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Functional diversity responses of a nearshore fish community to restoration driven by large-scale dam removal

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ABSTRACT

Large scale dams have numerous significant impacts on river and nearshore components of watersheds. Large scale dam removal is therefore an increasingly useful restoration tool that reestablishes physical processes and habitats that form nearshore ecosystems. Removing large scale dams will likely affect the functional ecology of nearshore ecosystems, but this concept has yet to be explored. Here we use data from a decade long study to define how the functional ecology of fish responded to large scale dam removal. Dam removal resulted in shifts in the nearshore through the reconnection of riverine and marine hydrodynamic system, large-scale and rapid creation of nearshore habitats, and a shift in nearshore habitats from tidally influenced to non-tidally influenced habitats. The functional diversity of the fish community within the system restored by dam removal was volatile during and after dam removal. Dam removal released sediment that formed new lower river and estuary. These new nearshore habitats supported a fish community of significantly greater functional dispersion and entropy relative to previously present beaches within and outside the new delta. That is, species unique in their diet, habitat use, morphology, and size were abundant relative to less functionally unique fish in newly formed beaches. These trends were temporary as there were no significant differences in functional diversity or entropy of fishes among sites after the restoration. Newly formed habitats proved to be more diverse but had lower resiliency after dam removal. Newly establishing nearshore sites appear more vulnerable to non-native and nuisance species that could disrupt the establishment of the watershed and shoreline. While functional richness at the original estuary sites dropped dramatically after dam removal, resiliency was higher after dam removal corresponding to a shift from estuary to lower river side channel habitat, indicating a more stable nearshore zone than new sites. We anticipate that functional diversity at the newly formed nearshore areas will stabilize as the habitats are vegetated and mature.

1. Introduction

Nearshore ecosystems are a critical ‘connective tissue’ that link marine and watershed ecosystems. In the northeast Pacific numerous endangered salmon and forage fish species depend on the nearshore zone for migration, foraging, refuge, and spawning (Simenstad et al 1982; Beck et al 2001; Shaffer et al., 2017a). Fish benefit from many features of shallow ecosystems (e.g., prey availability, predator refuge), and they are sensitive to anthropogenic disturbances (Munsch et al., 2016, 2017).

Large-scale dam removals are becoming an important tool for nearshore ecosystem restoration, but little is known about functional coastal response to large-scale dam removal (Shaffer et al., 2017a&b). In this study, we explore the long term functional diversity of fish communities of two estuaries on the north Olympic Peninsula, Strait of Juan de Fuca, with an emphasis on the functional metrics of the Elwha River estuary and the role of ecosystem restoration associated with large-scale dam removal in changing functional diversity. We detail the trait-based functional diversity and functional redundancy, and resulting functional stability of the Elwha estuary fish functional assemblage by species before, during, and after large-scale dam removals. The Elwha River dam removal project, which ended in 2014 resulted in 20 mcm of material liberated to the Elwha system approximately half of which is anticipated to be delivered to the coast within five years of dam removals.

We address the following questions:

1. What are the functional parameters of this regions nearshore

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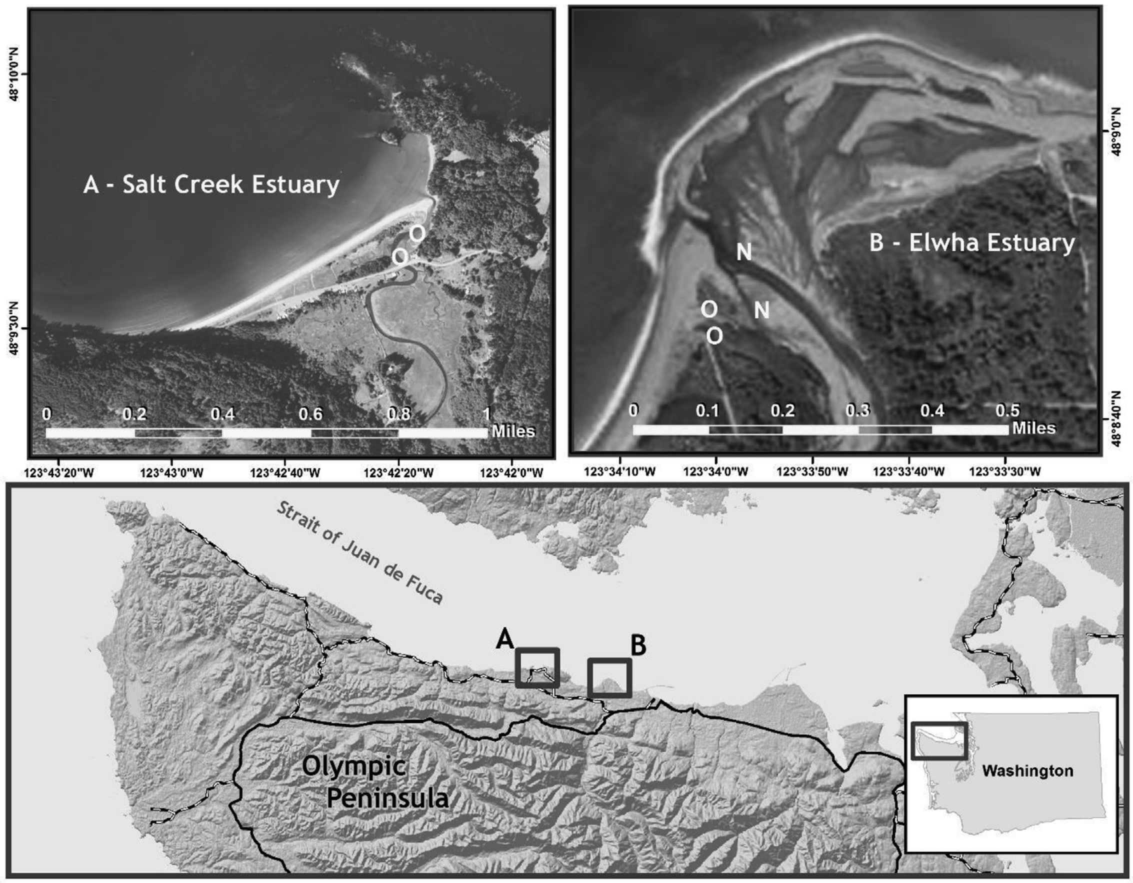

Fig. 1. A Salt Creek and B. Elwha River nearshore study sample sites. O original sites sampled 2008-present; N New sites created over the course of dam removals from delivery of dam removal sediment and sampled from 2013-present. Map by Terry Johnson, WDFW.

Table 1
Definitions of functional traits used in this analysis.

Metric	Definition	Citation
Functional richness	The amount of functional space occupied by a species assemblage	Laliberte et al., 2014
Functional dispersion	A multidimensional functional diversity matrix	Laliberte et al., 2014
Functional evenness	How regularly species abundances are distributed in the functional space.	Mouchet et al., 2010
Functional divergence	How far species abundances are from the center of the functional space	Mouchet et al., 2010
Rao's quadratic entropy (Q)	A distance matrix that defines the pairwise distances between species weighted by the relative abundance. Rao's Q takes into account abundances where functional richness cannot, thereby preventing overestimation of the influence of uncommon species	Bourdon 2016
Functional redundancy	The difference between species diversity and functional diversity. High redundancy indicates high stability and more resilience to ecosystem disruptions.	Guillemot et al., 2010, Kang et al., 2015

Table 2
The four trait categories used (Baptista et al., 2015).

Size	Small (< 70 mm)	1
	Medium (70–150 mm)	2
	Large (151–400 mm)	3
	Very large (> 400 mm)	4
Body transverse shape	< 0.5 (flat horizontally e.g. flatfish)	1
	0.5–1	2
	1–2	3
	> 2 (flat vertically e.g. perch/salmon)	4
Feeding guild	Omnivorous	1
	Planktivorous	2
	Piscivorous	3
	Zoobenthivorous	4
	Detritivorous	5
Vertical distribution	Benthic	1
	Pelagic	2
	Demersal	3

estuarine fish communities?

2. How do these functional parameters of the estuary fish community respond to ecosystem restoration associated with large-scale dam removal?
3. Are the functional elements of the estuary fish community more resilient after dam removals than before or during dam removal?
4. How does fish species community composition change functionally with dam removals?

Answering these questions will provide further understanding of ecosystem restoration, the functional linkages between nearshore coastal systems and large-scale dam removals, and how species assemblages may change functionally. All of these are important but poorly understood elements for future ecosystem restoration.

Fig. 2. Elwha dam removal project site. Both dams removed 2011–2014. Photos from: http://www.nps.gov/olym/naturescience/elwha-ecosystem-restoration.htm.

2. Methods

Subsets of the data used for this study have been previously published using different analyses and study focus and are provided with permission for this unique analysis (Quinn et al., 2013, 2014; Shaffer et al. 2009, 2012, 2017b). Field data collection methods are detailed in the most recent of these (Shaffer et al., 2017 b). In short, fish use of the Elwha and a comparative estuary of the Salt Creek system were assessed through monthly beach seining at established sites in the Elwha and comparative sites. While a much different system than Elwha, the Salt Creek is a nearby estuary that was unaffected by dam removal that allows us to control for general effects. The beach seine was a standard ‘small net’ as outline in the Puget Sound protocol (PSWQA, 1996). Sampling was conducted once a month, on the neap tide, during daylight hours at designated sampling locations. All sites were sampled within the same 8 h period. The sampling time period was broken into three periods: pre-dam removal (2008–2011), dam removal (2011–2014) and post dam removal (2014–2017). 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.

For each sample, all fish were identified to the lowest taxa possible and up to 25 fish of each species and life history stage (adult, juvenile, post larval) were measured. In March 2013, two additional sites, named Elwha ‘new’, were added to the sampling plan. These were located in new Elwha estuary areas created as a result of dam removal (Fig. 1). Therefore the first Elwha sites are hereafter titled ‘original’ sites and newly created Elwha sites ‘new sites’. Salt Creek sites are ‘comparative’ sites.

We aggregated the data by taking the mean of all measurements for each site, year, and thirds of the year (Jan–Apr, May–Aug, Sep–Dec). Initial data exploration revealed considerable variation in the data described by individual net samples, and aggregating the data reduced noise in the description of species present at a site, allowing trends in functional traits to emerge. We decided to use thirds of a year because this aligned with transitions in dam removal phases in August. We used linear mixed effects models to quantify functional metrics of the fish community among systems as dams were removed. The parameters in these models included the fixed effects of region (Elwha Original, Elwha New, and Salt Creek), dam removal phase (before, during, and after), and third of the year, and the random effect of site and year to account for non-independence of measurements taken in the same locations and times. Finally, we used non-metric multidimensional scaling (NMDS) to visualize how the functional traits of fish communities varied among sites and dam removal phases. We overlaid vectors onto these NMDS plots that indicated increasing gradients of functional traits in multivariate space to better visualize how species abundances corresponded to presence of functional traits. The statistical significance of these vectors was determined by bootstrapping (1000 permutations). We calculated relative positions of fishes in trait space using a Bray-Curtis dissimilarity matrix comparing the species (row data) according to their functional traits (column data). We intended for these visual tools to supplement the comparatively rigorous statistical tools of our mixed effects models. The purpose of the multivariate visualizations was to provide a window into the multidimensional details of differences in species abundances and corresponding functional traits among sites and dam removal phases. That is, the mixed effects models describe quantitatively differences in the arrangement of functional trait space and the NMDS plots enhance our understanding of the species and traits that contributed to these differences by qualitatively visualizing the data. Consequently, the NMDS plots should be interpreted cautiously and as supplemental to the statistical and more rigorous tools of the mixed effects models.

We selected a subset of functional traits that: 1. Encompass the widest selection of fish guilds observed in the Elwha delta and comparative sites, and; 2. Allow for comparison with published work in

Fig. 3. Elwha delta A) before (2010) and; B) after (2016) dam removals with area changes over the last 100 years. Reprinted with permission from Shaffer et al. (2017b).

other systems. The four traits selected for analysis were body size, body type, feeding strategy, and vertical distribution (Table 1). Abundance data for each species, by month and site, were converted to functional trait values (Table 2), and then all sample dates with a minimum of four species (required for analysis) were analyzed for functional metrics.

There are a number of functional diversity traits that are used to quantify biodiversity, ecosystem functioning and environmental constraints. It is important that traits selected to assess functional diversity accurately reflect the system (Petchey and Gaston, 2005). Functional trait space is often multidimensional because usually more than one trait is required to effectively describe species, including diversity, richness, dispersion and evenness. Functional divergence (in this paper also called 'functional diversity'), functional dispersion, richness, evenness, and Rao's quadratic entropy have been found to be useful for aquatic communities (Bourdon, 2016; Guillemot et al., 2010; Mouillot et al., 2007, 2013; Villeger et al., 2010), and so are the focus of this paper (see Table 2 for a synopsis of each metric). Functional divergence, functional richness, and Rao's estimate of quadratic entropy are the most informative functional diversity metrics defining the functional structure of the nearshore fish community central to this study (Botta-Zukat, 2005; Mouchet et al., 2010).

Functional redundancy, defined as the number of taxonomically distant species that exhibit similar ecological functions, is another important ecological parameter. Functional redundancy is the difference between species diversity and functional diversity (Guillemot et al., 2010; Kang et al., 2015). Systems that have high functional redundancy have a higher degree of stability and are more resilient to ecosystem disruptions. (Pillar et al., 2013; Kang et al., 2015). However, the

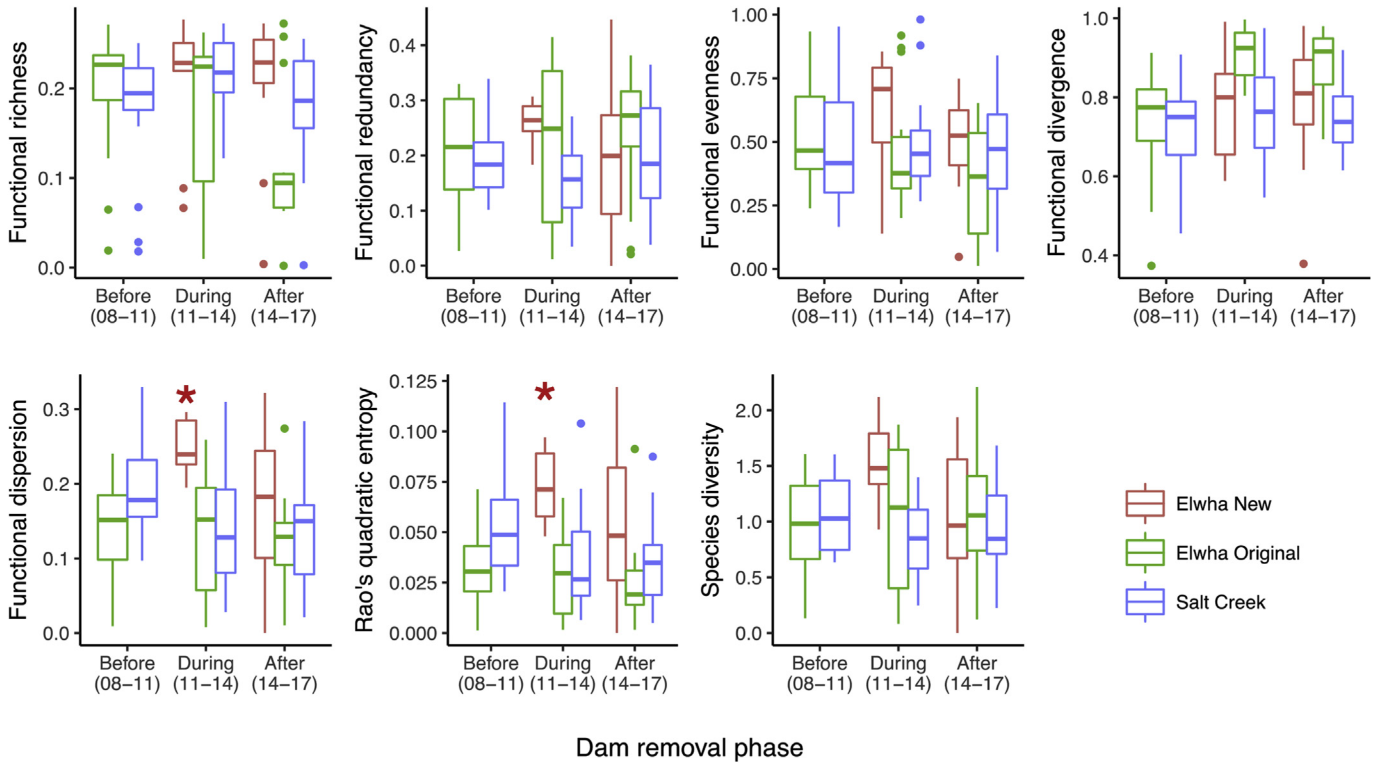

Fig. 4. Functional and species diversity compared among Elwha Original, Elwha New, and Salt Creek sites before, during, and after dam removal. Bold horizontal lines are median values; top and bottom of squares are first and third quartiles. Vertical lines with whiskers are the minimum and maximum values if no outliers are displayed. On boxes with outliers the whiskers represent 1.5 times the interquartile range. Numbers in parentheses are years within dam removal stage. Asterisks indicate statistically significant differences between Elwha New sites and sites from other regions, and arrows, when present, indicate which pair-wise differences are described.

removal of a function may be of higher impact in a system with high rather than low functional redundancy. Therefore, functional richness, evenness, divergence, dispersion, Rao's Q, and functional redundancy were generated for the three dam removal phases using the FD package in R (Debastiani and Pillar, 2012; Laliberté and Legendre, 2010; Laliberté et al., 2014).

Analysis occurred in R version 3.3.3 (R Core Team, 2018) using the package lme4 (Bates et al., 2016) and Vegan (Oksanen, 2015; Oksanen et al., 2018).

3. Results

The two dams in the Elwha River were removed from September 2011 to 2014 (Fig. 2) Overall the delta grew by approximately 35 ha to over 157 ha as of 2015 (Fig. 3; Shaffer et al., 2017b). A total of 37 species and life history stages were collected over the course of the study. Functional metrics varied with site and dam removal phase (Fig. 4; full summary statistics are in Table S1). Before the dam removal, there were no statistically significant differences in the functional ecology of the fish communities between the Elwha Original and Salt Creek regions (Table S1, Phase: Before). During the dam removal, (1) functional dispersion and Rao's quadratic entropy among sites were significantly greater at the Elwha New sites (Table S1, Phase: During, Responses: Functional dispersion and Rao's quadratic entropy) and (2) functional divergence among sites was significantly greater at the Elwha Original sites (Table S1, Phase: During, Response: Functional divergence). After the dam removal, functional evenness was significantly lower at Elwha Original sites than Elwha New sites (Table S1, Phase: After, Response: Functional evenness) and functional divergence remained significantly higher at the Elwha Original sites than Elwha New sites (Table S1, Phase: After, Response: Functional divergence).

Multivariate visualizations of the fish community in functional space showed how mean abundances of functionally distinct species varied among dam removal phases and regions (Fig. 5). Before the dam removal, the communities at Salt Creek and Elwha Original sites were similar: fish occupied most of the functional space, and fish that were least functionally extreme (i.e., those in the center of the ordinations) were generally most abundant. As the dams were removed, the community at Salt Creek remained virtually the same, the community at Elwha Original sites became more compact in functional space and its abundances more evenly distributed among species, and the community at the newly formed Elwha new sites included many species located peripherally in functional space (e.g., bull trout, English sole, eulachon, starry flounder, adult surf smelt, post-larval surf smelt, unidentified juvenile trout, unidentified cottids) while excluding others often abundant in the center. After the dam was removed, the communities at Salt Creek and Elwha Original sites did not markedly change, but at Elwha New sites, a few species that were least functionally extreme (e.g., pink salmon, fluffy sculpin) became present while the more functionally extreme English sole was absent. Overall, these multivariate visualizations were most clearly consistent with our univariate analyses showing that functional dispersion (i.e., abundance-weighted distribution of species away from the origins of functional trait space) and entropy were greatest at Elwha New sites during the dam removal (i.e., the pairwise, abundance-weighted distances between species in functional trait space), while more subtle relative changes (e.g., decreasing functional evenness at Elwha Original sites as lowest measures of evenness at Elwha New sites increased, resulting in significant differences between the two regions after the dam removal) were more difficult to discern.

4. Discussion

Here we show that the functional dispersion and entropy of a fish

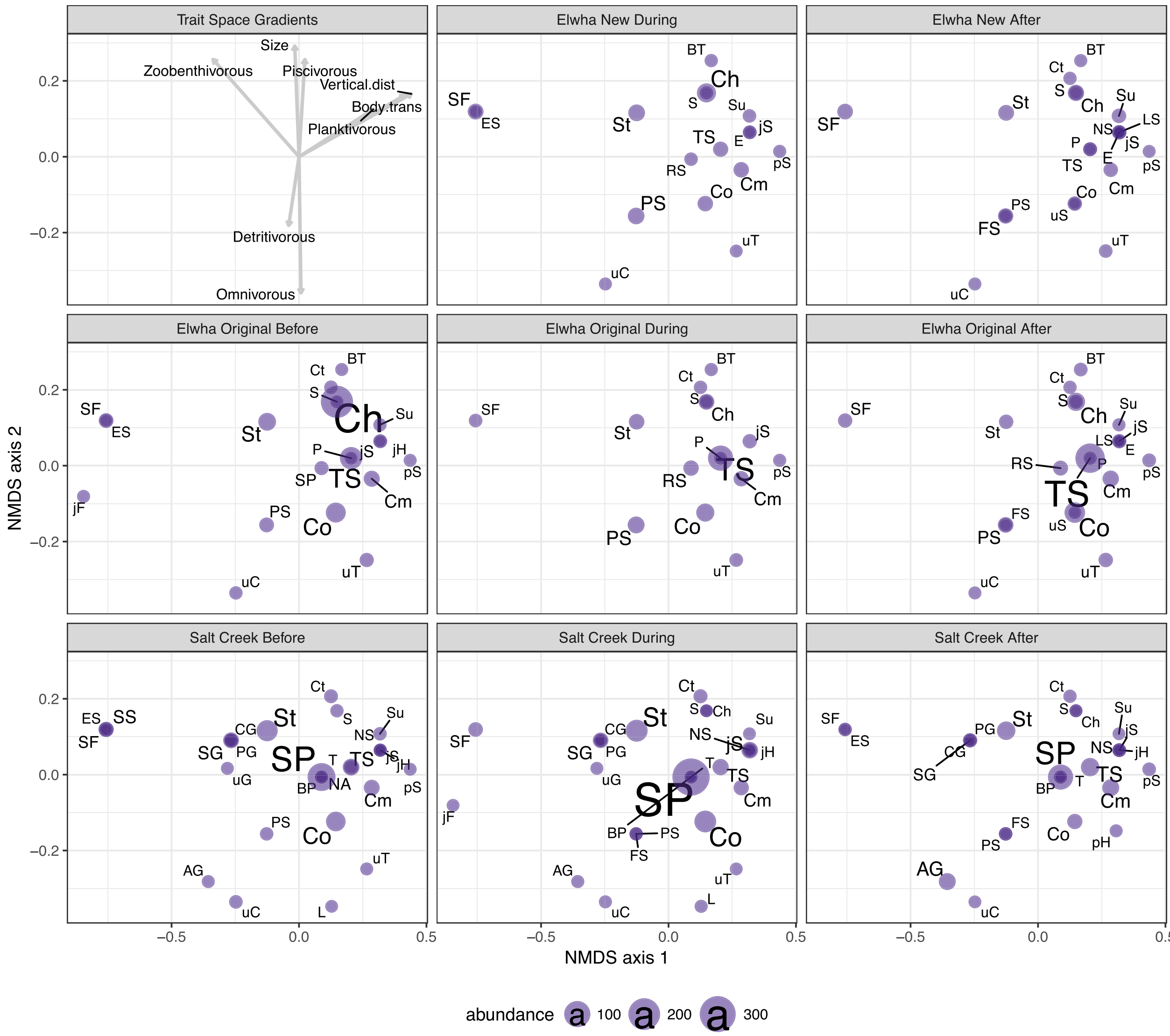

Fig. 5. Species and trait NMDS. Nonmetric multidimensional scaling plots visualizing how the functional composition of fish communities varied among sites and dam removal phases. Larger points indicate more abundant species. Fish are positioned according to their relative functional traits, and how gradients of functional traits in multivariate space are shown in the bottom left corner. All vectors in the bottom left panel are statistically significant (bootstrapping, $p < 0.05$) except "Detritivorous" ($p = 0.21$)). Abbreviations: AB = arrow goby, BP = bay pipefish, BT = bull trout, Ch = Chinook salmon, Cm = chum salmon, Co = coho salmon, CG = Crescent gunnel, Ct = Cutthroat trout, ES = English sole, E = eulachon, FS = fluffy sculpin, jH = juvenile herring, pH = postlarval herring, jF = juvenile flatfish, L = lingcod, LS = longfin smelt, NA = northern anchovy, NS = northern shad, PG = penpoint gunnel, P = pink salmon, PS = prickley sculpin, RS = redsided shiner, SG = saddleback gunnel, SS = sand sole, SP = shiner perch, jS = juvenile smelt, pS = postlarval smelt, St = staghorn sculpin, SF = starry flounder, S = steelhead, Su = adult surf smelt, TS = three-spine stickleback, T = Tubesnout, uC = unidentified cottids, uG = unidentified gunnel, uT = unidentified juvenile trout, uS = unidentified juvenile salmon.

community temporarily increased in portions of the Elwha estuary recently formed by the deposition of sediment released by dam removal. That is, species unique in their diet, habitat use, morphology, and size were abundant relative to less functionally unique fish. We did not see this at original sites in the same system or at sites in another system. In addition, the functional divergence of fish at original sites in the same system increased during and after the dam removal and remained higher than at newly formed sites in the same system as well as at our comparative site outside of the dam removal system. Finally, after dam removal was complete, the functional evenness of the community of the original sites was significantly lower than that of the newly formed sites. This is likely a result of the original sites transitioning from estuarine to lower river side channel, resulting in fewer species that use them. While functional diversity within the Elwha system disrupted by dam removal was volatile, at sites outside this system functional diversity was relatively constant.

Three major shifts in physical habitat are at the center of these changes in the 'new' sites relative to the original Elwha and Salt Creek comparative sites.

1. The expansion of the Elwha nearshore through the creation of both new lower river-side channels and estuary habitat formed in a severely constrained and small estuary (Shaffer et al., 2017 a,b);
2. High sediment loads delivered to the estuary (Warrick et al., 2015), and;
3. Shifts in habitat from estuarine to freshwater (East et al., 2015; Foley et al., 2015).

Combined, the extremely fast and large-scale changes to the estuary and lower river resulted in both higher functional diversity through the introduction of new, functionally distinct species to the system that also resulted in a disparate, and significantly lower redundancy in the still establishing new Elwha delta habitats relative to the original habitats. This lower redundancy, indicates a less resilient and more unstable community in the new regions of the Elwha estuary. Thus, while new sites have a higher functional diversity they may be more susceptible to disruption, including colonization by pioneering native species (e.g., eulachon, *Thaleichthys pacificus*, and non-native species (e.g., shad *Alosa sapidissima*). Shad have a warm water anadromous life history. As climate change advances, shad may be a future concern for the watershed (as they are in the nearby Columbia River, see Hasselman et al., 2012). With the advent and establishment of new nearshore spawning habitats in the Elwha nearshore, including along the lower river and side channel habitats, eulachon may re-establish in this watershed. As the sites and communities stabilize, the functional stability of the system should re-establish to a higher functional redundancy. As the sites stabilize we predict these sites to become more stable, and so more resilient.

In summary, functional ecology of nearshore systems is sensitive to large scale dam removal and may be less resilient and so more vulnerable to functional disruptions, particularly at new sites created as a result of dam removal. The disruption appears the highest during the dam removal phase. Overall, it appears that (1) large scale dam removal can affect the functional ecology of nearshore systems, particularly by including proportionally more functionally extreme species and (2) these changes are temporary as the functional ecology of the fish community tended to become less distinct at new sites after the dam removal was completed. Large scale dam removal restoration actions in the future should consider this disruptive phase not only for new, but also original nearshore habitats, which may offer more stable refuge during dam removal. Specifically, as much nearshore habitat as possible should be provided prior to dam removal beginning, and focus efforts to minimize ecosystem destabilizing events such as the establishment of non-native species, should be taken during and after dam removal to minimize destabilizing non-native species. Once the dam removal ends resiliency appears to improve, indicating a more stable nearshore system.

Author contribution

Dr Shaffer devised and led all elements of large scale dam removal study as a component of her PhD dissertation;

Dr. Munsch provided data analysis and scientific collaboration;

Dr Juanes, as Shaffer's committee chair, provided scientific collaboration and insights into Functional Diversity.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.ecss.2018.08.030.

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