

Intertidal Biotic Community Monitoring Following Elwha Dam Removal

February 13, 2019



**PUGET SOUND ECOSYSTEM
MONITORING PROGRAM**



**WASHINGTON STATE DEPT OF
NATURAL
RESOURCES**

Cover photo: Low tide in the morning at Freshwater Bay.

Intertidal Biotic Community Monitoring Following Elwha Dam Removal

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Megan N. Dethier
University of Washington

Helen Berry
Nearshore Habitat Program
Aquatic Resources Division



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Washington State Department of Natural Resources
Aquatic Resources Division
1111 Washington St. SE
P.O. Box 47027
Olympia, WA 98504-7027

www.dnr.wa.gov

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Executive Summary

The Washington State Department of Natural Resources (DNR) is steward of 2.6 million acres of state-owned aquatic lands. As part of its stewardship responsibilities, DNR monitors the condition of nearshore habitats. Monitoring results are used to guide land management decisions for the benefit of current and future citizens of Washington State.

This report summarizes collaborative University of Washington-DNR research quantifying changes from 2014 to 2018 in the intertidal zone near the mouth of the Elwha River. Removal of the dams from the river released pulses of sediments that had been accumulating behind the dams for over 100 years. The marine shoreline along this stretch of the Strait of Juan de Fuca had likely suffered chronic sediment deficits because of the sediment trapping. Abundance and mobility of shoreline sediment is critical to nearshore ecology; in beaches with mixed substrate types (e.g. cobble or pebble and sand), which are very common in the Salish Sea. An important factor determining biotic diversity is the abundance of relatively stable substrates (e.g. boulders and cobbles) versus mobile substrates (e.g. gravel and sand).

The UW-DNR team sampled sites beyond the mouth of the Elwha River to evaluate changes to biotic communities farther afield of the delta. This work is based on a spatial drift cell strategy developed for Elwha nearshore monitoring (Shaffer et al. 2008,) and complements biotic community sampling completed at the delta by the United States Geological Survey (Duda et al. 2011) and beach geomorphology sampling by Parks (2015), Miller et al. (2015), Gelfenbaum et al. (2015). Generally, abundant and persistent sediment deposition occurred at the river mouth, where changes in response to the dam removal continue. Physical and biotic effects to date decreased in magnitude with distance from the river mouth.

Sites in this study are co-located with a long-term study of sediment dynamics along bluff-backed shorelines led by David Parks (2015).

While we did not sample prior to dam removal, other scientists performed intertidal surveys in 2010-2012, with comparative sites sampled outside the Elwha drift cell. Although methodological differences make detailed before-after comparisons challenging, we qualitatively compare our biotic surveys (2014-2018) with those completed before dam removal. For species sampled effectively using both methods (e.g., not including algae or mobile invertebrates <1mm), species-abundance curves show that benthic communities were adequately sampled with both methods. In both datasets, sand-dominated beaches had dramatically different (and depauperate) communities relative to beaches with cobble. When just cobble-sand beaches are examined and species poorly sampled by one or the other methodology are excluded, we found strong similarities in the biotic communities distant from the delta. It is not possible to determine if small differences observed among years reflect methodology or genuine change following dam removal, but we suspect the

former. If dam removal was causing long-term change to the biota, we would expect increasing divergence from the 2011 communities through time, but this is not the case.

Spatial and temporal comparisons of biotic communities in the 2014-2018 samples (all using the same method) emphasize both the depauperate state of sand-dominated beaches (1-4 species per transect vs. 37-82 in the cobble-sand beaches), and relative biological stability of cobble-sand beaches through time. The two cobble-sand sites had consistently different communities from each other, but at each beach these communities changed in similar ways among years. The main differences from 2014 to 2018 were declines in many perennial macrophytes and in limpets, and increases in ephemeral algae and their snail consumers. There were also reductions in species richness through time in each transect, which were paralleled by an increase in sand. As seen elsewhere in the Salish Sea, there is a clear negative relationship between the amount of sand and the species richness on beaches. Overall, our sampling efforts in the low intertidal zone in the Strait of Juan de Fuca suggest that some sites have experienced influxes of sediment that have impacted the biota found there, but that most of these changes have been gradual. Intertidal sites closer to the mouth of the Elwha River presumably changed much more rapidly and dramatically following intense sediment influx. Because most geomorphological changes are slow, this system is still relatively early in the post restoration 'recovery' phase.

Introduction

The Washington State Department of Natural Resources (DNR) is steward of 2.6 million acres of state-owned aquatic land. The Aquatic Resources Division of DNR manages these aquatic lands for the benefit of current and future citizens of Washington State.

Program Background

The overall goal of the Intertidal Biotic Community Monitoring Project is to assess the condition of intertidal biota in greater Puget Sound. This work supports the mandate of the Washington State Department of Natural Resources (DNR) to ensure environmental protection of the 2.6 million acres of state-owned aquatic lands that it stewards (RCW 79.105.030). Additionally, this work supports the Puget Sound Partnership's effort to protect and restore Puget Sound through tasks that are defined in the Puget Sound Action Agenda (Puget Sound Partnership 2009), and in the monitoring plans by its predecessor, the Puget Sound Action Team (Puget Sound Action Team 2007).

DNR and the University of Washington (UW) have jointly monitored biotic communities since 1997, focusing on shoreline communities at Mean Lower Low Water elevation. These communities can be highly diverse and productive, harboring extensive populations of algae and seagrasses that contribute to food webs (both nearshore and in deeper water) and provide habitat for many other organisms (e.g., Duggins et al. 1989). Intertidal and nearshore communities also serve as useful 'indicators' of ecosystem health. Because most organisms in these habitats are relatively sessile and thus unable to move away from stressors, they are vulnerable to both natural and anthropogenic stressors from terrestrial and aquatic sources. A critical parameter determining the types of organisms, species diversity, and productivity of intertidal communities is the type of substrate – which on the shorelines of the Salish Sea ranges from continuous bedrock to soft mud. General types of biota found on shorelines of different substrates have been described in Dethier (2010) and can be seen in the Encyclopedia of Puget Sound (<https://www.eopugetsound.org/habitats/shore-types>). In beaches with mixed substrate types (e.g. cobble or pebble and sand), which are very common in the Salish Sea, a key factor determining biotic diversity is the abundance of relatively stable substrates (e.g. boulders and cobbles) versus mobile substrates (e.g. gravel and sand). Sediment that is held in place by surface cobbles can greatly increase local diversity by creating habitat for infaunal invertebrates such as polychaetes and clams; sediment that moves seasonally or in storms can decrease diversity by smothering organisms and being too unstable for most organisms to colonize effectively. Thus the type and behavior of sediment in a region is a significant determinant of nearshore ecology.

This report summarizes collaborative UW-DNR research quantifying changes from 2014 to 2018 in the intertidal zone near the mouth of the Elwha River, several years after the 2011 removal of the dams there. Removal of the Elwha dams on the Olympic Peninsula not only restored natural freshwater flows from a near-pristine watershed into the

nearshore marine environment of the Strait of Juan de Fuca, but released into the river, and thence into the nearshore, pulses of sediments that had been accumulating behind the dams for over 100 years. Sediment supply from rivers, streams, and eroding bluffs are a natural and integral part of nearshore ecosystem processes on Washington's coastlines (Parks 2015, Shipman 2010, Kaminsky et al. unpubl.), so this large-scale 'experiment' provides an opportunity to study how restoration of this key process affects marine communities. The shoreline along this stretch of the Strait of Juan de Fuca had likely suffered chronic sediment deficits because of the sediment trapping of the Elwha dams (Foley et al. 2017).

As the Elwha dams were removed in stages, an estimated 30 million tonnes of trapped sediment (Warrick et al. 2015) were released over the course of several years when winter rains and spring snowmelt flushed out sediments on the river and lake bottoms. This flushing was first seen in Spring 2012 and is continuing episodically at least through 2018. Modelling and measurements of hydrological and geomorphological changes have been done by USGS and other agencies (e.g., Foley et al. 2017). Biological changes in the subtidal environment off the mouth of the Elwha River have been studied in detail by Rubin et al. (2017), and changes in riverine habitats and fish use by Foley et al. (2017). Rubin et al. emphasize the role of sediment – both causing turbidity in the water column and deposition on the benthos – in creating major changes in shallow subtidal communities near the river mouth.

The UW-DNR team sampled intertidal sites beyond the mouth of the Elwha River to evaluate changes to biotic communities farther afield of the delta. This work complements biotic community studies at the delta by USGS and beach sediment dynamics studies by Washington SeaGrant. Generally, abundant and persistent sediment deposition occurred in the intertidal zone at the river mouth. Physical and biotic effects decreased in magnitude strongly with distance from the river mouth.

The UW-DNR intertidal biota sites are co-located with a long-term study of sediment dynamics along bluff-backed shorelines led by David Parks (Parks et al. 2013).

While UW-DNR did not sample this shoreline prior to dam removal, intertidal biotic community surveys were conducted in 2010-2012 by the H. Andersen through the Coastal Watershed Institute (2013). The methods used for these surveys differed from our standard methodology in several ways, making detailed before-after comparisons challenging. Here we present data comparing our biotic surveys with those done by CWI/Andersen before the dam removal, and a time-series of post-removal data using just UW-DNR methodology.

Methods

SCALE intertidal biotic community sampling design and statistical analyses have been described in previous peer-reviewed publications (Schoch and Dethier 1995, Dethier and Schoch 2005, Dethier and Schoch 2006) and technical reports (available through DNR at http://www.dnr.wa.gov/ResearchScience/Topics/AquaticHabitats/Pages/aqr_nrsh_publications.aspx). General methods are summarized here.

We quantitatively assessed patterns in benthic nearshore populations and communities along the shoreline at a number of the sites sampled by Andersen (2013) before dam removal. These included sites relatively far from the mouth of the Elwha, where no biotic changes were expected (e.g., Dungeness Bluff), as well as sites closer to the Elwha (Elwha Bluffs and Freshwater Bay). We sampled both low-diversity sand-pebble beaches and high-diversity cobble-sand beaches. Biological sampling was conducted during spring tides in late June and early July. Andersen (2013) sampled some sites during several seasons, but we compared our summer data only with her summer (2011) data. We sampled transects at all 3 regions in 2014, at Freshwater Bay only in 2015-2017, and at Elwha Bluffs and Freshwater Bay in 2018.

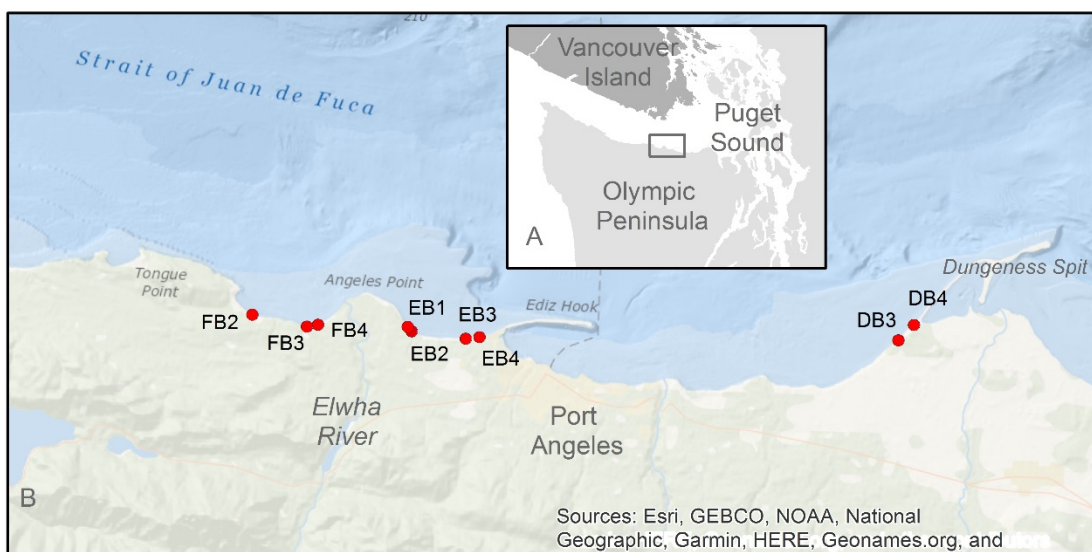


Figure 1. A. study area location on the Olympic Peninsula in Washington State; B. sites sampled in this study.

Precise transect locations were chosen to match sites where beach elevation data had been gathered for several years by CWI (Parks et al. 2013) using RTK-GPS surveying methods with vertical/horizontal accuracy of about 5 cm. In sites where sediments accumulated at MLLW, the physical location of the transect had to be moved further from the bluff to ensure that the same tidal elevation was being sampled each year. Each year that we sampled, we relocated transect sites with three methods: horizontal distance from survey markers at the base of the bluff, calculated using annual RTK-GPS survey; handheld GPS

coordinates; and water level at the time of the predicted MLLW tide. These locations generally agreed closely with each other; transect elevations are estimated to have a total elevation uncertainty of <15cm. In one case, when a survey marker was lost during winter storm activity, we relied on the GPS coordinates from the previous sampling year and water level line at the time of predicted MLLW tide.

Biotic community samples for the SCALE sampling included both epibiota and infauna from 10 randomly spaced sample units along a 50 m horizontal transect. Each sample unit consisted of a 0.25 m² quadrat to quantify abundance of surface macroflora and fauna, plus a 10 cm diameter x 15 cm deep core for macroinfauna. Percent cover was estimated for all sessile taxa in the quadrats, and all motile epifauna (organisms > ca. 3 mm) were counted. Fresh core samples were washed through 2 mm mesh sieves, thereby excluding meiofauna, juveniles of some worms, and adults of smaller crustaceans, such as cumaceans and harpacticoids. In 2014-2016 we also sieved samples through 1 mm sieves to capture more of the smaller organisms and make our methodology more similar to that of Andersen. The finest taxonomic resolution used in field sampling and laboratory identification was species level, although some difficult taxa were only identifiable to genus or higher levels (e.g., *Pagurus* spp., Phylum Nemertea). Taxonomic references were Kozloff (1996) for invertebrates and Gabrielson and Lindstrom (2018) for macroalgae.

While Andersen (2013) worked at the same sites and tidal elevations, her methods were somewhat different, in general examining fewer samples in greater detail; she chose sites and used methods developed in the 1970s for the MESA study (Nyblade 1979). She collected 5 stratified random samples along each 50 m transect. In sand/pebble beaches, she sampled infauna by digging all sediment to 15 cm depth from a 22.5 x 22.5 cm frame. This sediment was sieved to 1 mm in the field. Other quadrats were dug deeper to sample for clams, but we did not do any sampling parallel to this method. For mixed cobble-sand beaches, she first scraped all algae and collected all visible epibenthic organisms from a 50x50 cm frame. These samples were preserved and later sorted and enumerated into broad taxonomic groups (polychaetes, gastropods, etc.) under a dissecting microscope in the lab. Algal abundance was not quantified. She then dug a smaller core sample to 15 cm depth as in the sand samples, and sieved these to 1 mm in the field. We did additional taxonomic work on a subset of her scraped and dug samples to achieve a similar level of specificity as with our own samples, to make the data more comparable.

Multivariate analyses and PRIMER software (Clarke and Gorley 2006, Anderson et al. 2008) were used to detect patterns in the spatial and temporal distributions of communities. The data matrix of taxon abundances was square-root transformed to reduce the contribution of highly abundant species in relation to less abundant ones in the calculation of similarity measures. We used the ordination technique of non-metric multidimensional scaling (MDS) to group communities based on the Bray-Curtis similarity metric. Graphic plots of ordination results for the two axes explaining the greatest proportion of the variance were examined for obvious sample groupings. Analysis of similarity (ANOSIM) tested the significance of hypothesized differences among sample groups. Similarity percentage (SIMPER) analyses identified the variables (species) that contributed the most to different groupings.

Results

Comparison of Before (Andersen) and After (SCALE) Biota

We compared our monitoring data from the Elwha area in 2014, 2015, and 2016 (all post dam-removals), with those of Anderson's data from 2011 (pre-dam-removals). It is a challenge to compare these two sets of data with different sizes of sample devices (both quadrats and cores), numbers of samples per transect, and methodologies (e.g., scrapes of epiflora vs. quantification in the field). Because the 2011 samples were fewer but larger, we first examined 'species-accumulation curves', which illustrate how the number of expected species (based on how many were found in each sample) increases with the number of samples. Figure 2 shows curves from the SCALE data from Freshwater Bay 3 (FB3) and the more-diverse FB2. For each of these sites, the accumulation curves level off near 10 samples, illustrating that taking more samples would add relatively few additional species. For the Andersen samples (5 larger samples) from FB2, there is a similar leveling off after 5 samples and at a similar number of species (ca. 70 vs. ca. 60 in the SCALE data), showing that each method does a fairly good job representing the community.

For community-level analyses comparing Andersen's data with SCALE datasets, we had to scale biotic parameters to bring all Elwha samples into the same units (Table 1). This analysis could be done only for animals; all algal data were removed because Andersen did not quantify algae.

With all data modified in this manner, the other key manipulation of the data was removing taxa from each list that were not sampled effectively by both teams (Appendix 1). For the Andersen data, this meant eliminating very small organisms (copepods, several other small crustaceans) that were found when picking preserved algal scrapings, but which are not sampled by the SCALE method. For the SCALE data, this meant eliminating all algae and fishes, and pooling anemone species and numerous taxa that were not analysed to the same level in Andersen's samples. These modifications allowed similar data to be compared.

Appendix 2 lists all taxa collected at each site, scaled according to Table 1.

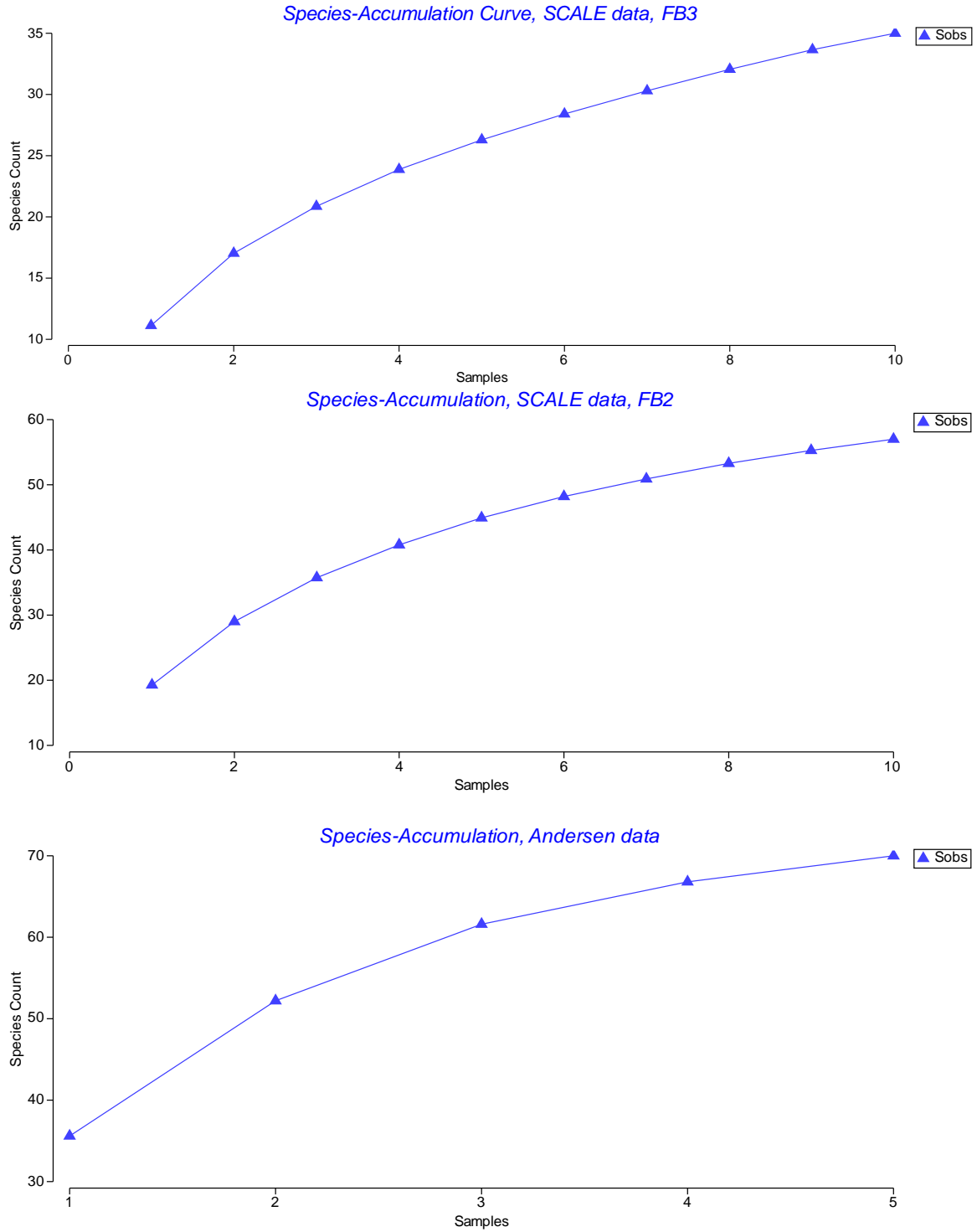


Figure 2. Species-accumulation curves for two sites using SCALE methods (top two panels) and for Andersen’s data from FB2 using fewer, larger samples.

Table 1. The 'correction' factors used to bring all samples to a per 50x50 cm area basis (2500 cm²).

Cobble sites (FB2, FB3, and EB1)

<u>Andersen Samples</u>	<u>multiply count by</u>
Animals in algal 'scrapes'	1
Epifauna	1
Infauna	5
<u>SCALE Samples</u>	
Quadrat animals	1
Infauna	32

Sand sites (EB3, EB4, DB3, DB4)

<u>Andersen Samples</u>	<u>multiply count by</u>
Infauna	5
<u>SCALE Samples</u>	
Quadrat animals	1
Infauna	32

With this reduced dataset, we ran community analyses to compare the sets of organisms present during each of the 4 years of sampling. The first analysis (Figure 3) shows that sand communities are very different from those on cobble shores, separating clearly into different regions of the plot.

Elwha Bluff (EB) 1 was categorized as Cobble by Andersen (and listed in Andersen 2013 as “open beach, cobble low-tide terrace”, with 53% cobble by volume at MLLW) and its biota cluster with the cobble-dominated Freshwater Bay 2 samples (green square in center right of plot). Yet, in 2014 the low shore was clearly sand-dominated (>70% cover sand), and its biota groups with the sand beaches (red triangle in upper left cluster). Andersen’s 2011 samples at EB1 contained some biota associated with hard substrates such as barnacles, gastropods, and cnidarians, and her notes list some algae (*Ulva* and *Porphyra*) at this site; our 2014 samples were sand-pebble dominated (see below) and contained only one taxon, fleshy algal crusts on some pebbles. These differences strongly suggest that this site became buried (in the low intertidal) by sediment, covering the boulders Andersen recorded at this site and dramatically changing the biotic communities.

All Elwha Sites and Years

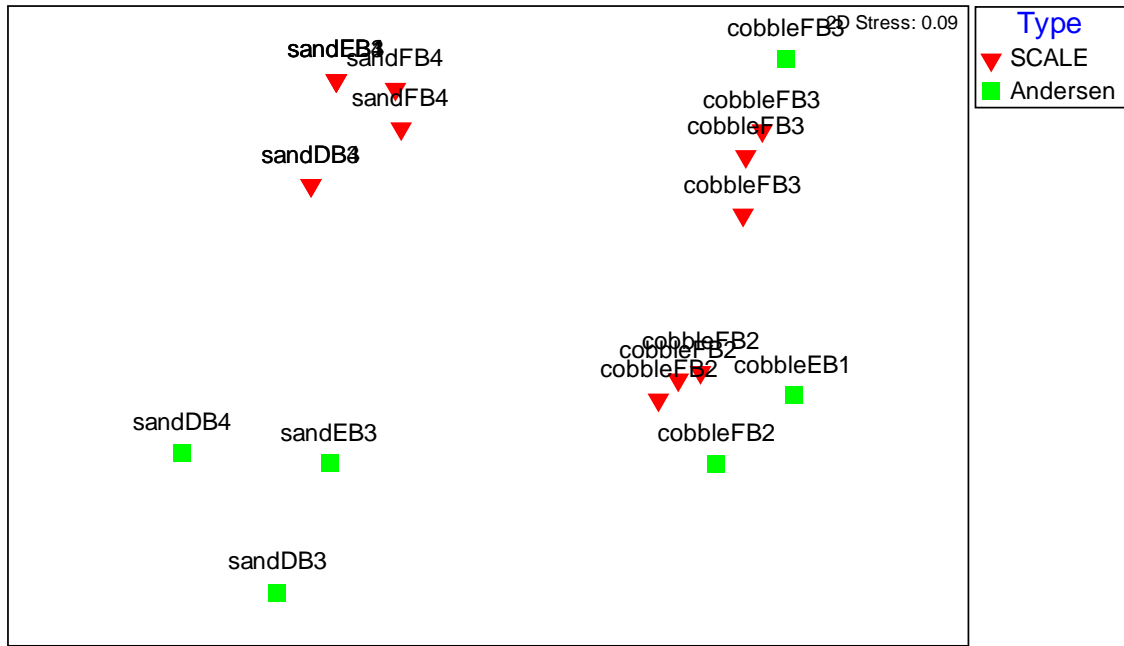


Figure 3. Non-metric multidimensional (MDS) plot of the biotic communities present at all Andersen summer sites (2011) that were also sampled by UW-DNR (2014-2016). Points closer together indicate more similar communities in terms of both species and abundances. The most upper left point comprises 3 sand sites: EB1, EB3, and EB4. The sand DB point below that comprises DB3 and DB4, with identical communities.

To perform a more informative analysis we then extracted just the data from the cobble beaches (not including Elwha Bluff 1) and ran a new MDS analysis (Figure 4).

This plot shows that the 3 years of SCALE sampling of both FB2 and FB3 were relatively similar to each other (i.e., low year-to-year variation, but substantial differences among beaches) and that each is different from the 2011 sampling effort at that site. A SIMPER analysis enumerated the taxa most responsible for the differences between 2011 and the other years. The 4 most important taxa driving these differences are oligochaetes, the amphipod *Americorophium brevis*, the small snail *Littorina sitkana*, the tiny spionid polychaete *Malacoceros gluteus*, and the gravel-loving amphipod *Paramoera bousfieldi*, all more abundant in the 2011 samples. We have found that even when using a 1-mm sieve (as we did for these samples), the SCALE sampling likely underestimates amphipod abundance and diversity (because when live-sieving, they squirm readily through even small mesh). Oligochaetes and very small polychaetes are rarely retained on 1 mm mesh when live-sieving, although some were found in our samples. Small snails that hide in crevices and among algae at low tide, such as *Littorina*, are readily under-counted in field sampling, but would be enumerated precisely in Andersen’s preserved, microscopic analyses.

Cobble Sites Only

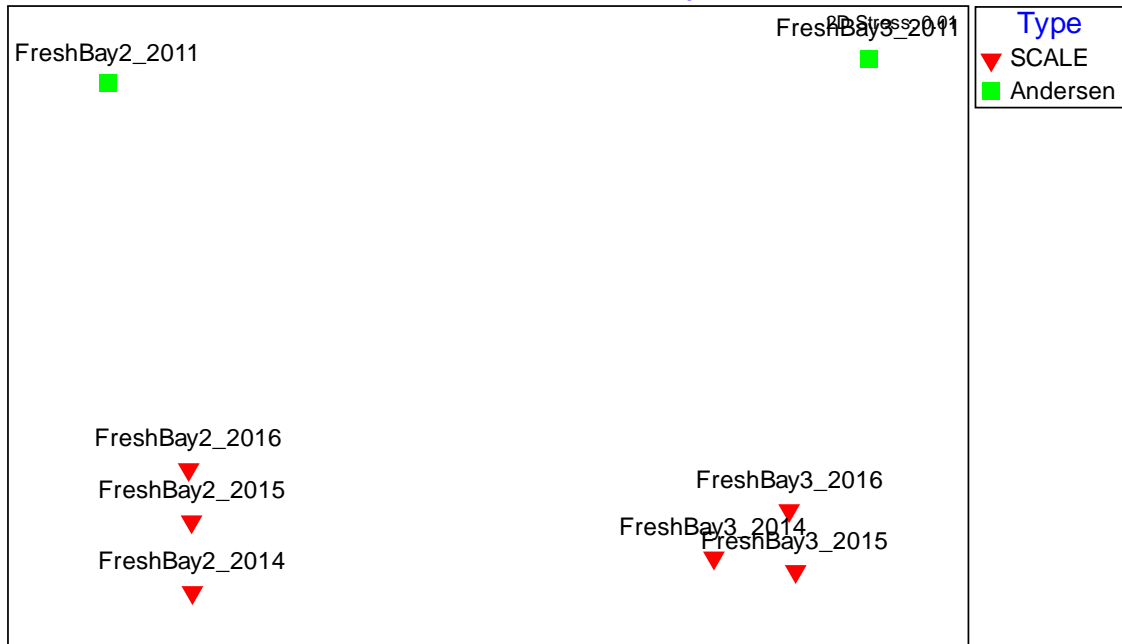


Figure 4. Non-metric multidimensional (MDS) plot of the biotic communities present at cobble sites sampled by Andersen (2011) and UW-DNR (2014-2016). Points closer together indicate more similar communities in terms of both species and abundances.

To make a more realistic comparison of communities similarly quantified with both sampling methods, we eliminated the first two species described above and reran the analysis. This had the effect of making the 2011 samples substantially more similar to the later samples (Figure 5).

Figure 5 raises the question: are the apparent differences from 2011 to 2014 and beyond a result simply of sampling differences, or might some of this ‘change’ be due to the dam removals on the Elwha? While it is not possible to answer this question definitively, it is likely that the ‘separation’ of the 2011 samples in the graph above relate largely to sampling differences. First, there is no way to make the datasets gathered with these different methods totally comparable, so that there are always likely to be differences in relative abundances, which would show up as slightly separated points in multivariate space. Second, the fact that the 2011 samples are close to the other points from the same sites shows that there are strong similarities through time. Finally and most tellingly, if dam removal was causing long-term change to the biotic communities on these cobble beaches, we would expect the points to be moving further away from the 2011 community, rather than closer through time as they have been doing for both sites. An alternative explanation is that the ‘more distant’ 2014 samples represent community change that happened in the first several years following dam removal (e.g., from sediment influx), and since 2014 the communities have been rebounding to a state more similar to their pre-

disturbance (2011) state. However, our sediment data described below (Figs. 6, 9) suggest a gradual increase since 2014 in sand abundance and impact rather than rebound from an initial pulse. Thus we conclude that to date the communities on cobble beaches in Freshwater Bay sampled before and after dam removal have changed very little, in contrast to the site closest to the river mouth (EB1) where cobble was rapidly buried by sand.

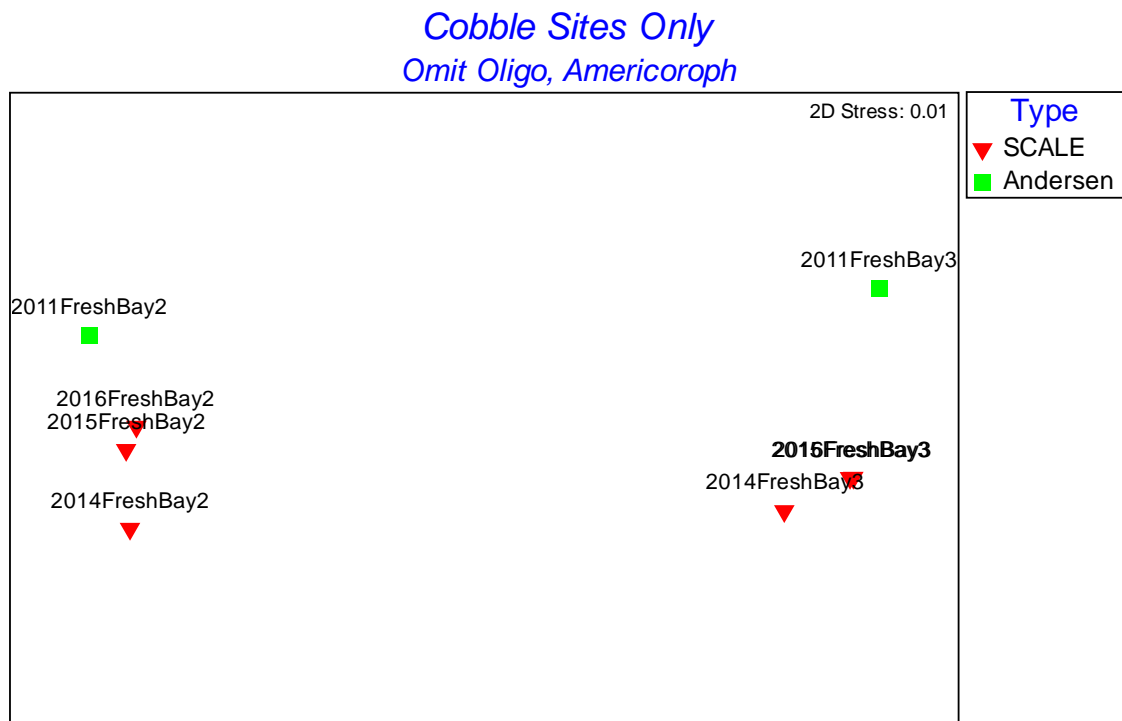


Figure 5. Non-metric multidimensional (MDS) plot of the biotic communities present at cobble sites sampled by Andersen (2011) and UW-DNR (2014-2016) omitting 2 groups of small organisms (oligochaetes and the amphipods *Americorophium*) under-sampled using SCALE methods. Points closer together indicate more similar communities in terms of both species and abundances.

2014 to 2018 SCALE Analyses

The SCALE sampling method quantifies (via visual estimation) the relative abundances of different sediment types at the surface of all quadrats. These substrate data show both the differences between the sampling sites, and the changes through time at the sites sampled more than once (Fig. 6).

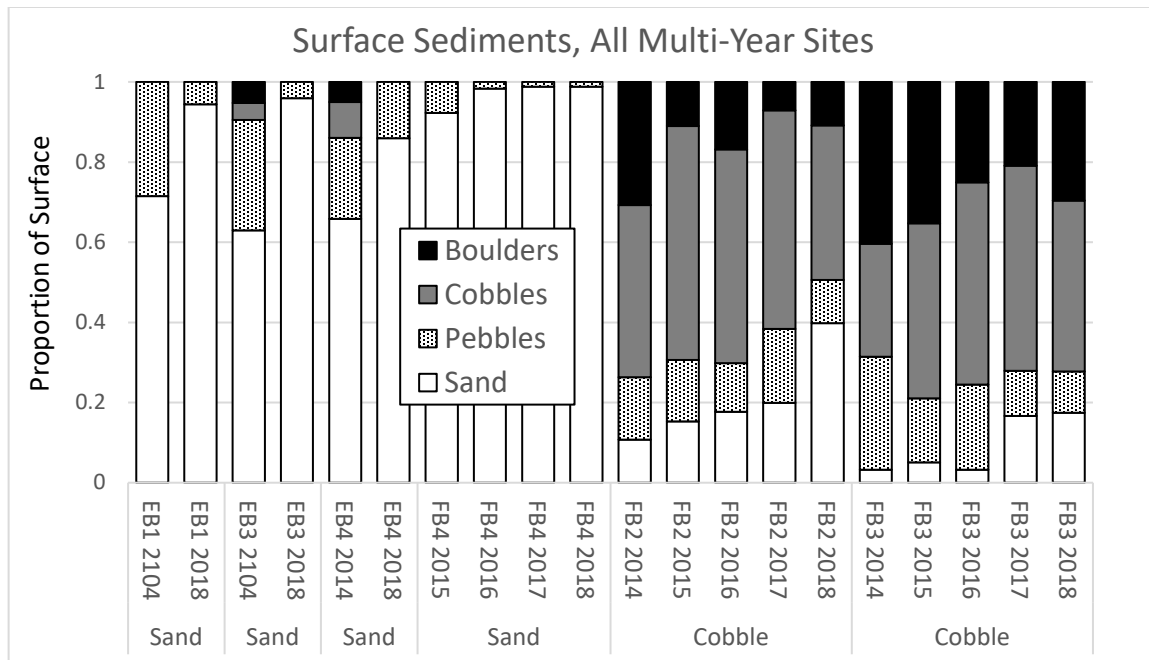


Figure 6. Surface sediment types in all sites and years sampled in more than one year with SCALE methodology, with sites categorized by dominant sediment type.

The Dungeness Bluff sites (not shown: sand and pebble-dominated) were both steep, high-energy sand-pebble beaches, as was the westernmost Elwha Bluff site (EB1). All Sand sites sampled in multiple years showed decreases in pebbles and increases in Sand between 2014 and 2018. The Cobble sites in Freshwater Bay (FB2 and FB3) showed more substantial substrate changes, with sand increasing at each site and contributing to declines in visible boulder cover.

Appendix 2 lists all taxa collected at each site. Biological communities at all sand sites were extremely depauperate. Figure 7 shows a multivariate plot of the biota from all sites and years using SCALE sampling; with the Andersen samples removed (cf. Fig. 3), the relative differences between sand and cobble communities become more striking. All the cobble sites in this analysis are in one 'location', showing great similarity relative to the sand sites. Among the sand sites, the Dungeness Bluff sites are distinct- these two transects had one individual each (among 10 samples) of the pebble-loving amphipod *Paramoera serrata*, seen nowhere else. The Elwha Bluff sites also had only one species each; this was an amphipod in EB3 and algal crusts on pebbles in EB1 and EB4. The Freshwater Bay sand site (FB4) had fewer pebbles (more sand: Fig. 6), and is less steep and experiences less wave energy than DB or EB; the transects there had 2, 4, and 1 species among the 3 sample years, almost all polychaetes. In 2015 we found two carnivorous polychaetes (a nephtyid and a syllid), in 2016 there were 3 different polychaetes plus larvae of a wrack-associated insect *Coelopa*, and in 2017 there was only a nephtyid polychaete. In 2018 we found no organisms at three of the sand sites: EB3, EB4, and FB4.

All SCALE Samples

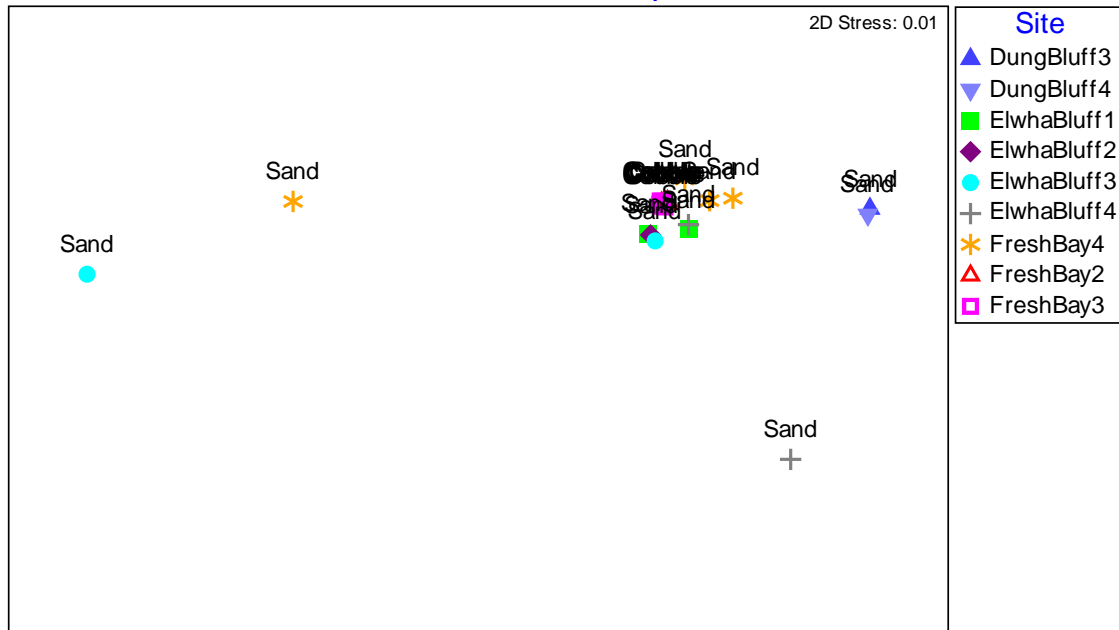


Figure 7. Non-metric multidimensional (MDS) plot of the biotic communities present at all sites sampled by UW-DNR (2014-2018). Points closer together indicate more similar communities in terms of both species and abundances.

In striking contrast, the Cobble sites had from 37 to 82 species per transect per year – a combination of surface flora and fauna on the boulders and cobbles, and infauna in the sediment beneath the cobbles. When cobble-site biota is analyzed without the sand sites, it is possible to see year-to-year as well as site-to-site differences in the communities (Figure 8).

The two Freshwater Bay sites have consistently different communities. Differences between the sites (regardless of year) were that FB2 had more macroalgae including ulvoids, *Fucus*, and *Saccharina sessilis*. Andersen, in her 2011 samples, similarly noted abundant macroalgae on the boulders and cobbles at this beach. FB2 also had more *Lacuna* snails (which consume macroalgae), tube-dwelling sabellid polychaetes, and a spionid polychaete. FB3 had more littorinid snails and limpets (which both may favor the large, stable boulders at that site) and more sphaeromid isopods.

Communities at Cobble Sites
SCALE, MLLW

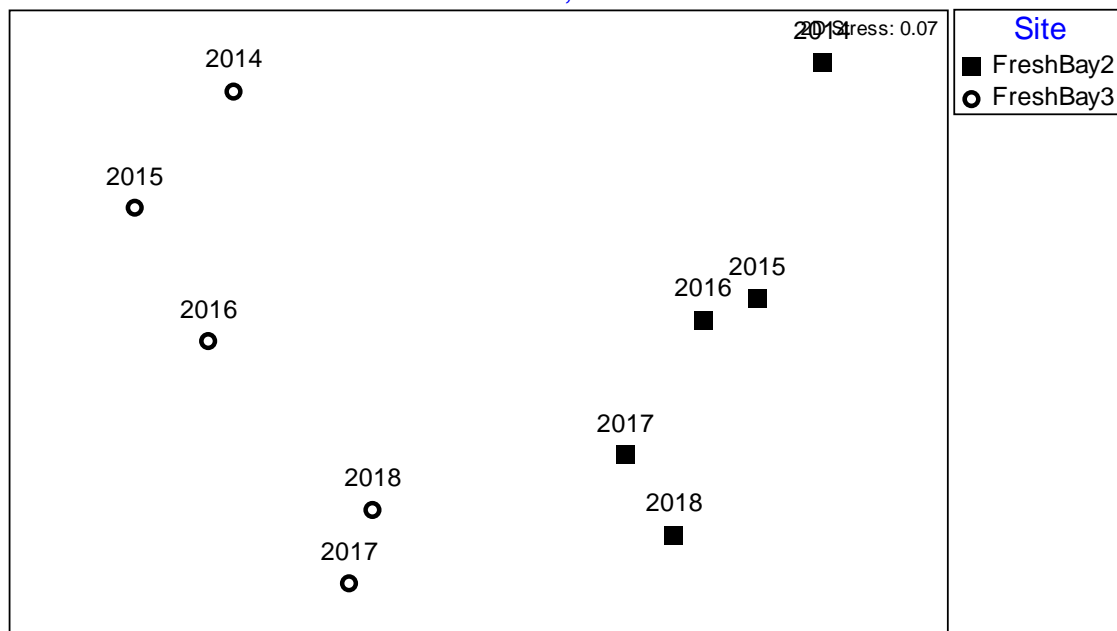


Figure 8. Non-metric multidimensional (MDS) plot of the biotic communities present at the cobble sites sampled by UW-DNR (2014-2018). Points closer together indicate more similar communities in terms of both species and abundances.

Figure 8 also shows differences among years at each of the cobble sites, with communities changing in similar ways among years (moving ‘down’ the plot in each case). The main differences from 2014 to 2018 were declines in many perennial macrophytes (*Saccharina*, *Fucus*, *Odonthalia*, and the surfgrass *Phyllospadix*) and in limpets and sedentary terebellid and sabellid polychaetes; and increases in the ephemeral algae *Porphyra*, *Acrosiphonia*, and *Chaetomorpha*, and their *Lacuna* consumers.

These changes in the dominant biota were accompanied by reductions in species richness through time in each transect (Fig. 9), and were paralleled by the increase in sand at each transect. As seen in other parts of the Salish Sea, there is a clear negative relationship between the amount of sand and the species richness in MLLW transects (Fig. 9).

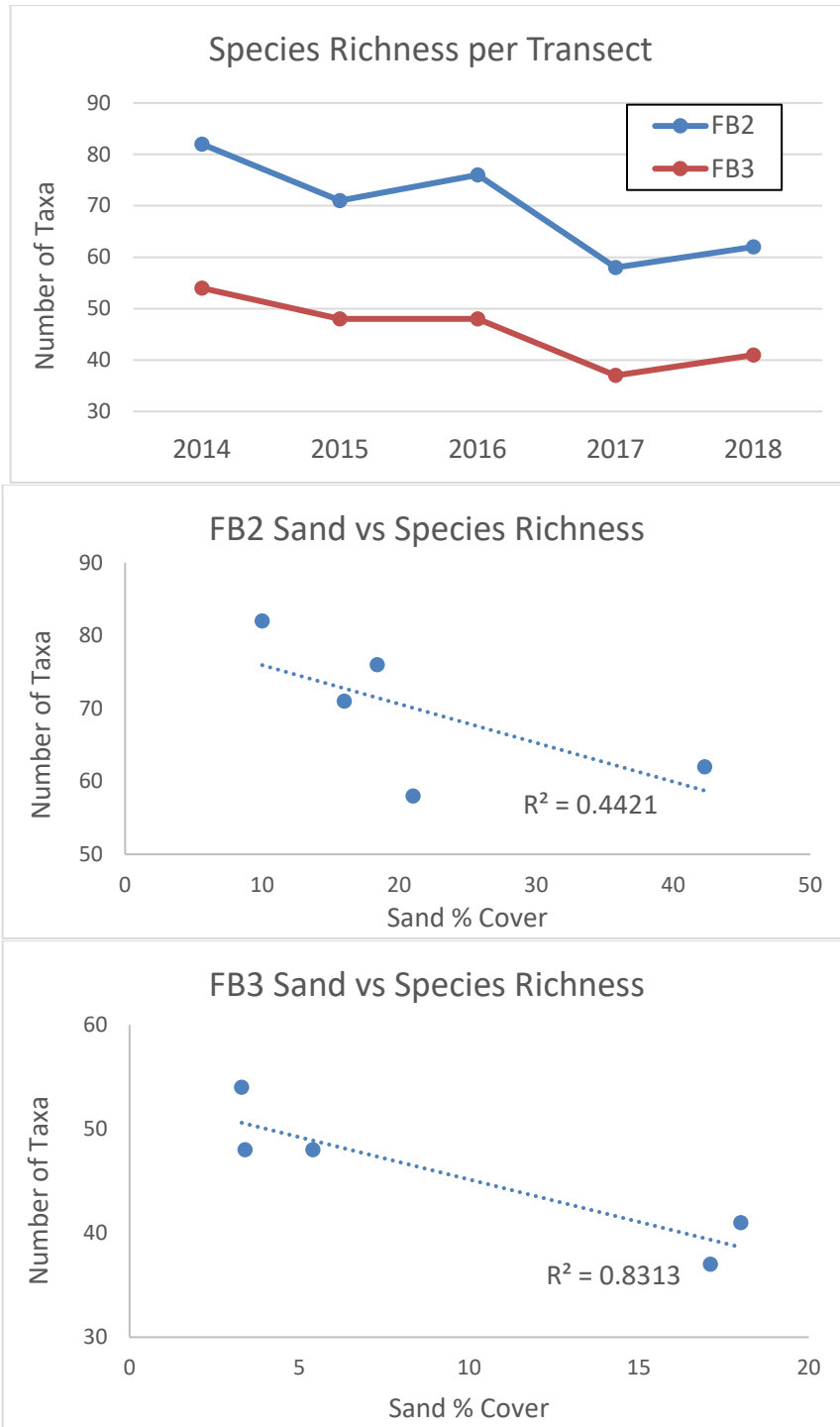


Figure 9. Patterns of species (taxa) richness at the two diverse transects in Freshwater Bay. Top panel: changes through time. Middle and lower panels: negative correlations between sand cover and taxa richness. Each point is one year's sample at that site.

Discussion

Overall, our sampling efforts in the low intertidal zone near the mouth of the Elwha River suggest that some sites have experienced influxes of sediment that have impacted the biota found there. Most of these changes have been subtle, with gradual increases in sand and decreases in sand-intolerant species in Freshwater Bay. Coarse-scale comparisons of data collected after dam removal with those of Andersen (2013) from before dam removal suggest one dramatic change, the apparent burial of boulders at the Elwha Bluffs site closest to the river mouth (EB1). This site experienced biotic change from a moderately diverse site with some epifauna (barnacles, cnidarians) and infauna (polychaetes, oligochaetes) in 2011 to a very depauperate site covered with sand and pebbles in 2014. Changes in beach sediment may have been caused by local bluff erosion or by sediment from the dam removal. The presence of abundant small, deteriorating woody debris in the intertidal zone suggests that the transformation was driven by sediment from the river. Future reports by DNR (David Parks personal communication) and Washington Sea Grant (Ian Miller, personal communication) will provide information on the spatial extent and timing of delivery of river-based sediment to beaches.

Sites in Freshwater Bay that we sampled over five years (2014 to 2018) included one sand-dominated site (FB4) and two cobble-dominated sites (FB2 and FB3); all three of these showed a trend towards an increasing proportion of sand over that time period, although the timing differed. FB4 showed a substantial decrease in pebbles and increase in sand after 2015; FB2 showed a steady increase in sand from 2014 onwards; and FB3 changed most clearly after 2016. At all three beaches we saw the highest proportion of sand in 2018. We know that sand naturally moves along Salish Sea shorelines with wind and tidally-driven currents; other sites regularly monitored (e.g., Possession Point on Whidbey Island) experience periodic sand waves without dam removals nearby. Thus we cannot prove that sand-correlated changes, such as the declines in species richness at the cobble sites, were necessarily caused by an influx of sediment following dam removals on the Elwha, although this is the most parsimonious explanation. One of these sites (FB4) clearly had a huge mass of sand deposited on the upper shore that had partly eroded at the time of our sampling in summer 2016, and non-sand-adapted vegetation species (*Pterygophora* and *Phyllospadix*) were buried by sand along the lower shore. Continued monitoring of sediments at these sites and impacts on the low-shore biota would be of interest, especially as sediment deposition and movement are a natural nearshore process and should continue now that the river is free-flowing, although at a much reduced rate. Presumably a steady-state should eventually be reached, although this is likely to be a dynamic one, i.e. with relatively unpredictable interannual variation in sand influx and corresponding biotic changes.

Rubin et al. (2017) documented marine subtidal impacts of dam removal, reporting on data linking sediment changes associated with Elwha River restoration with nearshore biotic community shifts. In the shallow subtidal zone, they found two different mechanisms of sediment-induced changes to benthic communities. Fine sediments carried down the Elwha

became suspended in marine nearshore waters as a very turbid plume; this turbidity apparently killed shallow subtidal algal communities that had otherwise been long-term dominants in this region. This reduction in primary producers continued for several years and then began to show recovery at some sites. A variety of invertebrates and fishes also showed changes at these sites, with some increasing in abundance as they benefited from the loss of algae. Different patterns were seen where suspended sediments actually became deposited on the bottom (on top of the previous gravel or sand substrate), smothering numerous benthic species including crustaceans, snails and bivalve molluscs, and echinoderms. Only a few invertebrates (cancerid crabs, burrowing anemones) and one fish species (sand lance) appeared to be truly tolerant of this deposition.

By design, some of the sites used by Rubin et al. were just offshore of our intertidal sites. In general, the changes they saw in shallow subtidal communities were much more substantial than the ones we observed intertidally. This likely can be explained by a combination of two factors: 1. Unlike subtidal algae, intertidal algae are never light-limited and thus are not expected to suffer from turbidity-induced loss of photosynthetic capacity. If they were buried beneath sediment or heavily scoured, they would decline in abundance, and this may have been the cause of some of the macrophyte losses from 2014 to 2017 at the Freshwater Bay cobble sites. 2. Regardless of riverine sediments, the algal and invertebrate communities in the intertidal zone along this shoreline likely have always been those that can tolerate both wave energy and sand movement. Even before removal of the dams, these sites had substantial amounts of sand, and such sediment tends to move both onto and off the beach and along the shore on an annual basis. Many of the algae (e.g. *Neorhodomela*, *Ahnfeltiopsis*) and some of the invertebrates (e.g. *Anthopleura* spp. anemones) actually are most commonly found on sand-impacted rocks, i.e. they have evolved to deal with this disturbance.

Thus in the absence of a major sediment deposition event that covers the low shore and remains for months (which would kill even sand-adapted species), the intertidal organisms found at the cobble-sand sites near the mouth of the Elwha are likely to survive well under the new riverine regime. Sites where there is a regular sediment supply (from the river or eroding bluffs) and where that sediment is not rapidly swept away by waves and currents are likely to be sand- or pebble-dominated, with relatively few macroscopic species in the low shore. These high-energy sand beaches have too little primary productivity to support a local food web, and the substrate is too unstable for most invertebrates. Sites where cobbles dominate the low shore because there is either limited sand supply or sand is only present for short time periods should continue to have much higher primary productivity (from annual and perennial algae on the cobbles) and animal species richness from species living on or under the cobbles or in the sediment beneath them.



Figure 10. Sand accumulation at FB4, in the backshore (top) and lower intertidal burying *Pterygophora* and *Phyllospadix* (bottom).

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Appendices

Appendix 1. Summary table of taxa from each set of studies that are likely to be under-represented in one or the other set of samples.

Species	Not sampled in 2011 by Andersen	Likely to be missed in 2014-2017
<i>Achelia chelata</i>		x
<i>Achelia nudiuscula</i>		x
<i>Allorchestes angusta</i>		
<i>Americorophium brevis</i>		
<i>Amphiodia</i> spp		
<i>Ampithoe</i> sp.		
Anemones (preserved)		x
<i>Anthopleura elegantissima</i>		
<i>Aoroides ?columbiae</i>		
<i>Aphelochaeta multifilis</i>		
<i>Armandia brevis</i>		
<i>Asabellides sibirica</i>		
<i>Boccardiella hamata</i>		
Boulder percentage	x	
<i>Branchiomaldane</i> sp.		
Bryozoa (miscellaneous)	x	
<i>Cancer oregonensis</i>		
<i>Capitella capitata</i>		
<i>Caulleriella ?pacifica</i>		
<i>Cirratulus cingulatus/robustus</i>		
<i>Cirratulus multioculatus</i>		
Cobble percentage	x	
<i>Cumella vulgaris</i>		
Dead barnacles (Class Cirripedia)	x	
<i>Eobrolgus chumashi</i>		
<i>Epiactis prolifera</i>	x	
<i>Eteone</i> spp.		
<i>Euclymene</i> spp.		
<i>Euphilomedes</i> spp.		x
<i>Exogone</i> and similar syllids		x
<i>Exosphaeroma amplicauda</i>		
Family Hesionidae		
Family Nereidae		
Family Terebellinae		

Species	Not sampled in 2011 by Andersen	Likely to be missed in 2014-2017
Flatworm (unident.)		
Gammarid amphipods	x	
<i>Glycinde picta</i>		
<i>Gnorimosphaeroma oregonense</i>		
Gobiesocidae (clingfish)		
<i>Halosydna brevisetosa</i>		
<i>Harmothoe imbricata</i>		
<i>Harrimania?</i>		
<i>Hemigrapsus nudus</i>	x	
<i>Hemigrapsus</i> spp.		
<i>Hemipodus borealis</i>		
<i>Hermisenda crassicornis</i>		
<i>Ianiropsis kincaidi</i>		
<i>Ianiropsis</i> sp.		
<i>Idotea</i> sp.		
<i>Idotea vosnesenskii</i>		x
Insect larvae (chironomids)		x
<i>Lacuna</i> spp.		
<i>Lamprops carinata</i>		x
<i>Lepidochitona dentiens</i>		
<i>Leptasterias hexactis</i>		
<i>Leptochelia dubia</i>		
<i>Leptosynapta clarki</i>		
<i>Leukoma staminea</i> juv.		
<i>Lirabuccinum dirum</i>		
<i>Lirularia</i> sp.		
<i>Littorina scutulata</i>		
<i>Littorina sitkana</i>		
Live barnacles (Class Cirripedia)	x	
<i>Lottia fenestrata</i>		x
<i>Lottia pelta</i>		x
<i>Lottia scutum</i>		x
<i>Lottia</i> spp. Juveniles		x
Lottid limpets		
<i>Lumbrineris zonata</i>		
<i>Macoma inquinata</i>		
<i>Macoma inquinata</i> juv.		

Species	Not sampled in 2011 by Andersen	Likely to be missed in 2014-2017
Majid (spider) crab		
<i>Malacoceros glutaesus</i>		
<i>Mediomastus californiensis</i>		
<i>Megalorchestia pugettensis</i>		
<i>Mooreonuphis stigmatus</i>		
<i>Mopalia lignosa</i>		
<i>Mopalia muscosa</i>		
<i>Mysella tumida</i>		
<i>Mytilus trossulus</i> juvenile		
<i>Naineris dendritica</i>		
<i>Nebalia pugettensis</i>		x
Nematodes		x
Nemertean (unident.)		
<i>Nereis procera</i>		
<i>Nereis vexillosa</i>		
<i>Notomastus tenuis</i>		
<i>Nucella lamellosa</i>		
<i>Nucella ostrina</i>		
<i>Nucella</i> sp.		
Oligochaetes		x
<i>Pagurus ?hirsutiusculus</i>		
<i>Pagurus</i> spp.		
<i>Paracalliopiella pratti</i>		
<i>Parallorchestes cowani</i>		
<i>Paramoera bousfieldi</i>		
<i>Paramoera serrata</i>		
Pebble percentage	x	
<i>Photis</i> spp.		
<i>Phoxichilidium femoratum</i>		x
<i>Phyllodoce</i> spp.		
Piddock clam (unident.)	x	
<i>Pinnixia schmitti/occidentalis</i>		
<i>Pisaster ochraceus</i> juvenile		
<i>Platynereis bicanaliculata</i>		
<i>Podarke pugettensis</i>		
<i>Polycirrus</i> n. sp. (L. Harris)		
<i>Polydora cardalia</i>		

Species	Not sampled in 2011 by Andersen	Likely to be missed in 2014- 2017
<i>Polydora columbiana</i>		
<i>Polydora proboscidea</i>		
Polynoid (unident., in quadrat)	x	
<i>Pontogeneia ivanovi</i>		
<i>Potamilla</i> sp.		
<i>Protohyale oclairi</i>		
<i>Pugettia</i> sp. Juvenile		
Pycnogonid		
<i>Rochefortia tumida</i>		
Sabellid (unident.)	x	
Sand percentage	x	
<i>Schizobranchia insignis</i>		
Sipunculids (unident.)		
<i>Sphaerodoropsis minuta</i>		
Sphaeromid isopods	x	
<i>Spio filicornis</i>		
Sponge, unidentified		
Stauromedusae		
Stichaeidae (gunnels and pricklebacks)		
Syllids (unident.)(incl. stewarti, heterochaeta)	x	
<i>Thelepus crispus</i>		
<i>Tonicella</i> sp. (unident)		
<i>Transennella tantilla</i>		
<i>Tresus capax</i> juveniles		
<i>Typosyllis</i> spp.		x

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	DB3	DB3	DB4	DB4	EB1	EB1	EB1	EB2	EB3	EB3	EB3	EB4
	2011	2014	2010	2014	2011	2014	2018	2018	2011	2014	2018	2014
<i>Achelia chelata</i>												
<i>Achelia nudiuscula</i>					2							
<i>Acrosiphonia</i> spp.												
<i>Ahnfeltia fastigiata</i>												
<i>Alia</i> spp.												
<i>Allorchestes angusta</i>					2							
<i>Americorophium brevis</i>					5							
<i>Amphiodia</i> spp.												
<i>Ampithoe dalli</i>												
<i>Ampithoe</i> spp.												
Anemones (preserved)					1							
<i>Anthopleura artemisia</i>												
<i>Anthopleura elegantissima</i>												
<i>Aoroides ?columbiae</i>					1							
<i>Aphelochaeta multifilis</i>	17											
<i>Arabella semimaculata</i>												
<i>Armandia brevis</i>					4							
<i>Asabellides sibirica</i>												
<i>Axiothella rubrocincta</i>												
<i>Boccardiella hamata</i>												
<i>Bossiella</i> spp.												
Boulder percentage										50		15
<i>Branchiomaldane</i> spp.					11							
Bryozoa (miscellaneous)												
<i>Callophyllis</i> spp.												
<i>Cancer magister</i>												
<i>Cancer oregonensis</i>												
<i>Cancer</i> spp. Juvenile												
<i>Capitella capitata</i>												
<i>Cauleriella ?pacifica</i>												
<i>Chaetomorpha</i> spp.												
<i>Cirratulus cingulatus/robustus</i>					10							
<i>Cirratulus multioculatus</i>												
<i>Clinocardium nuttallii</i> juveniles												
Cobble percentage										20		13
<i>Coelopa</i> spp.												
Cottidae (sculpins)												
<i>Crepidula adunca</i>												
Crust, coralline												
Crust, fleshy						1						5
<i>Cryptosiphonia woodii</i>												
<i>Cumella vulgaris</i>												
Dead barnacles (Class Cirripedia)												
<i>Desdimelita desdichada</i>												
<i>Desmarestia</i> spp.												

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	DB3	DB3	DB4	DB4	EB1	EB1	EB1	EB2	EB3	EB3	EB3	EB4
	2011	2014	2010	2014	2011	2014	2018	2018	2011	2014	2018	2014
Diatoms, chain-forming												
<i>Egregia menziesii</i>												
<i>Eobrolgus chumashi</i>					17							
<i>Epiactis prolifera</i>												
<i>Eteone</i> spp.					3							
<i>Euclymene</i> spp.												
<i>Eulalia</i> spp.												
<i>Euphilomedes</i> spp.												
<i>Evasterias troschelii</i>												
<i>Exogone</i> and similar syllids												
<i>Exosphaeroma amplicauda</i>					5							
<i>Exosphaeroma inornata</i>												
<i>Exosphaeroma</i> spp.												
Family Hesionidae					4							
Family Nereidae					4							
Family Terebellinae												
<i>Farlowia mollis</i>												
Flatworm									27			
<i>Foxiphalus falciformis</i>												
<i>Fucus gardneri</i>												
Gammarid amphipods							6	2		1		
<i>Gelidium</i> spp.												
<i>Glycinde picta</i>												
<i>Gnathopleustes pugettensis</i>												
<i>Gnorimosphaeroma oregonense</i>					14							
Gobiesocidae (clingfish)												
Green filaments												
Gunnel												
<i>Halosaccion glandiforme</i>												
<i>Halosydna brevisetosa</i>												
<i>Harmothoe imbricata</i>					5							
<i>Harrimania?</i>												
<i>Hemigrapsus nudus</i>												
<i>Hemigrapsus oregonensis</i>												
<i>Hemigrapsus</i> spp.												
<i>Hemipodus borealis</i>					79							
<i>Hermisenda crassicornis</i>												
<i>Ianiropsis kincaidi</i>					1							
<i>Ianiropsis</i> spp.												
<i>Idotea</i> spp.												
<i>Idotea vosnesenskii</i>					1							
Insect larvae (chironomids)					2							
<i>Katarina tunicata</i>												
<i>Lacuna</i> spp.					49							
<i>Lamprops carinata</i>					1							

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	DB3	DB3	DB4	DB4	EB1	EB1	EB1	EB2	EB3	EB3	EB3	EB4
	2011	2014	2010	2014	2011	2014	2018	2018	2011	2014	2018	2014
<i>Lepidochitona dentiens</i>												
<i>Leptasterias hexactis</i>												
<i>Leptocheilia dubia</i>												
<i>Leptosynapta clarki</i>												
<i>Leukoma staminea</i> juv.												
<i>Lirabuccinum dirum</i>												
<i>Lirularia</i> spp.												
<i>Littorina scutulata</i>												
<i>Littorina sitkana</i>												
Live barnacles (Class Cirripedia)												
<i>Lottia fenestrata</i>					2							
<i>Lottia pelta</i>												
<i>Lottia scutum</i>												
<i>Lottia</i> spp. Juveniles					1							
Lottid limpets												
<i>Lumbrineris zonata</i>					5							
<i>Macoma inquinata</i>												
<i>Macoma inquinata</i> juv.												
Majid (spider) crab												
Majid juvenile crab												
<i>Malacoceros glutaesus</i>					164							
<i>Mastocarpus jardinii</i>												
<i>Mastocarpus papillatus</i>												
<i>Mazzaella heterocarpa/oregona</i>												
<i>Mazzaella splendens</i>												
<i>Mediomastus californiensis</i>					6							
<i>Megalorchestia pugettensis</i>					5		2	1				
<i>Metridium</i> spp.												
<i>Microcladia borealis</i>												
<i>Monocorophium</i> spp.												
<i>Mooreonuphis stigmatus</i>												
<i>Mopalia lignosa</i>												
<i>Mopalia muscosa</i>												
<i>Mytilus californianus</i>												
<i>Mytilus trossulus</i> juvenile					1							
<i>Naineris dendritica</i>												
<i>Naineris uncinata</i>												
<i>Nebalia pugettensis</i>												
Nematodes					10							
Nemertean (unident.)					5							
<i>Neorhodomela oregona</i>												
<i>Nephtys longosetosa</i>												
<i>Nereis procer</i>												
<i>Nereis vexillosa</i>					15							
<i>Notomastus tenuis</i>												

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	DB3	DB3	DB4	DB4	EB1	EB1	EB1	EB2	EB3	EB3	EB3	EB4
	2011	2014	2010	2014	2011	2014	2018	2018	2011	2014	2018	2014
<i>Nucella canaliculata</i>												
<i>Nucella lamellosa</i>												
<i>Nucella ostrina</i>												
<i>Nucella</i> spp.												
<i>Nutricola lordi</i>												
<i>Odonthalia floccosa</i>												
Oligochaetes					1				15			
<i>Owenia fusiformis</i>												
<i>Pagurus ?hirsutiussculus</i>					1							
<i>Pagurus</i> spp.												
<i>Paracalliopiella pratti</i>												
<i>Parallorchestes cowani</i>												
<i>Paramoera bousfieldi</i>												
<i>Paramoera serrata</i>	5	1	8	1					8			
<i>Paramoera suchaneki</i>												
Pebble percentage		22		35		29	6	30		26	6	20
<i>Petalonia fascia</i>												
<i>Petrolisthes</i> spp.												
<i>Pherusa plumosa</i>												
<i>Phoronopsis harmeri</i>												
<i>Photis</i> spp.					1							
<i>Phoxichilidium femoratum</i>												
<i>Phyllodoce</i> spp.												
<i>Phyllospadix scoleri</i>												
<i>Phyllospadix serrulatus</i>												
Piddock clam												
<i>Pinnixia schmitti/occidentalis</i>					5							
<i>Pisaster ochraceus</i> juvenile												
<i>Platynereis bicanaliculata</i>					7							
<i>Podarke pugettensis</i>												
<i>Podarkeopsis glabrus</i>												
<i>Polycirrus</i> n. spp. (L. Harris)												
<i>Polydora cardalia</i>												
<i>Polydora columbiana</i>					2							
<i>Polydora proboscidea</i>					10							
Polynoid (in quadrat)												
<i>Polysiphonia</i> spp.												
<i>Pontogeneia ivanovi</i>					14							
<i>Porphyra</i> spp.												
<i>Potamilla</i> spp.												
<i>Prionitis</i> spp.												
<i>Prionospio steenstrupi</i>												
<i>Protohyale oclairi</i>					1							
<i>Pugettia</i> spp.												
<i>Pugettia</i> spp. Juvenile												

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	DB3	DB3	DB4	DB4	EB1	EB1	EB1	EB2	EB3	EB3	EB3	EB4
	2011	2014	2010	2014	2011	2014	2018	2018	2011	2014	2018	2014
Pycnogonid												
<i>Rochefortia tumida</i>												
Sabellid (unident.)												
<i>Saccharina sessilis</i>												
<i>Saccharina</i> spp.												
Sand percentage		78		64		72	94	71		60	97	66
<i>Saxidomus giganteus</i> juv.												
<i>Schizobranchia insignis</i>												
<i>Scolelepis squamata</i>												
<i>Scytosiphon simplicissimus</i>												
Sipunculids					5							
<i>Smithora naiadum</i>												
<i>Soranthera ulvoidea</i>												
<i>Sphaerodoropsis minuta</i>												
Sphaeromid isopods												
<i>Spio filicornis</i>												
Sponge, unidentified												
Stauromedusae					9							
<i>Stichaeidae</i>												
<i>Streblosoma</i> spp.												
Syllids					30							
<i>Thelepus crispus</i>												
<i>Tonicella</i> spp.												
<i>Transennella tantilla</i>												
<i>Traskorchestia</i> spp.												
<i>Traskorchestia traskiana</i>												
<i>Tresus capax</i>												
<i>Tresus capax</i> juveniles												
<i>Typosyllis</i> spp.												
Ulvoids												
<i>Urticina</i> spp.												
<i>Zirfaea pilysbryi</i> juvenile												
<i>Zostera marina</i>												

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	EB4	FB2	FB2	FB2	FB2	FB2	FB2	FB3	FB3	FB3	FB3	FB3
	2018	2011	2014	2015	2016	2017	2018	2011	2014	2015	2016	2017
<i>Achelia chelata</i>		2		1								
<i>Achelia nudiuscula</i>												
<i>Acrosiphonia</i> spp.			10	4	11	13	19		4	1	13	31
<i>Ahnfeltia fastigiata</i>			1	4		1	1			15	1	
<i>Alia</i> spp.										2		
<i>Allorchestes angusta</i>					1			1				
<i>Americorophium brevis</i>								143				
<i>Amphiodia</i> spp.		5	1		1		1					
<i>Ampithoe dalli</i>					1		1					
<i>Ampithoe</i> spp.		11										
Anemones (preserved)		8										
<i>Anthopleura artemisia</i>							1					
<i>Anthopleura elegantissima</i>			3	5	4	6	5		1		2	5
<i>Aoroides ?columbiae</i>												
<i>Aphelochaeta multifilis</i>		13		1	1		1					
<i>Arabella semimaculata</i>				1								
<i>Arandia brevis</i>		15		1	2							
<i>Asabellides sibirica</i>		4										
<i>Axiothella rubrocincta</i>							2	3				1
<i>Boccardiella hamata</i>			2									
<i>Bossiella</i> spp.			2	3	1				1			
Boulder percentage			35	29	44	15	29		46	38	29	24
<i>Branchiomaldane</i> spp.		43	2	2	2	1	1	3	3	1	2	
Bryozoa (miscellaneous)			3	4					3			
<i>Callophyllis</i> spp.			1	1								1
<i>Cancer magister</i>							1					
<i>Cancer oregonensis</i>			1									
<i>Cancer</i> spp. Juvenile				1		1						
<i>Capitella capitata</i>		13	2		1			10				
<i>Caulerella ?pacifica</i>			2									
<i>Chaetomorpha</i> spp.				17	6	10				3	6	7
<i>Cirratulus cingulatus/robustus</i>		13		3								
<i>Cirratulus multioculatus</i>			2									
<i>Clinocardium nuttallii</i> juveniles				1			1					
Cobble percentage			44	61	56	64	51		29	47	54	53
<i>Coelopa</i> spp.												
Cottidae (sculpins)										1		
<i>Crepidula adunca</i>										1		
Crust, coralline			1	2	3		1			3	1	
Crust, fleshy			36	32	13	23	17		9	8	8	16
<i>Cryptosiphonia woodii</i>			2		2	8	1					
<i>Cumella vulgaris</i>		54						3				
Dead barnacles (Class Cirripedia)			1	1	2	2	2		1	4	1	1
<i>Desdimelita desdichada</i>					1							
<i>Desmarestia</i> spp.				1								

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	EB4	FB2	FB2	FB2	FB2	FB2	FB2	FB3	FB3	FB3	FB3	FB3
	2018	2011	2014	2015	2016	2017	2018	2011	2014	2015	2016	2017
Diatoms, chain-forming			6	4	11	5	1		5	8	5	4
<i>Egorgia menziesii</i>			10									
<i>Eobrolgus chumashi</i>		34	4	2	1	1						
<i>Epiactis prolifera</i>									1	1		
<i>Eteone</i> spp.		3	1	1	1							
<i>Euclymene</i> spp.			2	2	4							
<i>Eulalia</i> spp.						1						
<i>Euphilomedes</i> spp.		7										
<i>Evasterias troschelii</i>						1						
<i>Exogone</i> and similar syllids		64										
<i>Exosphaeroma amplicauda</i>		100				4	1					
<i>Exosphaeroma inornata</i>					2							
<i>Exosphaeroma</i> spp.				4								
Family Hesionidae		1										
Family Nereidae		19										
Family Terebellinae		68										
<i>Farlowia mollis</i>									1	7	4	2
Flatworm									1			
<i>Foxiphalus falciformis</i>							1					
<i>Fucus gardneri</i>			21	11	3	12	9		1	3		
Gammarid amphipods				8	2	2	5		30	18		
<i>Gelidium</i> spp.				1		1						
<i>Glycinde picta</i>			1								1	
<i>Gnathopleustes pugettensis</i>					1							
<i>Gnorimosphaeroma oregonense</i>							1	138	5	6	7	1
Gobiesocidae (clingfish)									1		2	1
Green filaments			7									
Gunnel					1						1	
<i>Halosaccion glandiforme</i>			1	1	1	1	1		1	1	1	
<i>Halosydna brevisetosa</i>		12	3	2	2		1		1			
<i>Harmothoe imbricata</i>		4						4				
<i>Harrimania?</i>			1				1					
<i>Hemigrapsus nudus</i>					2				1	3	6	2
<i>Hemigrapsus oregonensis</i>							1			1	3	1
<i>Hemigrapsus</i> spp.								5				
<i>Hemipodus borealis</i>			1	0	2	1	1		1	1	2	1
<i>Hermisenda crassicornis</i>									1			
<i>Ianiropsis kincaidi</i>		9						34				
<i>Ianiropsis</i> spp.									1			
<i>Idotea</i> spp.			1	2	2	1			1	1	20	2
<i>Idotea wosnesenskii</i>		15			1			7				
Insect larvae (chironomids)		88						6				
<i>Katarina tunicata</i>				1						1		
<i>Lacuna</i> spp.		197	19	46	29	39	39	1	9	5	5	48
<i>Lamprops carinata</i>												

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	EB4	FB2	FB2	FB2	FB2	FB2	FB2	FB3	FB3	FB3	FB3	FB3
	2018	2011	2014	2015	2016	2017	2018	2011	2014	2015	2016	2017
<i>Lepidochitona dentiens</i>		2	2	1	1					1		
<i>Leptasterias hexactis</i>		1	1	1	1	2	1		1	1		
<i>Leptocheilia dubia</i>		4	2	1	1							
<i>Leptosynapta clarki</i>		4	2	1	2							
<i>Leukoma staminea</i> juv.			1		1		1					
<i>Lirabuccinum dirum</i>									2	2	6	2
<i>Lirularia</i> spp.		5										
<i>Littorina scutulata</i>								28		1	1	
<i>Littorina sitkana</i>								139	17	24	13	1
Live barnacles (Class Cirripedia)			4	12	16	9	10		6	11	9	5
<i>Lottia fenestrata</i>								17				
<i>Lottia pelta</i>		1						2				
<i>Lottia scutum</i>								8				
<i>Lottia</i> spp. Juveniles												
Lottid limpets			11	2	5	7	8		23	26	13	7
<i>Lumbrineris zonata</i>		126		2	4	3	4			1	1	
<i>Macoma inquinata</i>							1		1			
<i>Macoma inquinata</i> juv.		15		1	1						1	
Majid (spider) crab			3			1						
Majid juvenile crab				2								
<i>Malacoceros glutaesus</i>		211	2	4	4	2			1		1	
<i>Mastocarpus jardinii</i>			3						3			
<i>Mastocarpus papillatus</i>				8	10	9	3			5	4	9
<i>Mazzaella heterocarpa/oregona</i>						3					5	
<i>Mazzaella splendens</i>			7	7	10	1	3		2	9	5	13
<i>Mediomastus californiensis</i>		30		2	2							
<i>Megalorchestia pugettensis</i>												
<i>Metridium</i> spp.					1	1					1	1
<i>Microcladia borealis</i>			4	1	6				2	5	8	
<i>Monocorophium</i> spp.											1	
<i>Mooreonuphis stigmatus</i>			4	1	2	1	2	5	1	1		
<i>Mopalia lignosa</i>			1		2	1	1			1	1	
<i>Mopalia muscosa</i>		1	1	2	2	2	2					
<i>Mytilus californianus</i>											5	
<i>Mytilus trossulus</i> juvenile		42										
<i>Naineris dendritica</i>		17	4	3	2	1		5				
<i>Naineris uncinata</i>				1								
<i>Nebalia pugettensis</i>		4		1	1							
Nematodes		32		1								
Nemertean (unident.)		23	1	1	1	1	2		1	1		1
<i>Neorhodomela oregona</i>			5	30	23	2	3		15	7	12	6
<i>Nephtys longosetosa</i>												
<i>Nereis procera</i>			1									
<i>Nereis vexillosa</i>				1	1	1	1	6	1	1	0	1
<i>Notomastus tenuis</i>		78	4	1	2	2	2		2	1	3	

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	EB4	FB2	FB2	FB2	FB2	FB2	FB2	FB3	FB3	FB3	FB3	FB3
	2018	2011	2014	2015	2016	2017	2018	2011	2014	2015	2016	2017
<i>Nucella canaliculata</i>												2
<i>Nucella lamellosa</i>			2	2	3	5	2			11	3	2
<i>Nucella ostrina</i>								8			5	
<i>Nucella</i> spp.			1									
<i>Nutricola lordi</i>						1	2					
<i>Odonthalia floccosa</i>			18	5	3	1	2		1	3	3	3
Oligochaetes		82		3	1			227			15	
<i>Owenia fusiformis</i>						1						
<i>Pagurus ?hirsutiusculus</i>		3						3				
<i>Pagurus</i> spp.			4	18	6	3	3		3	14	6	3
<i>Paracalliopiella pratti</i>		7			3							
<i>Parallorchestes cowani</i>		19										
<i>Paramoera bousfieldi</i>								92		1		
<i>Paramoera serrata</i>												
<i>Paramoera suchaneki</i>											1	
Pebble percentage	15		16	16	16	22	16		29	17	23	12
<i>Petalonia fascia</i>			2	1	1				1	5	1	
Petrolisthes spp.					1							
<i>Pherusa plumosa</i>				1	1							
<i>Phoronopsis harmeri</i>							1					
<i>Photis</i> spp.												
<i>Phoxichilidium femoratum</i>		2										
<i>Phyllodoce</i> spp.			1	1								
<i>Phyllospadix scoleri</i>							75				1	
<i>Phyllospadix serrulatus</i>			15						25			75
Piddock clam									1			
<i>Pinnixia schmitti/occidentalis</i>		5			1							
<i>Pisaster ochraceus</i> juvenile		1										
<i>Platynereis bicanaliculata</i>		45	2		1							
<i>Podarke pugettensis</i>			1		1							
<i>Podarkeopsis glabrus</i>				1								
<i>Polycirrus</i> n. spp. (L. Harris)			2		1							
<i>Polydora cardalia</i>			13	18	2							
<i>Polydora columbiana</i>		3	2	4			2		1			
<i>Polydora proboscidea</i>												
Polynoid (in quadrat)			1	1	3				1			
<i>Polysiphonia</i> spp.			10	5	12	16	13		6	26	23	23
<i>Pontogeneia ivanovi</i>		9			1				2			
<i>Porphyra</i> spp.			1	3	6	17	6		4	6	10	53
<i>Potamilla</i> spp.		2	2									
<i>Prionitis</i> spp.					1				1	5	1	1
<i>Prionospio steenstrupi</i>				1								
<i>Protohyale oclairi</i>		109	2	1			3	2				
<i>Pugettia</i> spp.					1							
<i>Pugettia</i> spp. Juvenile		3										

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	EB4	FB2	FB2	FB2	FB2	FB2	FB2	FB3	FB3	FB3	FB3	FB3
	2018	2011	2014	2015	2016	2017	2018	2011	2014	2015	2016	2017
Pycnogonid			1									
<i>Rochefortia tumida</i>		1	2	3	4	1	3					
Sabellid (unident.)			19	10	24	9	2					
<i>Saccharina sessilis</i>			39	15	15		3					
<i>Saccharina</i> spp.						1						
Sand percentage	90		11	16	18	21	42		4	5	3	17
<i>Saxidomus giganteus</i> juv.											1	
<i>Schizobranchia insignis</i>		5										
<i>Scolelepis squamata</i>					2							
<i>Scytosiphon simplicissimus</i>			1		1	1						
Sipunculids												
<i>Smithora naiadum</i>												50
<i>Soranothera ulvoidea</i>			1									
<i>Sphaerodoropsis minuta</i>		1	1									
Sphaeromid isopods				17		6			19	29	12	13
<i>Spio filicornis</i>			1									
Sponge, unidentified			0	1	1		1					
Stauromedusae		1										
<i>Stichaeidae</i>			1	1		1	1		1			
<i>Streblosoma</i> spp.							3					
Syllids			1	2			1		1			
<i>Thelepus crispus</i>		21	11	4	2	1	1			1	1	1
<i>Tonicella</i> spp.			1									
<i>Transennella tantilla</i>		47	2	2	4							
<i>Traskorchestia</i> spp.							2					
<i>Traskorchestia traskiana</i>				2								
<i>Tresus capax</i>				1		1						
<i>Tresus capax</i> juveniles		19	3	1	1	3	3		2			
<i>Typosyllis</i> spp.		62			2	1		20				
Ulvoids			28	75	80	68	42		23	6	24	32
<i>Urticina</i> spp.				3	1	5	1					
<i>Zirfaea pilysbryi</i> juvenile												
<i>Zostera marina</i>									1			

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	FB3	FB4	FB4	FB4	FB4
	2018	2015	2016	2017	2018
<i>Achelia chelata</i>					
<i>Achelia nudiuscula</i>					
<i>Acrosiphonia</i> spp.	43				
<i>Ahnfeltia fastigiata</i>	1				
<i>Alia</i> spp.					
<i>Allorchestes angusta</i>					
<i>Americorophium brevis</i>					
<i>Amphiodia</i> spp					
<i>Ampithoe dalli</i>	1				
<i>Ampithoe</i> spp.					
Anemones (preserved)					
<i>Anthopleura artemisia</i>					
<i>Anthopleura elegantissima</i>					
<i>Aoroides ?columbiae</i>					
<i>Aphelochaeta multifilis</i>					
<i>Arabella semimaculata</i>					
<i>Arandia brevis</i>					
<i>Asabellides sibirica</i>					
<i>Axiothella rubrocincta</i>					
<i>Boccardiella hamata</i>					
<i>Bossiella</i> spp.	1				
Boulder percentage	31				
<i>Branchiomaldane</i> spp.					
Bryozoa (miscellaneous)					
<i>Callophyllis</i> spp.					
<i>Cancer magister</i>					
<i>Cancer oregonensis</i>					
<i>Cancer</i> spp. Juvenile					
<i>Capitella capitata</i>					
<i>Cauleriella ?pacifica</i>					
<i>Chaetomorpha</i> spp.					
<i>Cirratulus cingulatus/robustus</i>					
<i>Cirratulus multioculatus</i>					
<i>Clinocardium nuttallii</i> juveniles					
Cobble percentage	44				
<i>Coelopa</i> spp.			6		
Cottidae (sculpins)					
<i>Crepidula adunca</i>					
Crust, coralline					
Crust, fleshy	11				
<i>Cryptosiphonia woodii</i>	1				
<i>Cumella vulgaris</i>					
Dead barnacles (Class Cirripedia)	1				
<i>Desdimelita desdichada</i>					
<i>Desmarestia</i> spp.					

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	FB3	FB4	FB4	FB4	FB4
	2018	2015	2016	2017	2018
Diatoms, chain-forming	1				
<i>Egregia menziesii</i>					
<i>Eobrolgus chumashi</i>					
<i>Epiactis prolifera</i>	2				
<i>Eteone</i> spp.					
<i>Euclymene</i> spp.					
<i>Eulalia</i> spp.					
<i>Euphilomedes</i> spp.					
<i>Evasterias troschelii</i>					
<i>Exogone</i> and similar syllids					
<i>Exosphaeroma amplicauda</i>					
<i>Exosphaeroma inornata</i>					
<i>Exosphaeroma</i> spp.					
Family Hesionidae					
Family Nereidae					
Family Terebellinae					
<i>Farlowia mollis</i>	2				
Flatworm					
<i>Foxiphalus falciformis</i>					
<i>Fucus gardneri</i>	1				
Gammarid amphipods	5				
<i>Gelidium</i> spp.					
<i>Glycinde picta</i>					
<i>Gnathopleustes pugettensis</i>					
<i>Gnorimosphaeroma oregonense</i>	2	3			
Gobiesocidae (clingfish)					
Green filaments					
Gunnel					
<i>Halosaccion glandiforme</i>	1				
<i>Halosydna brevisetosa</i>					
<i>Harmothoe imbricata</i>					
<i>Harrimania?</i>					
<i>Hemigrapsus nudus</i>	1				
<i>Hemigrapsus oregonensis</i>					
<i>Hemigrapsus</i> spp.					
<i>Hemipodus borealis</i>			1		
<i>Hermisenda crassicornis</i>					
<i>Ianiropsis kincaidi</i>					
<i>Ianiropsis</i> spp.					
<i>Idotea</i> spp.	2				
<i>Idotea vosnesenskii</i>					
Insect larvae (chironomids)					
<i>Katarina tunicata</i>					
<i>Lacuna</i> spp.	85				
<i>Lamprops carinata</i>					

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	FB3	FB4	FB4	FB4	FB4
	2018	2015	2016	2017	2018
<i>Lepidochitona dentiens</i>					
<i>Leptasterias hexactis</i>					
<i>Leptocheilia dubia</i>					
<i>Leptosynapta clarki</i>					
<i>Leukoma staminea</i> juv.					
<i>Lirabuccinum dirum</i>	1				
<i>Lirularia</i> spp.					
<i>Littorina scutulata</i>					
<i>Littorina sitkana</i>					
Live barnacles (Class Cirripedia)	7				
<i>Lottia fenestrata</i>					
<i>Lottia pelta</i>					
<i>Lottia scutum</i>					
<i>Lottia</i> spp. Juveniles					
Lottid limpets	32				
<i>Lumbrineris zonata</i>			1		
<i>Macoma inquinata</i>					
<i>Macoma inquinata</i> juv.					
Majid (spider) crab					
Majid juvenile crab					
<i>Malacoceros glutaeus</i>					
<i>Mastocarpus jardinii</i>					
<i>Mastocarpus papillatus</i>	8				
<i>Mazzaella heterocarpa/oregona</i>					
<i>Mazzaella splendens</i>	6				
<i>Mediomastus californiensis</i>					
<i>Megalorchestia pugettensis</i>					
<i>Metridium</i> spp.	1				
<i>Microcladia borealis</i>	3				
<i>Monocorophium</i> spp.					
<i>Mooreonuphis stigmatus</i>					
<i>Mopalia lignosa</i>					
<i>Mopalia muscosa</i>	1				
<i>Mytilus californianus</i>					
<i>Mytilus trossulus</i> juvenile					
<i>Naineris dendritica</i>			1		
<i>Naineris uncinata</i>					
<i>Nebalia pugettensis</i>					
Nematodes					
Nemertean (unident.)					
<i>Neorhodomela oregona</i>	10				
<i>Nephtys longosetosa</i>		1		1	
<i>Nereis procera</i>					
<i>Nereis vexillosa</i>					
<i>Notomastus tenuis</i>	4				

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	FB3	FB4	FB4	FB4	FB4
	2018	2015	2016	2017	2018
<i>Nucella canaliculata</i>					
<i>Nucella lamellosa</i>	1				
<i>Nucella ostrina</i>					
<i>Nucella</i> spp.					
<i>Nutricola lordi</i>					
<i>Odonthalia floccosa</i>	4				
Oligochaetes					
<i>Owenia fusiformis</i>					
<i>Pagurus ?hirsutiusculus</i>					
<i>Pagurus</i> spp.	2				
<i>Paracalliopiella pratti</i>					
<i>Parallorchestes cowani</i>					
<i>Paramoera bousfieldi</i>					
<i>Paramoera serrata</i>					
<i>Paramoera suchaneki</i>					
Pebble percentage	11	7	2	2	2
<i>Petalonia fascia</i>	1				
<i>Petrolisthes</i> spp.					
<i>Pherusa plumosa</i>					
<i>Phoronopsis harmeri</i>					
<i>Photis</i> spp.					
<i>Phoxichilidium femoratum</i>					
<i>Phyllodoce</i> spp.					
<i>Phyllospadix scoleri</i>	10				
<i>Phyllospadix serrulatus</i>					
Piddock clam					
<i>Pinnixia schmitti/occidentalis</i>					
<i>Pisaster ochraceus</i> juvenile					
<i>Platynereis bicanaliculata</i>					
<i>Podarke pugettensis</i>					
<i>Podarkeopsis glabrus</i>					
<i>Polycirrus</i> n. spp. (L. Harris)					
<i>Polydora cardalia</i>					
<i>Polydora columbiana</i>					
<i>Polydora proboscidea</i>					
Polynoid (in quadrat)					
<i>Polysiphonia</i> spp.	8				
<i>Pontogeneia ivanovi</i>					
<i>Porphyra</i> spp.	24				
<i>Potamilla</i> spp.					
<i>Prionitis</i> spp.	8				
<i>Prionospio steenstrupi</i>					
<i>Protohyale oclairi</i>					
<i>Pugettia</i> spp.					
<i>Pugettia</i> spp. Juvenile					

Appendix 2. Mean Taxa Density by Site and Year (count for mobile organisms, % cover for sessile organisms)

species	FB3	FB4	FB4	FB4	FB4
	2018	2015	2016	2017	2018
Pycnogonid					
<i>Rochefortia tumida</i>	1				
Sabellid (unident.)					
<i>Saccharina sessilis</i>					
<i>Saccharina</i> spp.					
Sand percentage	20	93	98	99	99
<i>Saxidomus giganteus</i> juv.					
<i>Schizobranhia insignis</i>					
<i>Scolelepis squamata</i>					
<i>Scytosiphon simplicissimus</i>					
Sipunculids					
<i>Smithora naiadum</i>					
<i>Soranothera ulvoidea</i>					
<i>Sphaerodoropsis minuta</i>					
Sphaeromid isopods	1				
<i>Spio filicornis</i>					
Sponge, unidentified	1				
Stauromedusae					
<i>Stichaeidae</i>	1				
<i>Streblosoma</i> spp.					
Syllids		1			
<i>Thelepus crispus</i>	1				
<i>Tonicella</i> spp.					
<i>Transennella tantilla</i>					
<i>Traskorchestia</i> spp.					
<i>Traskorchestia traskiana</i>					
<i>Tresus capax</i>					
<i>Tresus capax</i> juveniles					
<i>Typosyllis</i> spp.					
Ulvoids	19				
<i>Urticina</i> spp.					
<i>Zirfaea pilysbryi</i> juvenile	1				
<i>Zostera marina</i>					