.31		

Month values are averaged to consolidate table

DRS2 dam removal stage, DRS3 post dam removal stage SL sample location, Site2 salt creek. Month values are averaged to consolidate table

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