EPIBENTHIC INVERTEBRATES AND JUVENILE CHUM SALMON (*ONCORHYNCHUS KETA*) PREY AVAILABILITY ALONG AN ECO-ENGINEERED SHORELINE: A CASE STUDY AT THE SEAWALL IN SEATTLE, WASHINGTON

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Abstract

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Shoreline development can alter coastal processes resulting in habitat loss and species assemblage shifts, but eco-engineered enhancements, or modifications to hard structures that mimic or support ecological processes, may improve ecosystem functioning and benefit shoreline dependent species. Seawalls and piers can reduce the quality and quantity of shallow water habitat available to out-migrating juvenile salmon (*Oncorhynchus* spp.) by deepening nearshore water and shading the shoreline environment. Previous studies along Seattle's Elliott Bay waterfront have shown that common prey of migrating juvenile salmon, small epibenthic crustaceans such as amphipods and harpacticoid copepods, are negatively impacted by pier shading, presumably due to the reduced light intensity necessary to support primary production, and that juvenile salmon occurring there feed less on these types of prey. To reduce the impacts on out-migrating salmon and increase epibenthic prey availability a section of the Seattle seawall was replaced with an eco-engineered design including a raised marine bench to reduce shoreline water depths, a textured seawall and ledge to increase habitat diversity, and a cantilevered, glass-paneled walkway to allow light penetration to the water below. In 2018, we sampled epibenthic invertebrates along the raised bench and seawall-ledge, covered (under) and not covered (outside) by piers to compare the availability of epibenthic invertebrate prey among the eco-engineered habitats. The following year, juvenile chum salmon were collected for diet analysis from outside piers along the eco-engineered seawall, the adjacent original seawall with no eco-engineering, a nearby restored pocket beach, and two other riprap armored locations along the Seattle waterfront to compare prey selection among modified shorelines with and without the eco-engineered enhancements.

Epibenthic invertebrate assemblages varied by exposure (under-pier and outside-pier) and surface type (seawall shelf and bench) with higher relative densities and taxa richness outside piers and on the bench. Total epibenthic invertebrate densities and densities of juvenile chum salmon prey were higher on the bench positioned outside piers than on all other eco-engineered strata (the marine bench under piers, the seawall shelf under piers, and the seawall shelf outside piers) combined. Taxa richness and total densities along the eco-engineered seawall increased after enhancement and were more like values at a nearby un-armored and enhanced pocket beach site suggesting a positive effect of the eco-engineering. However, juvenile chum salmon consumed mostly planktonic prey and we did not observe a significant difference in the number or biomass of epibenthic or terrestrial prey consumed along the eco-engineered seawall relative to the un-enhanced seawall. Prolonged daytime shading from the cantilevered sidewalk may have influenced juvenile chum salmon to move away from the eco-engineering preventing access to epibenthic prey. However, previously observed changes in behavior, shoreline distribution,

and under-pier use of the eco-engineering by juvenile salmon suggest it has enhanced juvenile salmon habitat.

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Chapter 1. Introduction

General Introduction

Coastal cities and human development along shorelines have historically used artificial shoreline defenses, such as armoring, to prevent erosion and protect infrastructure from regular wave action and extreme weather events (Dugan et al. 2011). However, these structures also reduce connectivity among terrestrial and aquatic environments and alter coastal processes, resulting in habitat loss and assemblage shifts of resident and migratory shoreline species (Bulleri and Chapman 2010, Dugan et al. 2016, Munsch et al. 2017). In-water and over-water structures such as pilings and piers can also alter species distributions and trophic structure, and interrupt migration of juvenile Pacific salmon (*Oncorhynchus* spp.) (Duffy-Anderson et al. 2003, Toft et al. 2007, Munsch et al. 2014, Pereira 2017). The extent of shoreline armoring globally has not been determined, but one study estimated the footprint of marine shoreline structures to be over 32,000 km^2 (Bugnot et al. 2021). Regional studies have shown that coastlines in Canada, Australia, China, Japan, and Europe are extensively armored (Airoldi et al 2005, Ma et al. 2014, Masucci and Reimer 2019, Sauvé et al. 2020) and 14% of outer-coast shorelines in the USA are armored (Gittman et al. 2015). Yet, climate change and sea level rise are contributing to more extreme storms resulting in increased coastal flooding and economic damage along unprotected shorelines (Vitousek et al. 2017, Kirezci et al. 2020) which may eventually push beyond the limits of current shoreline defenses. These impacts will likely be exacerbated when coupled with continued human population growth and expected coastal migration (Neuman et al. 2015), magnifying the need to expand shoreline defense structures.

Hard armoring such as seawalls, bulkheads, riprap, and dikes, can be long lasting, and effective shoreline defenses. However, such structures interrupt ecological processes and impact the upland, intertidal, and nearshore aquatic communities (Gittman et al. 2016b). Armoring can reduce beach width (Chapman and Bulleri 2003) and alter sediment composition by facilitating erosion of finer grain sediments and reducing future sediment transport and deposition (Ruggiero 2010, Dethier et al. 2016). Wrack-associated and upland terrestrial invertebrates that supplement nearshore food webs are also threatened by armoring. Armoring that encroaches into the intertidal can reduce or prevent the recruitment of wrack, altering wrack associated invertebrate communities (Dethier et al. 2016, Jaramillo 2021). Similarly, armoring adjacent to upland terrestrial habitats can reduce insect abundances and biodiversity in upland habitats (Sobocinski et al. 2010), reducing their availability as prey. Coupled with sea level rise, armoring that backs marsh habitat contributes to "coastal squeeze" by preventing marsh retreat, leading to the loss of these habitats (Borchert et al. 2018). Recent efforts to reduce the ecological impacts of armoring have included complete removal and restoration of shorelines (Toft et al. 2013, Lee et al. 2018), transition from hard to soft armoring (Bilkovic et al. 2017, Toft et al. 2021), and eco-engineering of hard shorelines when a transition to soft armoring is not feasible (Cordell et al. 2017a, Morris et al. 2017, Strain et al. 2018, Bradford et al. 2020, Sawyer et al. 2020).

Soft armoring and living shorelines, such as sills, utilize natural elements like small rock or sand, planted vegetation, and oyster reefs can provide similar benefits as hard armoring, but with reduced ecological impacts and improved ecosystem services, like carbon sequestration (Davis et al. 2015, Bilkovic et al. 2017). Softened shorelines can support higher species diversity and abundances than hardened shorelines (Gittman et al. 2016a, Isdell et al, 2021), and given sufficient time, living shoreline techniques can provide improved ecosystem function nearing the level of nearby unaltered shorelines (Toft et al. 2021). This approach is becoming increasingly affordable to private property owners and supported by coastal governing agencies (Bilkovic et al. 2017, Stafford et al. 2020). However, shoreline softening may not be feasible in highly urbanized areas such as marine ports and waterfronts built into or beyond the intertidal. Instead, engineering or modifying hard structures following ecological principles, termed "eco-engineering," could be beneficial (Bergen et al. 2001, Strain et al. 2018).

Eco-engineered armoring could improve ecosystem functioning and benefit shoreline dependent species while providing the same level of protection as traditional hard armoring. Experimental studies have generally focused on increasing surface area and diversity by texturing armored surfaces, adding crevices and water retaining structures, and adding horizontal or gently sloping surfaces (shelves) at multiple elevations (Chapman & Blockley 2009, Firth et al. 2016, Cordell et al. 2017a, Evans et al. 2021). Other approaches considered the use of sessile taxa as ecological engineers, such as bivalves, coral, and algae, to provide structure for other species on artificial structures (Perkol-Finkel et al. 2012). In general, the most successful eco-engineered treatments showed increases in species abundances and richness (Strain et al. 2018). Most eco-engineered shoreline armoring applications have occurred on small scales (i.e., temporary experimental test plots attached to established armoring and monitored for less than two years), thus large-scale effectiveness remains untested (Strain et al. 2018).

In Puget Sound, WA, USA, efforts are underway to remove or soften shoreline armoring to restore terrestrial-aquatic connectivity and sedimentary processes and improve habitat for spawning forage fish (e.g., Pacific sand lance (*Ammodytes hexapterus*) and surf smelt (*Hypomesus pretiosus*)) and migrating juvenile salmon (*Oncorhynchus* sp.) (Cereghino et al. 2012). Unaltered Puget Sound shorelines consist of barrier, bluff-backed, rocky platform, and sand or gravel pocket beaches (Simenstad et al. 2011) which are maintained in part by shoreline erosion, particularly of bluffs (Johannessen and MacLennan 2007), thus requiring land-sea connectivity. Wind, waves, beach cardinal position, and a complex sediment transport system contribute to shoreline sediment maintenance, but shoreline armoring interrupts these processes and has degraded Puget Sound beaches and nearshore marine habitats (Dethier et al. 2016).

Pacific salmon and trout are ecologically and culturally important species in the eastern Pacific region but have experienced precipitous declines particularly along the southern reaches of several species' ranges, and many are listed as threatened or endangered under the Endangered Species Act (Ford 2022, Pacific Fishery Management Council 2022). Historic over-harvest, hydropower infrastructure, hatchery production, and habitat degradation (including shoreline development) have been identified as the key factors contributing to these declines (Toft et al. 2018, Hodgson et al. 2020). Juvenile salmon in habitats altered by armoring and piers may experience reduced prey densities (Toft et al. 2013, Morley et al. 2012, Toft et al. 2013, Munsch et al. 2015, Cordell et al. 2017a, Cordell et al. 2017b), altered behavior and migration (Ono and Simenstad 2014, Heerhartz and Toft 2015, Munsch et al. 2014, Sawyer et al. 2020), and potentially increased predation (Simenstad et al. 1999, Williams et al. 2003). Juvenile Puget Sound (ocean-type) Chinook (*Oncorhynchus tshawytscha*), chum (*O. keta*), and pink (*O. gorbuscha*) salmon are more impacted by estuarine habitat degradation than other species because they migrate and rear in estuarine and nearshore marine waters as small juveniles typically confined to shallow water habitats (Simenstad et al. 1982).

The most extensively armored region of Puget Sound is the central part (Simenstad et al. 2011) which includes Elliott Bay and the City of Seattle, WA. The Seattle waterfront has been heavily modified by a 2100 meter long seawall built beyond the intertidal, a cruise ship terminal, and nine connected piers. A large shipping port wharf, artificial island, and industrial infrastructure along most of the adjacent Duwamish River delta leave less than 5% natural nearshore habitat important to juvenile salmon.

In the 1930s, a seawall was built in Seattle to support water-based commerce and reclaim land area from tidal marshlands and the Duwamish River delta (Williams 2015). The seawall was composed of a flat concrete wall supported by wood beams and occasionally fronted by riprap (Figure 1). In 2001, the seawall was damaged during an earthquake and following inspection it was discovered the wooden support beams had been further damaged by wood-boring marine isopods.

Figure 1. A section of the original flat concrete seawall fronted by rip-rap and a dark, shaded under-pier area in the upper left.

The old seawall and pier structures and concurrent shading altered the movement and distribution of out-migrating juvenile salmon along the shoreline by forcing them into deeper water (Munsch et al 2014). Feeding behaviors were also reduced at high tide relative to nearby un-armored sites which likely contributed to atypical diets dominated by zooplankton rather than epibenthic amphipods and harpacticoid copepods (Munsch et al. 2015b) more typical of small juvenile Chinook, chum, and some pink salmon (Simenstad et al. 1982). City planners considered the need to replace the seawall as an opportunity to apply eco-engineering to reduce these impacts and provide more functional habitat for out-migrating juvenile salmon (City of Seattle, 2013). As part of the effort to reduce the impacts of armoring to juvenile salmon, in 2017 nearly half of the aging Seattle waterfront seawall was replaced with an eco-engineered seawall. The eco-engineered design includes a cantilevered glass-paneled overhanging sidewalk (light penetrating surface, LPS), a textured concrete seawall with attached ledges, and an elevated seafloor bench (herein "marine bench") directly adjacent to the seawall to increase surface area available for prey and other invertebrates (Figure 2) (Cordell et al 2017a). The glass panels allow some daylight penetration to the areas underneath the piers to support juvenile salmon migration and provide photosynthetically active radiation (PAR) to the water below to promote the growth of algae and other primary producers on the eco-engineered surfaces. Sawyer et al. (2020) showed that after addition of LPS, light levels under piers increased by as much as 4% and juvenile salmon were more abundant under piers than before enhancement. The surface of the eco-engineered seawall is textured with various grooves, crevices, and raised shapes to increase habitat complexity and the surface area available to algae and invertebrates. Two rows of continuous concrete ledges attached to the seawall add nearly horizontal habitat within the tidal range occupied by the new seawall (Figure 2). Lastly, a shorter, corrugated steel wall was constructed 3m offshore of and parallel to the concrete seawall that rises to Mean Low Low Water. The gap between the two walls is filled and overlayed with flexible mesh frames filled with coarse aggregate stone to raise the seafloor adjacent to the seawall creating shallow habitat for out-migrating juvenile Pacific salmon (Figure 2). These enhancements may also provide shallow habitat to support algal production and epibenthic invertebrate grazers available to juvenile salmon.

Figure 2. Seattle seawall eco-engineered enhancements. **Left**: In the foreground is the marine bench at low tide under a pier. On the right is the textured seawall with added shelves outside and under piers. Above are the cantilevered glass-paneled sidewalks (LPS). **Right**: View of LPS from below.

Objectives

Post-construction monitoring suggests the eco-engineering along the Seattle seawall has improved juvenile salmon passage along the seawall and access to previously unavailable under-pier habitat (Sawyer et al. 2020, Accola et al. 2022). In this study, I investigated how the eco-engineered seawall has affected the availability and access by juvenile salmon to typical prey. In the following, I examine the epibenthic prey communities produced on the four strata of the eco-engineered seawall (Chapter 2) and compare the diets of juvenile chum salmon feeding at the new seawall with those feeding at the original seawall and three other nearby locations (Chapter 3). We expect that if the eco-engineering supports the production of sufficient densities of the typical epibenthic invertebrate prey of small juvenile chum salmon, under and between piers, and if juvenile chum salmon can access the eco-engineered shallow water habitat where those prey are produced, then juvenile chum salmon will predominately consume those prey. But, if epibenthic invertebrate prey are not sufficiently abundant or juvenile chum salmon do not consistently occupy the shallow water habitat along the marine bench, then juvenile chum salmon will predominately consume other (e.g., planktonic) prey.

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Chapter 2: Epibenthic invertebrate assemblages and juvenile chum salmon (*Oncorhynchus keta*) prey availability along an eco-engineered shoreline

Introduction

Small epibenthic invertebrates in shoreline waters are subject to the impacts of shoreline development. Harpacticoid copepods are ubiquitous in the epibenthos of nearshore marine and estuarine waters and often one of the most abundant invertebrate taxa (Hicks and Coull 1983). Species and habitat diversity is high among harpacticoids and includes both sediment dwelling and phytal associated species (Hicks and Coull 1983, Boxshall and Halsey 2004). Amphipods also occupy epibenthic habitats and can dominate the epibenthic invertebrate community by weight in some regions (Thom et al. 1989). Harpacticoids and amphipods graze on a wide variety of algae, detritus, bacteria, and yeast (Hicks and Coull 1983) and can be important links in nearshore food webs (Alheit and Scheibel 1982, Simenstad et al. 1988, Coull 1999) since many fish species consume them as juveniles (Brezina 1979, Alheit and Scheibel 1982, Coull et al. 1995, Duffy-Anderson and Able 2001), including commercial species like flatfish and salmonids (Simenstad et al. 1988, Gee 1989). Although epibenthic prey are critical to many ecologically and economically important fish species (Gee 1989, Coull et al. 1995), the effects of shoreline structures on epibenthic invertebrate communities have not been widely studied (Connell and Glasby 1999, Glasby 2000). However, recent studies in Puget Sound have investigated the effects of seawalls and piers on the epibenthos (Toft et al. 2013, Morley et al. 2012, Cordell et al. 2017a, 2017b).

Puget Sound is armored along approximately one-third of its shoreline along with nearly two-thirds of the shoreline in central Puget Sound which includes Seattle, WA (Simenstad et al.

2011). Studies on the impacts of this armoring and piers to the epibenthic community have been conducted in and around Seattle. Morley et al. (2012) observed lower epibenthic invertebrate densities and taxa richness at armored shorelines relative to unarmored shorelines along with significant changes to harpacticoid assemblages along the Duwamish River estuary, which flows into Elliott Bay in Seattle. A similar study also found lower harpacticoid densities and taxa richness along the flat, vertical, concrete surface of the Seattle waterfront seawall relative to nearby un-armored beaches in Elliott Bay (Munsch et al. 2015b). Piers also alter epibenthic invertebrate assemblages in Puget Sound and these effects may be magnified where piers are clustered like along the Seattle waterfront (Cordell et al. 2017b).

Juvenile chum (*Oncorhynchus keta*), pink (*Oncorhynchus gorbuscha*), and sub-yearling Chinook (*Oncorhynchus* tshawytscha) salmon in Puget Sound and nearby waters occupy nearshore habitats (Simenstad et al. 1982) where they may consume epibenthic, planktonic, and terrestrial invertebrate prey (Healy 1979, Sibert 1979, Simenstad et al. 1980, Cordell 1986, D'Amours 1987). Small juvenile chum and pink salmon preferentially consume the harpacticoid species *Harpacticus uniremis* and genera *Tisbe* and *Zaus* which can account for a high proportion of their diets throughout their range in the northern Pacific (Harris and Hartt 1977, Healy 1979, Sibert 1979, Simenstad et al. 1982, Cordell 1986, D'Amours 1987, Webb 1991, Mayama & Ishida 2003). Some studies have shown *H. uniremis* and *Tisbe* spp. to be highly abundant in the epibenthos (Cordell et al. 1986, Thom et al. 1989) while others have shown them to be quite rare (Sibert 1979). *Zaus* spp. are generally less abundant in the environment and in juvenile salmon diets than the other two taxa. The *Harpacticus uniremis* group also includes *H. uniremis* and related species that are probably within a species complex (Cordell et al. 2018). Some studies of harpacticoids in the environment (Sibert 1979, Simenstad et al 1980, D'Amours

1987) or in juvenile salmon diets (Healy 1979, Simenstad et al 1980, D'Amours 1987) do not provide data on other species in the *H. uniremis* group and it is unclear if these were absent or not separated from *H. uniremis*. However, other studies that did discuss all taxa observed *H. uniremis* in relatively similar if not higher abundances than other species in the *H. uniremis* group in the environment (Cordell 1986, Thom et al. 1989) and in juvenile salmon diets (Cordell 1986). These disparities may not only be due to level of identification but also likely due to differences in location (studies referenced range from Washington to Alaska), sampling technique (Sibert 1979, Cordell 1986, D'Amours 1987), substrate composition (Sibert 1979), flow (Cordell 1986), seasonality and life history stage of harpacticoids (Cordell 1986), and high spatial and temporal variability. What is clear is that in many habitats *Harpacticus* species in the *uniremis* group (including *H. uniremis*) are an important prey source for juvenile pink and chum salmon. Juvenile Chinook salmon also consume epibenthic invertebrates but focus more on gammarid amphipods (Simenstad et al. 1982) primarily from the genera *Calliopius*, *Paracalliopiella*, and *Photis* (Brennan et al. 2004, Toft et al. 2007).

Changes to the epibenthic invertebrate community impact out-migrating juvenile salmon that feed on epibenthic invertebrates (Toft et al. 2007, Toft et al. 2013, Munsch et al. 2015b). Epibenthic invertebrate prey of juvenile salmon can be significantly reduced or eliminated by armoring and piers (Toft et al. 2013, Munsch et al. 2015b, Cordell et al. 2017b), reducing their availability to out-migrating juvenile salmon. Specifically, Cordell et al. (2017b) found reduced densities of *H. uniremis* group (including *H. uniremis*) and *Zaus* spp. under piers on the Seattle waterfront seawall. *Tisbe* spp., densities were also reduced by pier shading but dominated the depauperate under-pier epibenthic assemblages (Cordell et al. 2017b). Toft et al. (2013) found reduced densities of *Harpacticus* spp. on armored versus unarmored shorelines and that rehabilitation by removal and construction of a pocket beach can increase densities. A variety of gammarid amphipod taxa can be abundant along unaltered shorelines but armoring may reduce abundances of some taxa (e.g., *Calliopius* spp.) while increasing others (e.g., *Paracalliopiella pratti*) (Simenstad et al. 1980, Toft et al. 2013).

Armoring and pier removal, and shoreline rehabilitation in Puget Sound has shown promising results in restoring invertebrate prey assemblages to conditions at comparable reference sites or to pre-armoring conditions (Toft et al. 2021). However, removal may not be an option for some areas and eco-engineering is increasingly tested as a functional alternative. Efforts to enhance habitat at armored shorelines in Elliott Bay have shown promising results. At the Olympic Sculpture Park (OSP) (Figure 3) significant increases in epibenthic invertebrate densities, taxa richness, and prey taxa followed the removal of a section of riprap armoring and construction of a pocket beach (Toft et al. 2013). Also, at OSP, an eco-engineered compacted-sediment bench was placed in the low intertidal along a section of the intertidal seawall that could not be removed (Toft et al. 2013). Post-construction monitoring showed the epibenthic invertebrate assemblage had changed along the eco-engineered section and was more like the assemblage along the restored pocket beach and different than at the adjacent riprap armored shoreline and seawall section without the eco-engineering. Taxa richness also increased and was higher at the sediment bench and pocket beach sites.

Figure 3. Olympic Sculpture Park (OSP) pocket beach. Seattle waterfront and seawall are in the background and south of OSP.

To mitigate the impacts of the Seattle seawall on juvenile salmon and their epibenthic prey, the southern reach of the seawall was replaced with eco-engineering based on the designs and lessons learned from the OSP study and the seawall test panels (Figure 2). A description of the design can be found in Chapter 1.

Construction of the eco-engineered Seattle seawall was completed in 2017 and post-construction sampling began the following year. Light penetration under piers and over the marine bench has increased with construction of the LPS sidewalk but PAR remains low relative to outside of piers (Sawyer et al. 2020). In 2018, epibenthic invertebrate samples were collected from four outside-pier and under-pier paired sites along the eco-engineered seawall. Four strata were designated based on the four possible combinations of light exposure (outside of piers and under piers) and surface type and orientation (textured seawall shelf and marine bench) (Figure 4). The objectives of this study were to investigate the impacts of the newly constructed Seattle seawall to the epibenthic invertebrate community and to salmon-specific prey. I predicted that the four newly constructed engineered strata (seawall outside of piers (outside-seawall shelf; OS), seawall under piers (under-seawall shelf; US), marine bench outside of piers (outside-bench; OB), and marine bench under piers (under-bench; UB)) would support different epibenthic invertebrate assemblages due to the differences in surface orientation and light exposure. Specifically, I predicted that total epibenthic invertebrate densities, taxa richness, and densities of salmon prey taxa would be higher on the OB and OS strata where light levels are highest than on the UB and US strata. Because the seawall shelf and marine bench were both nearly horizontal surfaces, I predicted that there would be no difference between the seawall and marine bench surfaces within the outside-pier strata or the under-pier strata (i.e. no difference between OB and OS or between UB and US).

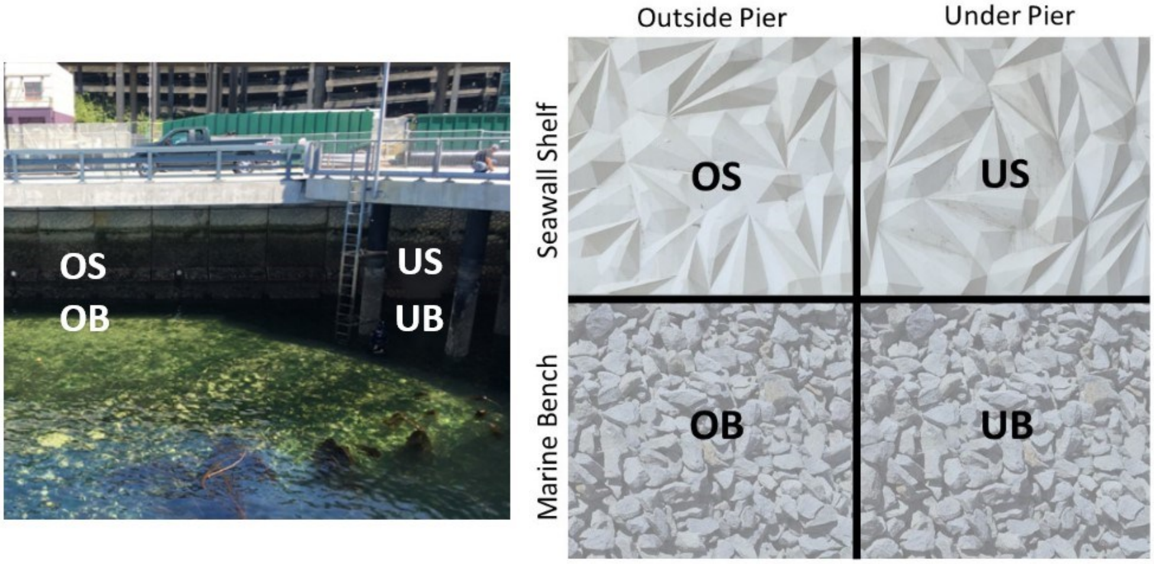

Figure 4. Eco-engineered seawall strata. **Left**: Seawall with example locations of outside-pier and under-pier seawall and marine bench sampling areas. **Right**: Conceptual diagram.

Methods

Study Area

Puget Sound in Washington, USA and the shared waters of the Straits of Georgia and Juan de Fuca comprise the greater Salish Sea in Washington, USA and British Columbia, Canada (Figure 5). Puget Sound is a complex of estuaries that experiences high seasonal freshwater input from twelve major rivers in a 31,440 km^2 watershed. Elliott Bay is an estuarine delta and embayment adjacent to Seattle, WA in the central Puget Sound that receives freshwater input from the Duwamish River watershed. The highly urbanized shorelines of Seattle were designed for shipping and ferry boat access and include a system of in and over-water structures including pilings and piers and is almost entirely armored.

Figure 5. Map of Elliot Bay. Epibenthic invertebrate sampling sites: A. Seattle Aquarium, B. Pier 56, C. Piers 55 and 54.

Four sampling sites were selected from the 1150 m section within the Seattle seawall replacement corridor: Seattle Aquarium, Pier 56, Pier 55, and Pier 54, construction of this section was completed in 2017. Each site includes all three eco-engineered features: a raised marine bench, textured seawall, and an overwater cantilevered LPS sidewalk (Figure 2) and all four strata.

Data Collection and Processing

In Spring 2018, epibenthic invertebrates were sampled monthly (April through July) along the Seattle waterfront at the four sites (Figure 5) and on each of the four combinations of exposure (outside of pier and under pier) and surface (seawall shelf and the marine bench) (Figure 4). We sampled the epibenthic invertebrate community using an epibenthic suction pump, consisting of an enclosure with 106 micrometer mesh ports attached to a manual bilge pump, that sampled an area of 0.02 m^2 over which we pumped twenty times per sample volume (Figure 6). Five discrete samples were collected randomly along a 25-m transect from both seawall shelf and marine bench, under piers and outside piers resulting in twenty samples from each site and per sampling event (month). Samples were preserved in 10% formalin and returned to a laboratory for processing.

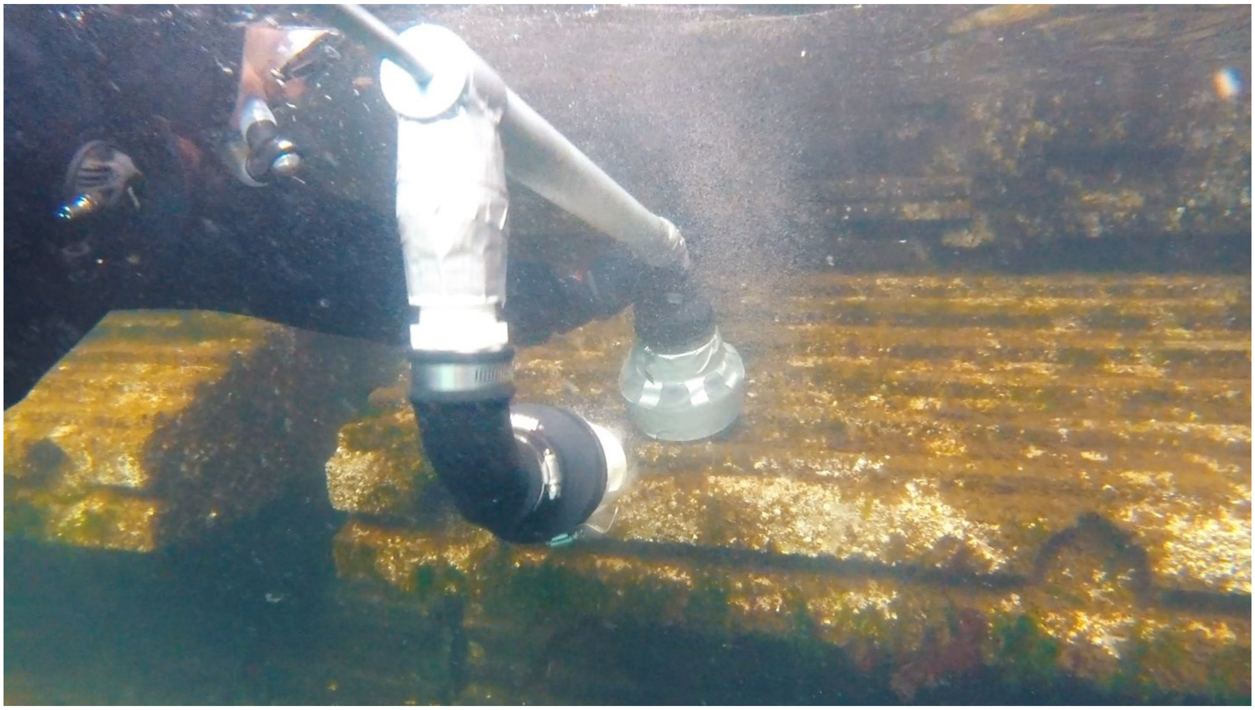

Figure 6. Epibenthic invertebrate sampling of the shelf along the Seattle seawall.

In the laboratory, samples were processed by rinsing the entire contents through a 106-µ sieve. Invertebrates were then placed in a Petri dish, examined, and enumerated under a high-powered dissecting microscope. Harpacticoid copepods and gammarid amphipods were identified to family, genus, or species. Other epibenthic crustaceans were typically identified to the same taxonomic levels but juvenile harpacticoid and cyclopoid copepodids that could not be identified further were counted as such. The remaining groups of epibenthic invertebrates, mostly Acari (mites) and annelid polychaete worms were enumerated at higher taxonomic levels. Strictly planktonic, benthic, or terrestrial invertebrates were not counted unless they were in an epibenthic stage, (e.g., barnacle cyprids, Diptera larvae) or could have been either terrestrial or epibenthic (e.g., Collembola, Acari).

Data Analysis

The four sites were treated as replicates due to their proximity and similar design. Data were typically log(x+1) transformed to account for zeros in the data and improve normality.

Non-metric multidimensional scaling (NMDS) was used to explore and visualize differences in the epibenthic community composition among the four engineered strata using the ‘metaMDS’ function (Oksanen et al. 2020) in R (R Core Team 2020). NMDS is an unconstrained multivariate ordination technique which may be used as a visual aid when interpreting species count data that is not normally distributed. A stress value is estimated that represents the degree of difference between the ordination in reduced dimension compared to the original dissimilarity matrix. A stress value less than 0.10 is preferred and indicates good separation; between 0.10 and 0.20 may be usable but values closer to 0.20 should be considered with caution (Clarke 1993). To maximize the probability of reaching a global solution and thus convergence, 999 NMDS permutations were performed for each analysis. The Bray-Curtis dissimilarity metric (Bray & Curtis 1957) was calculated to characterize the compositional dissimilarities between samples, exposure, surface, sites, and months using the ‘vegdist’ function in R. Species vectors were calculated by performing a linear regression between the species scores from the NMDS axes using the ‘envfit’ function in R. Taxa in fewer than 3% of samples were removed prior to NMDS analysis to reduce the influence of rare taxa. Counts of taxa were log-transformed prior to analysis.

PERMANOVA was used to test for significant differences in taxa densities among the four engineered strata with site and month as fixed factors using the ‘adonis2’ function in R. The ‘betadisper’ function in R was used to test for homogeneity of variances prior to PERMANOVA. PERMANOVA can be robust to heterogeneity when study designs are balanced (Anderson & Walsh 2013) as in this study. Densities of each taxa were log-transformed prior to analysis. Multivariate analyses were performed using the ‘vegan’ package (Oksanen et al. 2020) in R version 4.0.2 (R Core Team 2020).

Two-way ANOVAs (Analysis of Variance) with interaction were used to test for differences in taxa richness, total invertebrate densities, and densities of potential epibenthic invertebrate prey of juvenile Pacific salmon (Harpacticoida, Gammaridea, and Insecta) among the four engineered strata and among months. Individual analyses were conducted on gammarid amphipods and harpacticoid taxa with high overall densities, taxa with NMDS R^2 loadings >0.28, or taxa known to be consumed by juvenile Chinook, chum, and pink salmon. *Tisbe* spp., was the only salmon prey taxa that could be analyzed individually so prey taxa were analyzed together (*Calliopius* spp., *H. uniremis* group, *Tisbe* spp., and *Zaus* spp.). Due to the uncertainty surrounding the taxonomy of *H. uniremis* group and selection by juvenile salmon, and because *H. uniremis* was rare, *H. uniremis* and *H. uniremis* group were analyzed together.

I used Tukey's HSD (Honestly Significant Difference) test for pairwise differences by strata and month when significant differences ($p<0.05$) were detected in two-way ANOVAs with no interaction. Pairwise t-tests with a Bonferroni correction were used instead of Tukey's HSD to reduce the chance of Type 1 error when variances appeared unequal. If there was a significant interaction in the two-way ANOVA, multiple pairwise comparisons were performed using a Bonferroni adjustment.

Results

A total of 111 invertebrate taxa (Table 6) were identified in the 320 samples collected. The majority of taxa were harpacticoid copepods with minor contributions by gammarid amphipods, cyclopoid copepods, Cirripedia cyprids, and Chironomidae larvae (Figure 7). Overall invertebrate densities were highest at the OB strata and lowest at the US strata (Figure 7) and densities generally increased on all strata throughout the sampling season.

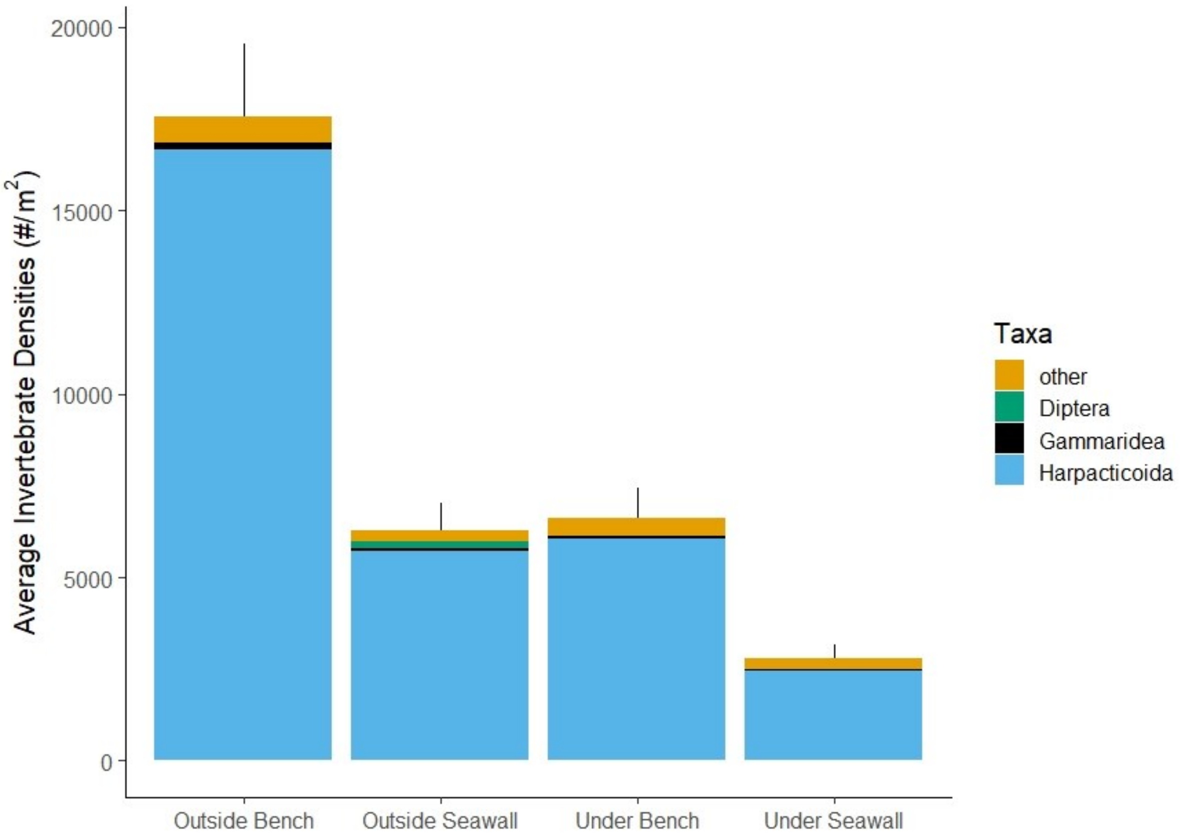

Figure 7. Mean densities of epibenthic invertebrate groups from all months and sites on the four strata. Error bars are standard error.

Epibenthic Assemblage Comparison

Multivariate analysis showed surface (marine bench or seawall) and exposure type (under-pier or outside-pier) influenced epibenthic assemblages. The NMDS showed separation among the four strata in ordination space (Figure 8) and there were significant differences among the strata, (PERMANOVA) (Table 1). Moderate stress was observed in the NMDS ordination, and a Monte Carlo randomization test of stress indicated that stress value to be reasonable at maintaining the rank order distances ($k = 3$, stress = 0.149). There was some overlap between the marine bench and seawall shelf surfaces, but separation among the outside and under pier strata was distinct, indicating assemblage differences were greatest by exposure. Many taxa exhibited highly significant loadings on the NMDS ordination so only those with R-values > 0.28 were displayed (Supplementary, Table 7). Several taxa, including *Ameira longipes*, Cirripedia, *D.vulgaris*, Diarthrodes, Ectinosomatidae, *H. obscurus* group, *H. uniremis* group, *Paradactylopodia* spp., and *Tisbe* spp., were the strongest drivers of differences among the eco-engineered strata (Figure 8). Cirripedia cyprids (not shown in NMDS plot) were more associated with under-pier strata (Figure 9) while harpacticoid taxa were more associated with between-pier strata (Figure 8).

Table 1. Summary statistics from a sequential PERMANOVA of epibenthic invertebrates among the four seawall strata. Site and month were used as blocking factors. Significant p-values (<0.05) are bold.

	Df	Sum of Squares	Mean Squares	F model	R^2	p
OB	1	4.193	4.1933	26.236	0.06710	**0.001**
OS	1	3.768	3.7682	23.576	0.06030	**0.001**
UB	1	4.028	4.0282	25.204	0.06446	**0.001**
Residuals	316	50.505	0.1598		0.80815	
Total	319	62.495			1.00000	

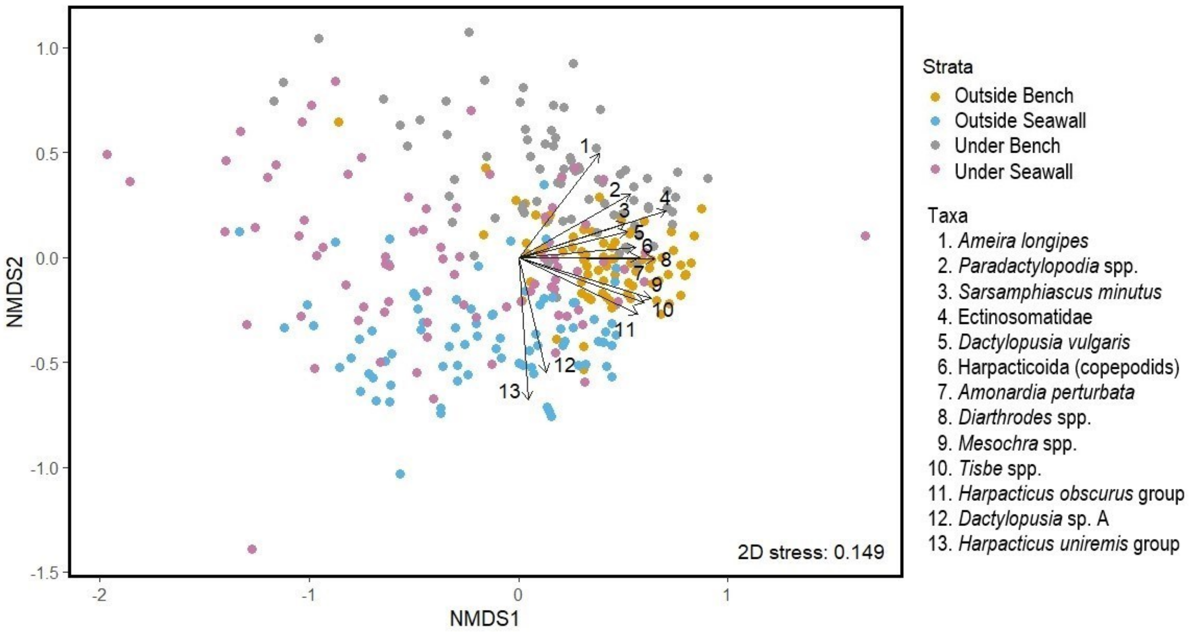

Figure 8. NMDS of epibenthic invertebrate samples at all four treatments. Stress = 0.149; linear fit $R^2 = 0.89$. Taxa with $R^2 > 0.28$ are displayed.

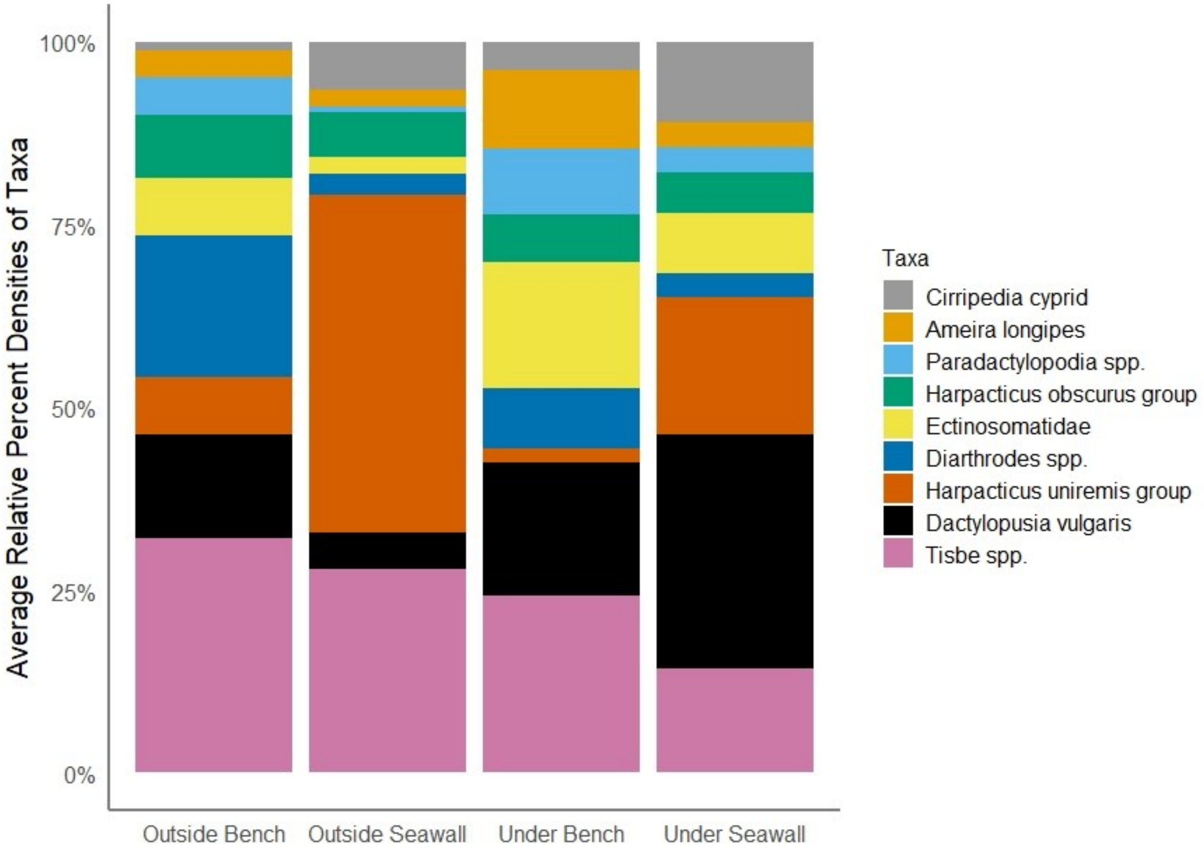

Figure 9. Average numeric proportion of taxa that had the greatest influence on the NMDS ordination.

Taxa Richness and Densities of Epibenthic Invertebrates and Juvenile Salmon Prey

Taxa Richness

The marine bench strata were associated with more taxa rich communities than the seawall strata and the outside-pier strata were associated with more taxa rich communities than the under-pier strata. Taxa compositions were significantly different among the four engineered strata and among the four months with no interaction effect (ANOVA $p < 0.05$) (Table 2). Taxa richness was higher on the outside-bench (OB) strata than on the other three strata (Figure 10), and higher on the under-bench (UB) strata than the two seawall-shelf strata (outside-seawall

(OS) and under-seawall (US)), which were not different from each other (Tukey's HSD $p < 0.05$) (Table 8).

Table 2. Summary statistics from two-way ANOVAs of epibenthic invertebrate taxa according to the factors of seawall strata and month. Significant p-values (<0.05) are bold.

Taxa group	Factor	df	SS	MS	F-value	p
Taxa Richness	Strata	3	6822	2273.8	66.855	**< 0.001**
	Month	3	5196	1732.1	50.927	**< 0.001**
	Strata x Month	9	552	61.3	1.803	0.0671
	Residuals	304	10340	34.0		
Total Density	Strata	3	32.26	10.75	57.015	**< 0.001**
	Month	3	13.26	4.42	23.440	**< 0.001**
	Strata x Month	9	2.12	0.24	1.248	0.265
	Residuals	304	57.33	0.19		
Potential Salmon Prey	Strata	3	36.55	12.18	64.750	**< 0.001**
	Month	3	17.45	5.82	30.910	**< 0.001**
	Strata x Month	9	3.52	0.39	2.080	0.031
	Residuals	304	57.19	0.19		
Prey Taxa	Strata	3	28.86	9.62	46.654	**< 0.001**
	Month	3	6.93	2.31	11.921	**< 0.001**
	Strata x Month	9	3.11	0.35	1.783	0.071
	Residuals	304	58.90	0.19		

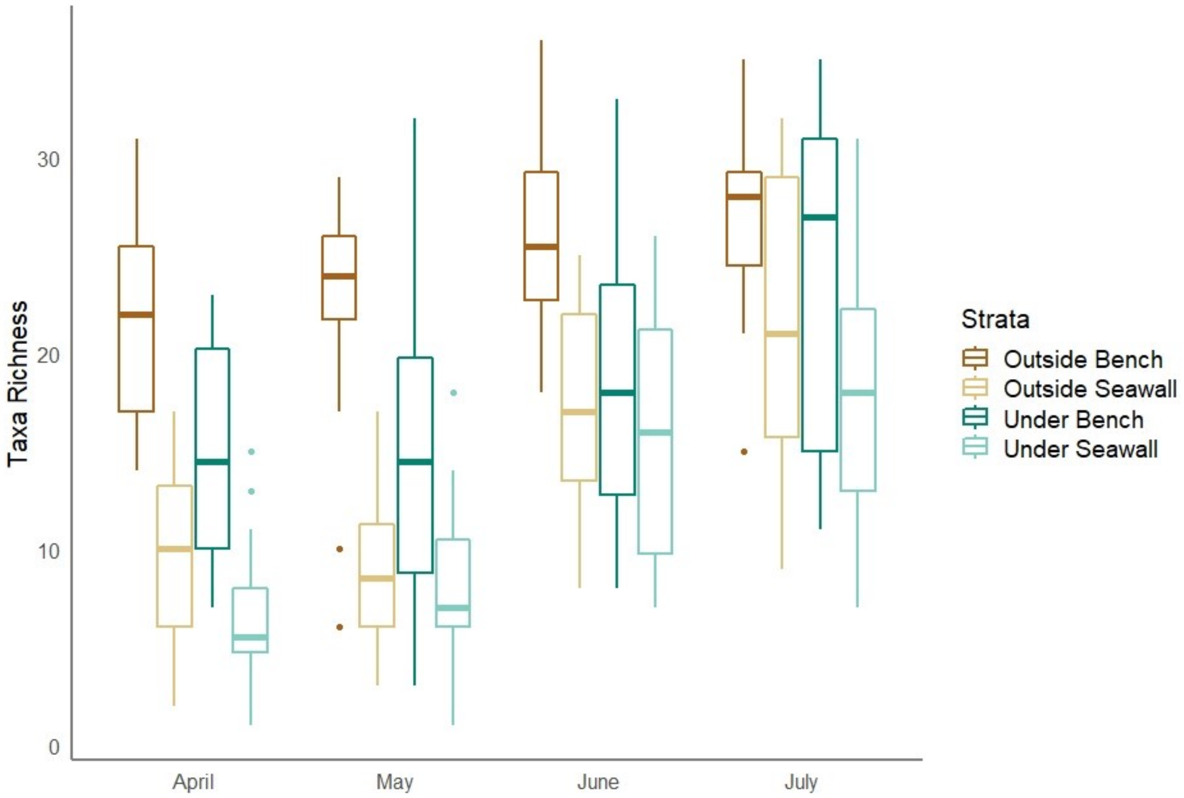

Figure 10. Taxa richness of epibenthic invertebrates on seawall strata by month. Box hinges show the interquartile range with the 25th (lower) and 75th (upper) percentiles, and median (thicker middle line). Whiskers depict 1.5 x the interquartile range and outliers are shown as points.

Overall Epibenthic Invertebrate Densities

Higher epibenthic invertebrate densities were associated with the marine bench strata than the seawall strata, and with the outside-pier strata than the under-pier strata (Figure 7). There were significant differences in overall epibenthic invertebrate densities among strata and months with no interaction (ANOVA $p < 0.05$) (Table 2). The outside-bench strata (OB) had higher densities than the other three strata while densities at the under-seawall shelf (US) were the lowest (Tukey's HSD $p < 0.05$) (Table 8, Figure 7). No statistical difference was found between the outside-seawall shelf strata (OS) and the under-bench (UB) strata (Table 8).

Grouped Taxa

Densities of potential prey of juvenile Pacific salmon were higher on the marine bench than on the seawall strata and were higher outside of piers than under piers. There were significant differences in density among strata and months with a significant interaction effect (ANOVA $p < 0.05$) (Table 2). Post-hoc pairwise comparisons using a Bonferroni correction showed that potential prey densities were generally highest on the OB strata and lowest on the US strata with intermediate densities at the other strata (Figure 11).

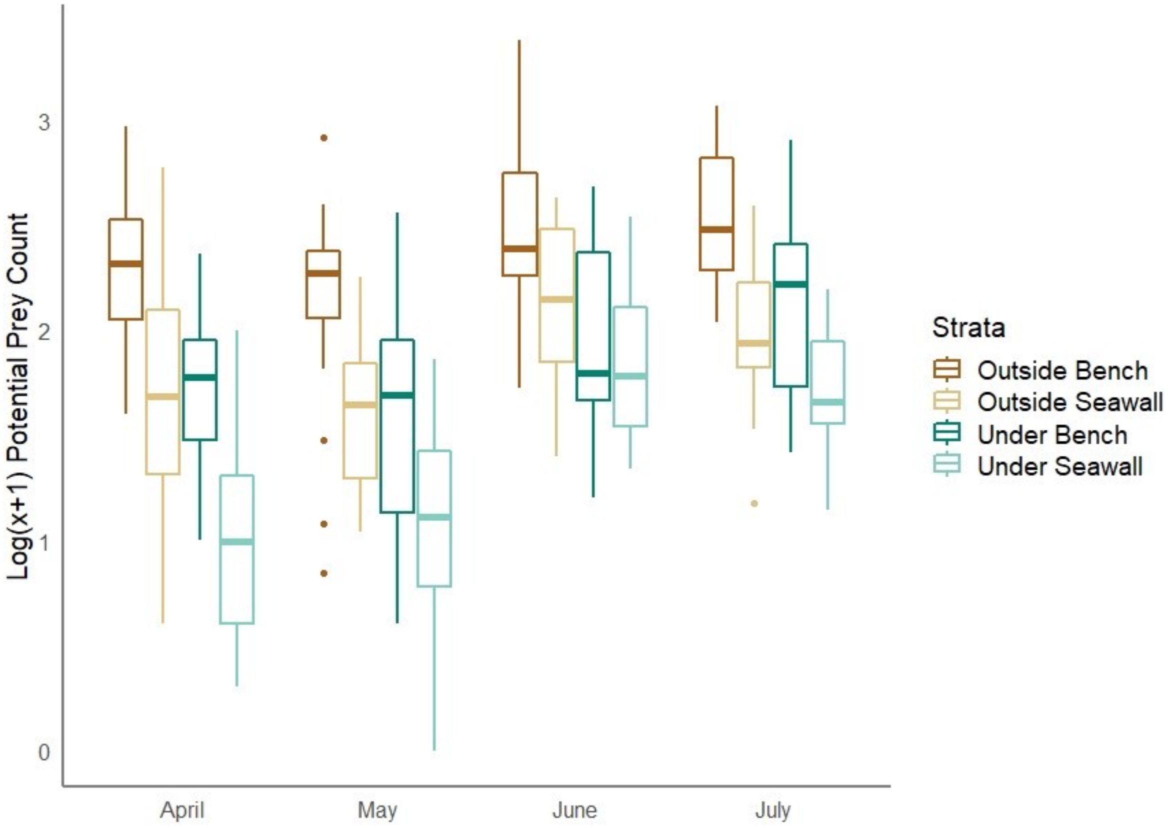

Figure 11. Potential juvenile pacific salmon prey taxa group (harpacticoids, gammarid amphipods, and insects) densities on seawall strata by month.

Prey important to juvenile chum salmon were found in highest densities at OB and lowest at US. There were significant differences among the strata and months of the prey taxa group densities (Table 2) but pairwise comparisons revealed those differences were not consistent (Table 8). Prey taxa densities were higher at the outside-strata than the under-strata, but there were not differences between surfaces within the same exposure (Figure 12).

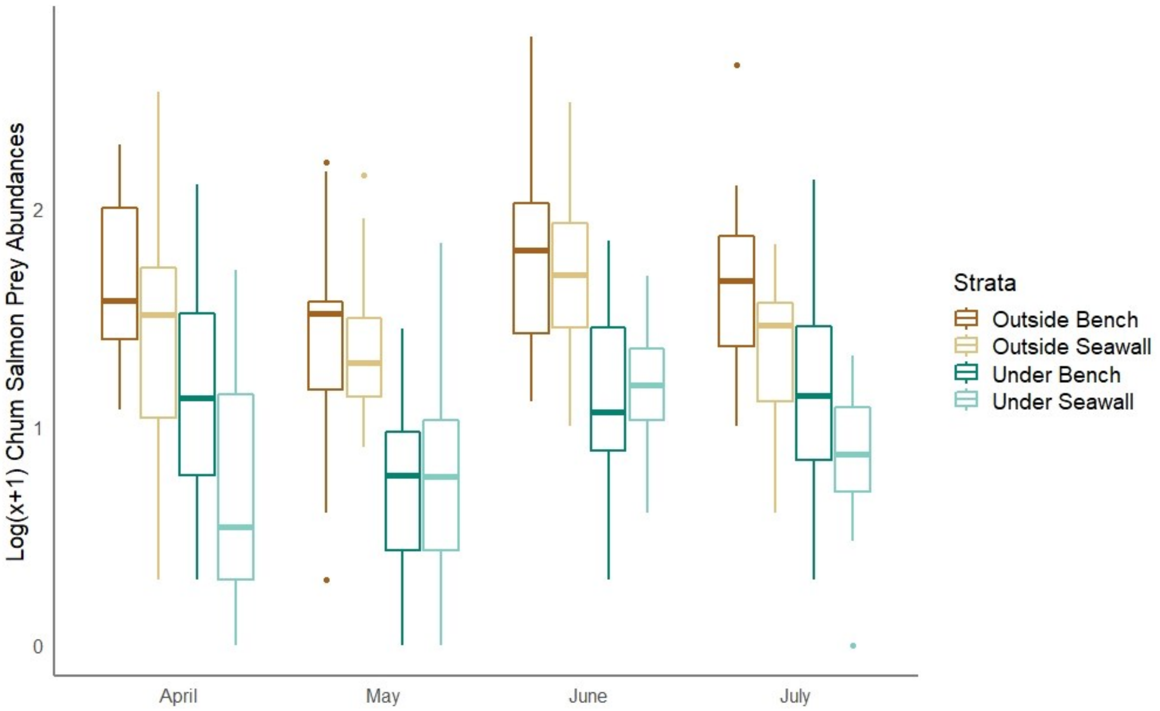

Figure 12. Prey taxa (*H. uniremis* group (including *H. uniremis*), *Tisbe* spp., *Zaus* spp., *Calliopius* spp.) densities on seawall strata by month.

Discussion

Epibenthic invertebrate assemblages varied by exposure (under-pier and outside-pier) and surface type (seawall shelf and bench). Taxa richness, overall epibenthic invertebrate densities, and densities of prey taxa important to juvenile salmon were positively correlated with the relative intensity of PAR received in support of my hypothesis that exposure would influence epibenthic invertebrate assemblages and congruent with previous studies that showed intertidal assemblages vary with light intensity (Struck et al. 2004, Blockley 2007, Cordell et al. 2017b). Assemblage structure also varied between surfaces within a level of exposure, and this may be attributed to the physical structure of the surfaces (textured concrete shelves versus the crushed rock marine bench). Eco-engineered surfaces that increase habitat heterogeneity along flat vertical seawalls have been shown to increase the numeric abundance and species diversity in benthic invertebrate communities (Chapman & Blockley 2009, Firth et al. 2016, Strain et al. 2018), but increased habitat complexity associated with the textured seawall had little effect on the epibenthic invertebrate community relative to the original seawall in the seawall-shelf design study (Cordell et al. 2017a). The interstitial space and crevices formed by the crushed rock lining the marine bench may have provided greater opportunity for algae to anchor and increased surface area and protection for the epibenthic community (Lee & Li 2013, Toft et al. 2013, Cordell et al. 2017a).

The seawall and bench surfaces experience varying photoperiods based on the position of the sun; for example, the OB strata may receive more PAR when the sun is rising or directly above the LPS and the west facing OS strata may receive more PAR when the sun is setting and lower on the horizon. Similar effects may extend to the under-pier strata, but the US strata likely experiences the lowest PAR due to the position of the piers. A reduction in PAR reaching nearshore waters can impact algae and other primary producers by reducing or preventing photosynthesis, leading to reductions or elimination of habitat available to phytal-associated epibenthic invertebrate communities (Blanton et al. 2001). Tidal height and seasonality may confound these effects by moderating light attenuation. Algae and invertebrates on the mid-tidal seawall shelf strata likely experienced greater levels of desiccation than those on the low-tidal bench strata. Wave energy is also probably higher on the seawall strata (Blockley and Chapman 2008) and disturbance from objects floating on or near the surface of the water more frequent, governing which taxa can reside there. Quantifying the interaction of these factors is needed to determine what eco-engineered designs and environmental setting provide the most ecological benefit.

Although we did not test these differences statistically, densities of all epibenthic invertebrates outside and under piers along the un-enhanced seawall were higher in 2014 (Cordell et al. 2017b) than on the respective eco-engineered seawall and bench strata in 2018 which may be a negative effect of the eco-engineering or due to interannual variation. The old un-enhanced seawall lacked overhanging structure or had a cantilevered ledge that was narrower than the three-meter-wide cantilevered sidewalk along the new eco-engineered seawall, so more unfiltered sunlight reached the outside-pier seawall surface throughout the day. Even with the LPS, the expansion of overhanging structure resulted in a reduction in daily photoperiod that may have had a negative effect on overall algal growth on the outside-pier seawall shelves relative to the old seawall surface (Sawyer et al. 2020). However, total densities and taxa richness on the outside-pier strata (OB and OS) were similar to what was found at the OSP pocket beach (where densities and taxa richness have been shown to be higher than at armored sites) in 2018 (un-published) suggesting differences between 2014 and 2018 were more likely due to interannual variability.

Similar densities of the harpacticoids *H. uniremis* group and *Zaus* spp. and the amphipod *Calliopius* spp. among the outside-pier strata and OSP (un-published) suggest the eco-engineering structures support higher prey densities relative to the un-enhanced seawall. *Tisbe* spp. were also found in similar densities among the outside-pier strata and OSP (un-published) in

2018, but they were in lower densities under-piers than they were outside piers, contrary to pre-eco-engineering conditions (Cordell et al 2017b). *H. uniremis* group and *Zaus* spp. are phytal associated taxa (Hicks and Coull 1983, Boxshall 2004) so were expected in higher densities outside piers where algae production would be the greatest, but *Tisbe* spp. is more ecologically diverse with epiphytic species and non-phytal associated species that can be sediment or benthic dwelling and found in deep sea environments (Hicks and Coull 1983, Boxshall 2004, Ivanenko et al. 2011). Non-phytal *Tisbe* spp. may have been more abundant in 2014 and it is unclear if this is an effect of the eco-engineering, increased light under-piers, or interannual variability. The outside-pier eco-engineering supports preferred harpacticoid prey of small juvenile chum salmon (*H. uniremis* group, *Tisbe* spp., *Zaus* spp., and *Calliopius* spp.) in densities similar to what is considered more natural or appropriate habitat. If prey produced on the bench and seawall strata are accessible to juvenile salmon, the combination of the two habitats may have increased the overall densities of prey available to juvenile salmon migrating along the eco-engineered seawall. However, diet studies are needed to determine if juvenile salmon can access that prey and benefit from the increased production. It remains unclear and may require multiple years of monitoring to determine if shading from the LPS negatively impacts the density and taxa richness of the epibenthic community or if those differences are simply an effect of interannual variability.

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Chapter 3: Juvenile chum salmon (*Oncorhynchus keta*) diets among a mosaic of developed and eco-engineered shorelines

Introduction

Puget Sound and the larger Salish Sea region support nine species of Pacific salmon and trout. Several populations in the region are listed as threatened or endangered under the Endangered Species Act, including Puget Sound Chinook salmon (*Oncorhynchus tshawytscha*) and Puget Sound steelhead trout (*O. mykiss*). Chum (*O. keta*) and pink salmon (*O. gorbuscha*) are the numerically dominant species but certain populations also have exhibited significant declines. Estuarine and nearshore marine residence times and habitat preferences vary among and within species and populations (Quinn 2018) and due to nearshore extended residence of some populations, these habitats appear to be important to juvenile salmon population viability (Thorpe 1994, Fresh 2006).

Small juvenile chum salmon (<50 mm forklength (FL)) show an affinity for shallow and intertidal estuarine shorelines (Quinn 2018) but transition to deeper waters when between 50 and 60 mm (Healey 1982, Simenstad et al. 1982). Along unaltered shorelines, smaller juvenile chum salmon generally consume epibenthic prey (harpacticoid copepods and gammarid amphipods) in shallow marine waters and terrestrial prey (often as aquatic early life history stages like chironomid fly larvae and other insects) (Healey et al. 1979, Levy et al. 1979, Sibert 1979, Simenstad et al. 1982) in both estuarine and marine waters. Larger fish that have transitioned to deeper water consume a variety of planktonic prey (calanoid copepods, decapod larvae, larvaceans, hyperiid amphipods, euphausiid larvae, fish larvae) and (in estuarine waters) drift insects (Quinn 2018). Similar prey preferences have been observed for juvenile chum salmon in restored habitats (Shreffler et al. 1992, Cordell et al. 2011). However, altered shorelines can affect juvenile salmon behavior and the availability of and access to prey (Morley et al. 2012, Toft et al. 2013, Munsch et al. 2014, 2015a, 2015b, 2017, Cordell et al. 2017a, Cordell et al. 2017b).

The shoreline in Seattle, WA, USA has been highly modified since the 1930s by the development of a seawall, large shipping port, piers, and other in- and over-water structures. The seawall was built into the intertidal and shallow subtidal where at high tides, water at the seawall interface could be as much as 10 m deep, preventing juvenile salmon from accessing shallow habitat while out-migrating along the shoreline. Several studies have investigated the effects of these structures on juvenile salmon behavior and access to epibenthic invertebrate prey along the Seattle waterfront (Toft et al. 2013, Munsch et al. 2014, 2015a, 2015b, 2017, Cordell et al. 2017a, Cordell et al. 2017b, Sawyer et al. 2020, Accola et al. 2022). Munsch et al. (2014) found that juvenile salmon behavior around piers varied among species and was influenced by tidal height. At high tide, juvenile salmon avoided the shade cast by piers and tended to aggregate in the pier-seawall corners however, at low tide, when light penetrated deeper under the pier, juvenile chum and pink salmon were observed under piers (Munsch et al. 2014). Chinook salmon were never observed under the piers and instead presumably continued around the pier into deeper water. Overall juvenile salmon were observed feeding in the open area between piers and in the corners (where piers meet the seawall) more than under piers at high tides. Juvenile chum and pink salmon also fed less under piers at low tide, but these differences were not significant (Munsch et al. 2014) and Chinook salmon were never observed feeding under piers. Ono and Simenstad (2014) found similar avoidance of pear shading by juvenile salmon around a pier in another area of Puget Sound. Shading is also associated with composition of epibenthic invertebrate on shorelines and armoring directly below (Munsch et al. 2015, Cordell et al. 2017b, Chapter 2) and the flat, vertical surface of the seawall also results in lower abundances and diversity of juvenile salmon epibenthic prey compared to unaltered beaches (Goff 2010, Toft et al. 2013, Cordell et al. 2017a).

Following an earthquake in 2001 that damaged the original Seattle seawall, local agencies elected to replace it with an eco-engineered design that could reduce the negative impacts to out-migrating juvenile salmon. Originally, a street and sidewalk ran along the edge of the seawall, but the new seawall was built three meters landward of the original position. To preserve pedestrian access, a three-meter-wide cantilevered sidewalk was built over the water. Glass panels were embedded in the sidewalk (LPS) (Figure 2) to allow some level of light to pass through, illuminating the seawall and water below to encourage juvenile salmon to swim under the piers rather than around them. In addition, a steel wall was also placed three meters in front of and parallel to the new seawall up to the MSL elevation and the space between the two walls was filled with rocks, creating a marine bench to provide shallow water habitat to migrating juvenile salmon. Lastly, the new seawall surface included shallow sloped ledges and complex texture which have been shown to support higher densities and greater diversity of juvenile salmon prey (Goff 2010, Cordell et al. 2017a, Chapter 2).

Construction of the new eco-engineered seawall was completed in 2017 and post construction monitoring began in 2018. Post-construction monitoring showed changes in juvenile salmon feeding behavior and distribution among nearshore areas (3 m from the seawall) and offshore areas (10 m from the seawall) under and between-piers along the eco-engineered seawall (Sawyer et al. 2020). Juvenile salmon were more evenly distributed among nearshore areas (under and between-piers) and the offshore between-pier area. The only significant difference found among the four areas was between the two offshore areas where higher juvenile salmon densities were found between piers, suggesting the eco-engineered seawall is promoting juvenile salmon migration under piers likely due to increased under-pier light from the LPS sidewalk (Sawyer et a. 2020). Interestingly though, the proportion of juvenile salmon occupying offshore between-pier areas was higher than at all other strata suggesting a relative offshore shift. This trend may have been due to the LPS sidewalk because overall light intensity decreased in the nearshore between-pier areas with the setback of the new eco-engineered seawall and cantilever of the sidewalk. Epibenthic invertebrate prey of juvenile chum salmon were observed in similar or elevated abundances along the eco-engineered habitat relative to the original seawall (Chapter 2) and juvenile salmon were observed feeding above the marine bench and along the nearshore habitat (Sawyer et al. 2020, Accola et al. 2022).

Recent studies have observed juvenile salmon migrating and feeding above the habitat benches and under piers that they previously avoided (Sawyer et al. 2020, Accola et al. 2022), and that the marine bench and seawall ledge surfaces between piers are supporting epibenthic prey typically preferred by juvenile salmon (Chapter 2). However, it is unclear if juvenile salmon occupying these eco-engineered habitats can utilize prey produced there, or if they are feeding on prey from other sources. Here, I investigate the diets of juvenile chum salmon migrating along the eco-engineered Seattle seawall and from four other nearby locations representing a variety of altered shorelines (Figure 13). These sites include the original seawall, a restored pocket beach, a rip-rap armored beach, and an armored beach with an eco-engineered habitat bench similar to the marine bench along the eco-engineered seawall. I hypothesized that if the type of shoreline alteration affects juvenile chum salmon prey consumption, then terrestrial and epibenthic prey would be consumed at the unarmored and restored pocket beach (Beach), epibenthic prey at the eco-engineered seawall (New), planktonic prey at the original seawall (Old), and from epibenthic and planktonic sources at the habitat bench (Bench) and river mouth (Riprap).

Methods

Study Area

Puget Sound is an estuarine fjord in the Pacific Northwest, USA, positioned between the Olympic Mountains to the west and Cascade Range to the east and the southern reach of the larger shared waters of the Salish Sea with British Columbia, Canada to the north. This study was conducted along the Seattle, WA waterfront and the eastern shoreline of Elliott Bay in central Puget Sound (Figure 13). Most juvenile chum salmon found in Elliott Bay enter from the Duwamish River watershed which empties into the southern end of Elliott Bay and typically migrate northward along the shoreline. The shoreline in Elliott Bay is mostly armored and the Duwamish River delta has been almost entirely developed.

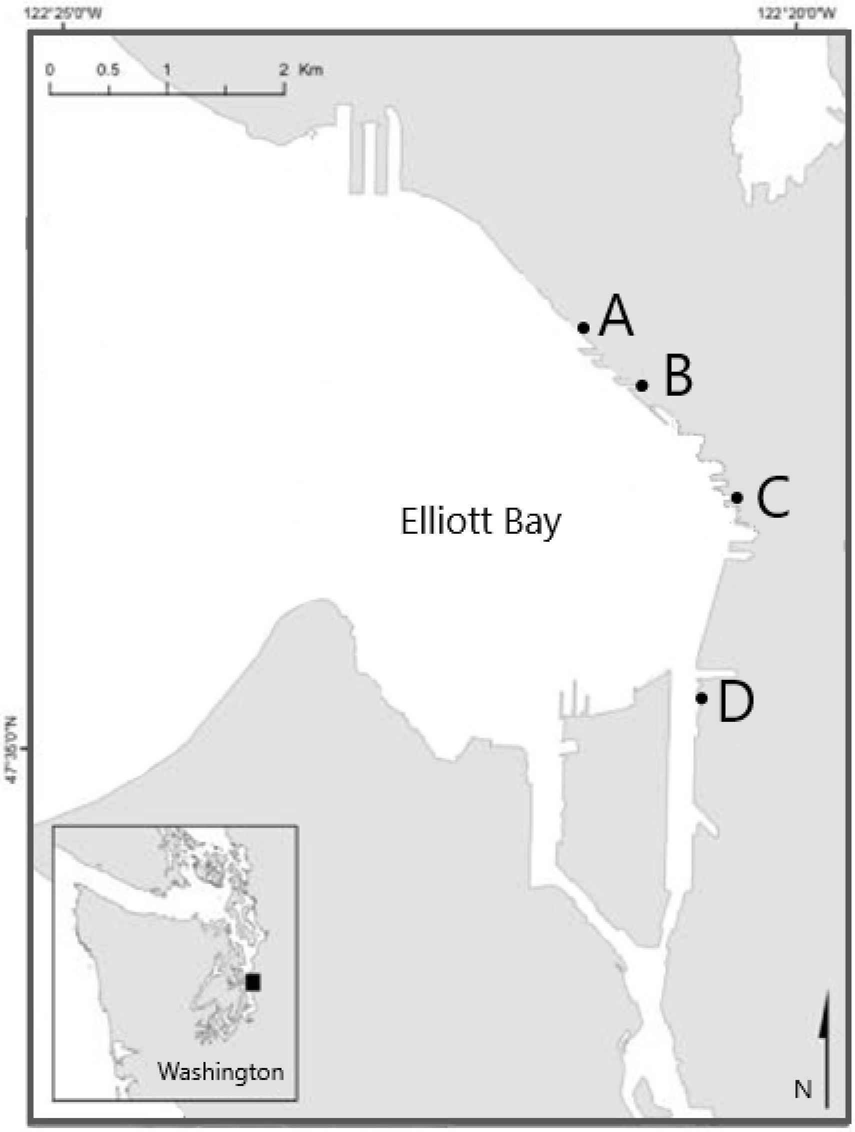

Figure 13. Map of Elliot Bay. Juvenile chum salmon collection sites: A. OSP Pocket Beach (Beach) & Habitat Bench (Bench), B. Seawall without eco-engineering (Old), C. Seawall with eco-engineering (New). D. Riprap pocket beach at Duwamish River Mouth (Riprap)

Sampling Design

Sampling occurred twice during the typical out-migration period for juvenile chum salmon in early and mid-May 2019 at five sites along the waterfront (Figure 13). The southernmost site, hereafter Riprap, is a small riprap armored beach adjacent to a derelict pier, at the mouth of the Duwamish River, and across from the artificial Harbor Island (Figure 14).

North of Riprap is the eco-engineered seawall site (New) followed by the original seawall site (Old). The two remaining sites are immediately north of the waterfront at the Olympic Sculpture Park and part of an urban habitat enhancement project (Toft et al. 2013). The habitat bench (Bench) is a stretch of eco-engineered shallow habitat similar to the bench at New but is fronted by sloping habitat rather than a steel wall and backed by riprap and a concrete seawall. Beach is a small, pocket beach composed of pebbles, naturally recruited driftwood, and a narrow strip of riparian vegetation.

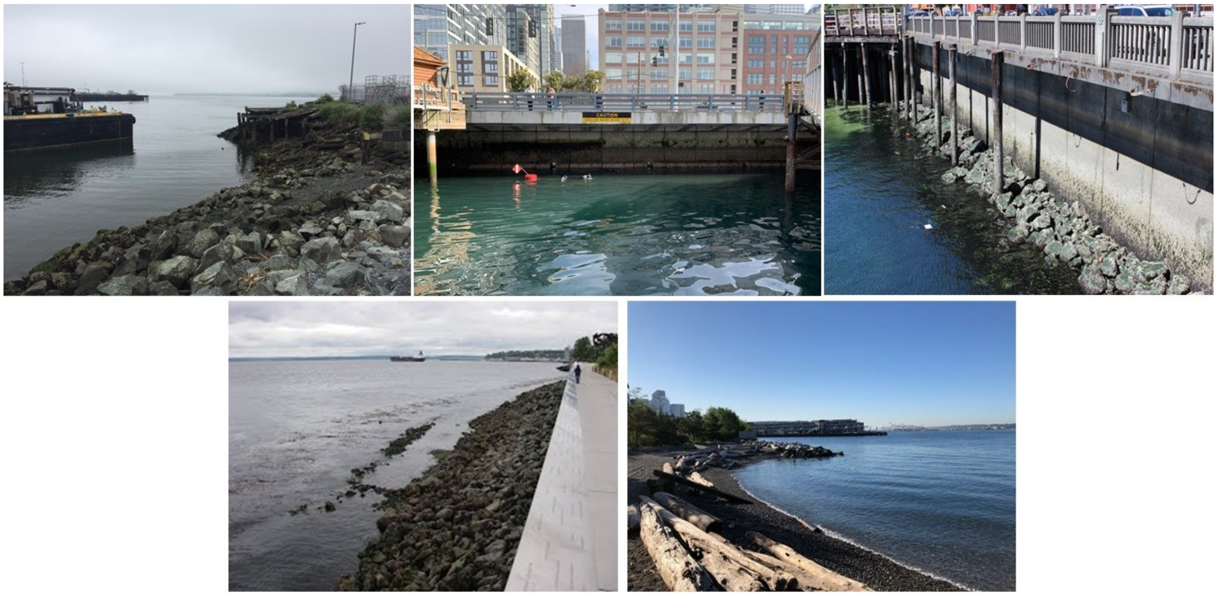

Figure 14. Juvenile salmon diet collection sites arranged from South to North along the Elliot Bay Shoreline: **Top Left**: Riprap, **Top Center**: New, **Top Right**: Old, **Bottom Left**: Bench, **Bottom Right**: Beach

Juvenile chum salmon were netted using either a beach seine (37 m x 2 m, with 0.64 cm mesh) or pole seine (9.1 m x 1.2 m, with 0.64 cm mesh). At Beach, one snorkeler swam perpendicular to shore pulling one end of the beach seine while another person waited on shore. The net was extended to its full length or until an observer detected a school of salmon accessible for netting, after which the snorkeler would swim parallel to shore before returning to shore to close the net. The net was then pulled to shore and any catch promptly processed as described below. Netting with a beach seine was not possible at the other sites due to the position of adjacent piers (New and Old) or water depth (Riprap, Old, and Bench). Instead, two snorkelers directed by over- and in-water observers targeted a school of salmon by quickly circling the fish with a pole seine (Figure 15). Targeted fish were then hand netted and transferred to buckets. In both methods, juvenile chum salmon were identified and up to 10 individuals less than 50 mm FL were euthanized using a lethal dose of MS-222 and preserved in 10% Formalin. Fish of this size class were targeted because juvenile chum salmon typically transition from epibenthic feeding to planktonic feeding above 50 mm FL (Simenstad et al. 1982). All remaining fish were released.

Figure 15. Netting for juvenile chum salmon using a pole seine at New.

The preserved fish were returned to the lab for further processing, weighed and measured, and the stomach was then removed and weighed prior to dissection. Gut contents were sorted, identified, enumerated, and weighed along with the empty stomach. Prey were typically identified to family, genus, or species for insects, harpacticoids, gammarid amphipods, decapods, and polychaetes; all other taxa were identified to higher taxonomic levels.

Juvenile chum salmon are highly mobile and both the sites and the distances between sites in this study are small. To increase the likelihood of detecting prey consumed specifically from the site or very near where fish were collected, stomachs were subdivided into three sections to stratify relative time since consumption (Figure 16) and we repeated the analysis using only prey from the first gut partition (1), the most anterior section of the stomach. However, many of the analyses could not be performed due to low prey content in the first partition but an NMDS ordination of prey counts and the results from the plankton univariate analyses in the first partition could be presented.

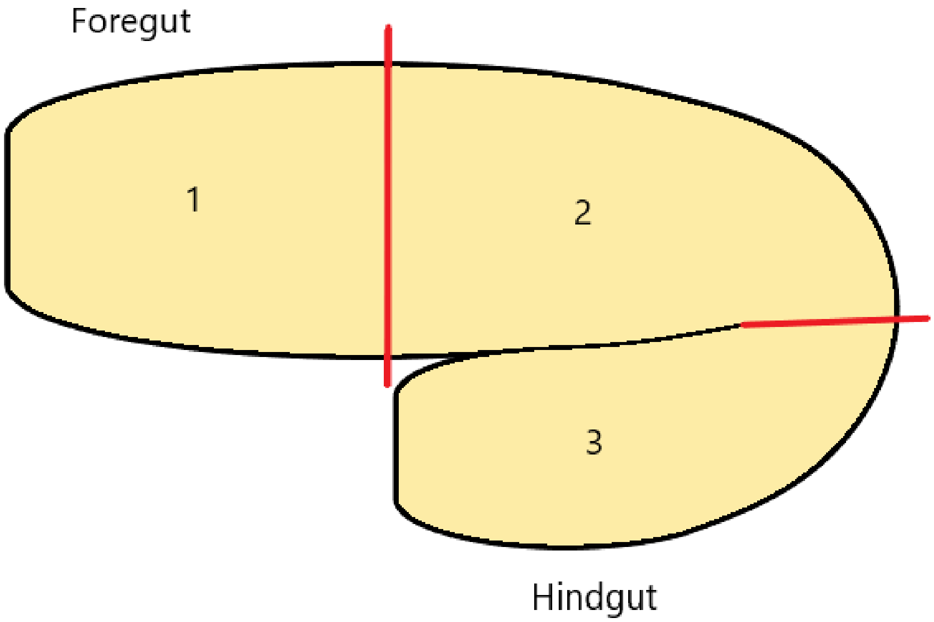

Figure 16. Juvenile chum salmon gut partitions. Contents of all three partitions were used in the entire gut analyses. Only prey contents of partition 1 were used in the first gut partition analyses.

Diet Assemblage Analysis

Prey count and weight data were analyzed separately. Prey taxa were grouped into larger taxonomic and ecologically relevant categories to reduce the abundance of zeros in the raw data and the dissimilarity matrices. Extremely rare taxa accounting for less than 0.07% of counted individuals were removed from the count data. Extremely rare taxa (<0.3%) and diet material (<10%) by weight that could not be identified were removed from the weight data. Count and weight data were square-root transformed to stabilize variances and reduce the effects of rare and abundant taxa.

Non-metric multidimensional scaling (NMDS) ordination was used to characterize differences in the diet composition of juvenile chum salmon among the five shoreline sites and between sampling events. Species vectors representing prey taxa from the chum salmon diets were fit onto the ordination using the ‘envfit’ function in R with 999 permutations. Site (Bench, New, Old, Beach, and Riprap) and sampling event (Event 1 & 2) were included as grouping factors. Diet composition of juvenile chum salmon collected from the five shoreline sites were compared using a permutational multivariate analysis of variance (PERMANOVA) on a Bray-Curtis similarity matrix with 999 permutations. Site and sampling event were included as fixed factors. nMDS ordinations and PERMANOVAs were performed using the ‘vegan’ package in R (Oksanen et al. 2020).

Prey Source Analysis

Prey taxa were further grouped into habitat sources (plankton, epibenthic, and terrestrial) for univariate analysis. “Plankton” refers to neritic taxa (e.g., calanoid copepods, euphausiid larvae, larvaceans) that reside in the water column and likely would have been consumed there. “Epibenthic” taxa are those that typically reside in the epibenthos (e.g., harpacticoid copepods, amphipods), are usually associated with biogenic substrata (e.g., sessile invertebrates, algae), and would have been consumed from or near the shoreline surface. “Terrestrial” taxa were mostly insects that would have fallen onto the surface of the water (or were pupal stages of Diptera that migrated to the water surface to emerge) and could have been consumed at the water surface or in the water column. Prior to analysis, Tukey’s Ladder of Powers test was used to determine transformations that would best normalize the data. Plankton count and weight data were square-root transformed and the epibenthic and terrestrial count and weight data were $x^{1/5}$ transformed.

I used two-way analysis of variance (ANOVA) tests with interaction to test for differences among sites and sampling events in chum salmon diets followed by multiple pairwise comparison tests (PWC). When two-way interactions were non-significant, multiple pairwise comparison tests with a Bonferroni adjustment were used to test for pairwise differences among sites and between events if main effects were significant. If a significant interaction ($p<0.05$) was detected, simple pairwise comparison tests with a Bonferroni adjustment were used.

Results

Site Fidelity

Due to low total contents in the first gut partitions and because the NMDS ordinations of the first gut partitions and the entire guts were similar (Figure 23), this study focused on the entire gut and the interpretation assumes the entire gut contents represent feeding within the site fish were collected. Distinct differences in diets among sites would have provided greater confidence to associate prey with specific sites, so the similarities among the diets at New, Old, and Bench require cautious consideration.

Prey Composition of Entire Gut

A total of 69 juvenile chum salmon FL < 50mm were collected from the five Seattle waterfront sites over two sampling events: 14, 20, 13, 10, and 12, respectively, from Riprap, New, Old, Bench, and Beach respectively (Table 3). In Event 1, the targeted 10 fish were collected from Riprap, New, Old, and Bench and 7 from Beach. The remainder were collected in Event 2. No fish were caught at Bench in Event 2.

Table 3. Fish sizes and the number of diets that contained harpacticoid copepods at the five shoreline sites.

Site	Number of Fish ≤ 49mm	Size Range (mm)	Mean Size (mm)	Median Size (mm)	# Diets Containing Harpacticoids	Total Harpacticoids Counted
Riprap	14	37 - 49	44	45	6	13
New	20	36 - 49	43	43	5	5
Old	13	40 - 49	44	44	2	3
Bench	10	39 - 45	42	42	2	3
Beach	12	37 - 49	43	43	5	17

The overall (total stomach) diet composition of juvenile chum salmon were numerically and gravimetrically dominated by planktonic prey (Figure 17, Figure 18). Planktonic (neritic) calanoid and cyclopoid copepods were the dominant prey taxa in the diets of fish collected from Riprap (n=14) (Figure 19, Figure 20) but several fish consumed terrestrial chironomid pupae, teneral adults (emerging from pupae to adult form typically at the water's surface), and adults almost exclusively (Figure 21, Figure 22). Fish collected sequentially north along the shoreline from New (n=20), Old (n=13), and Bench (n=10), also consumed mostly planktonic taxa, but the proportion of calanoids decreased as euphausiids became increasingly prominent at the northern sites (Figure 19, Figure 20). Terrestrial and epibenthic taxa were rare in the diets from New, Old, and Bench (Figure 21, Figure 22). Fish from Beach (n=12) consumed a much more varied diet with higher contributions of terrestrial and epibenthic prey by weight as chironomid and hemipteran insects, and gammarid amphipods, respectively (Figure 19, Figure 20). Epibenthic harpacticoid copepods were rare among all sites and were mostly found in the diets of fish from

Beach (Figure 21, Figure 22). *H. uniremis* group accounted for nearly 60% of harpacticoids in the diets while all other harpacticoid taxa were rare.

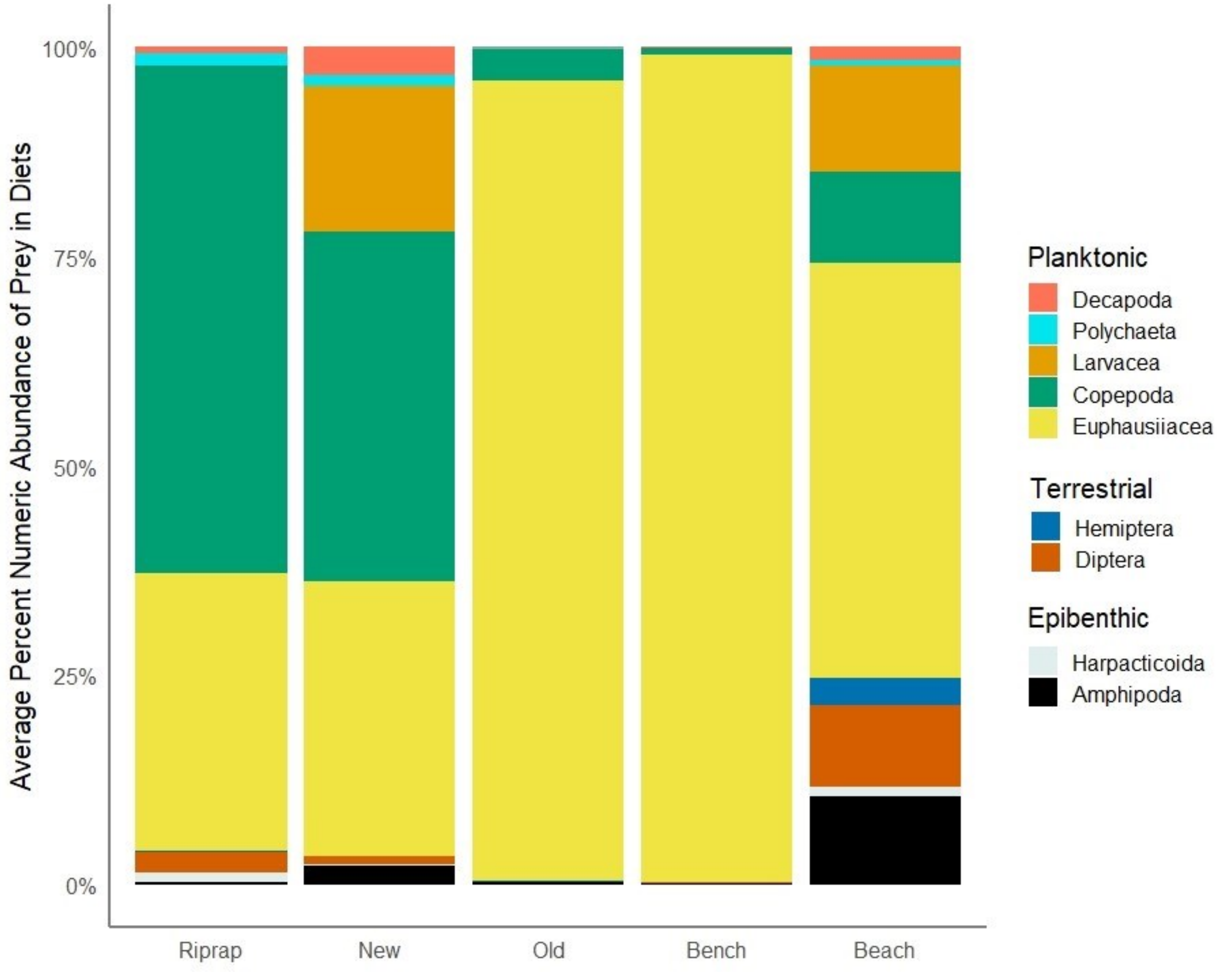

Figure 17. Average percent numeric abundance of prey in the entire gut of juvenile chum salmon from both Events among the five shoreline sites. Prey within the source categories are ordered from bottom to top by increasing total abundance from all sites combined.

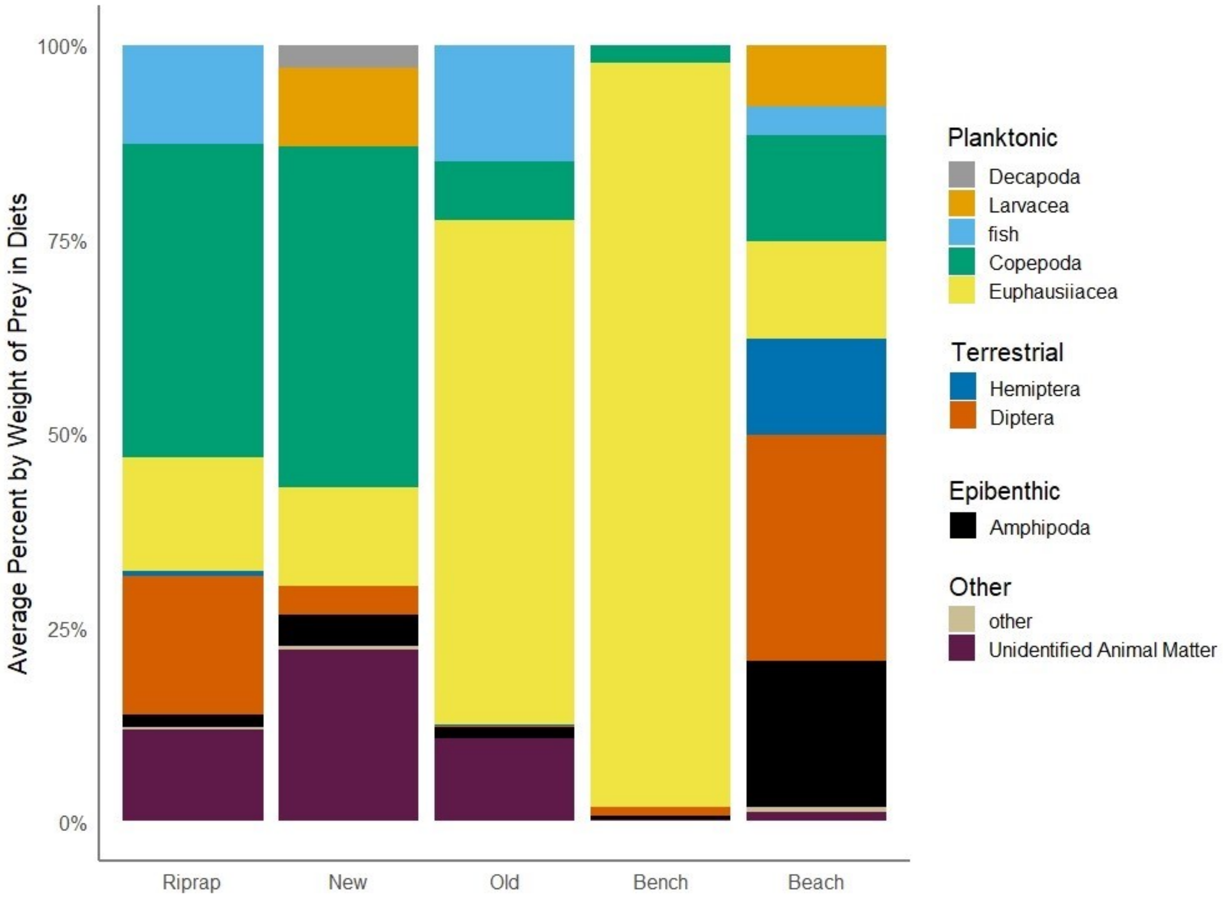

Figure 18. Average percent by weight of prey in the entire gut of juvenile chum salmon from both Events among the five shoreline sites. Prey within the source categories are ordered from bottom to top by increasing total weight from all sites combined. To simplify plots, prey from all sources that had very low relative weights are grouped into “other.” “Unidentified Animal Matter” refers to animal matter that was too digested to identify.

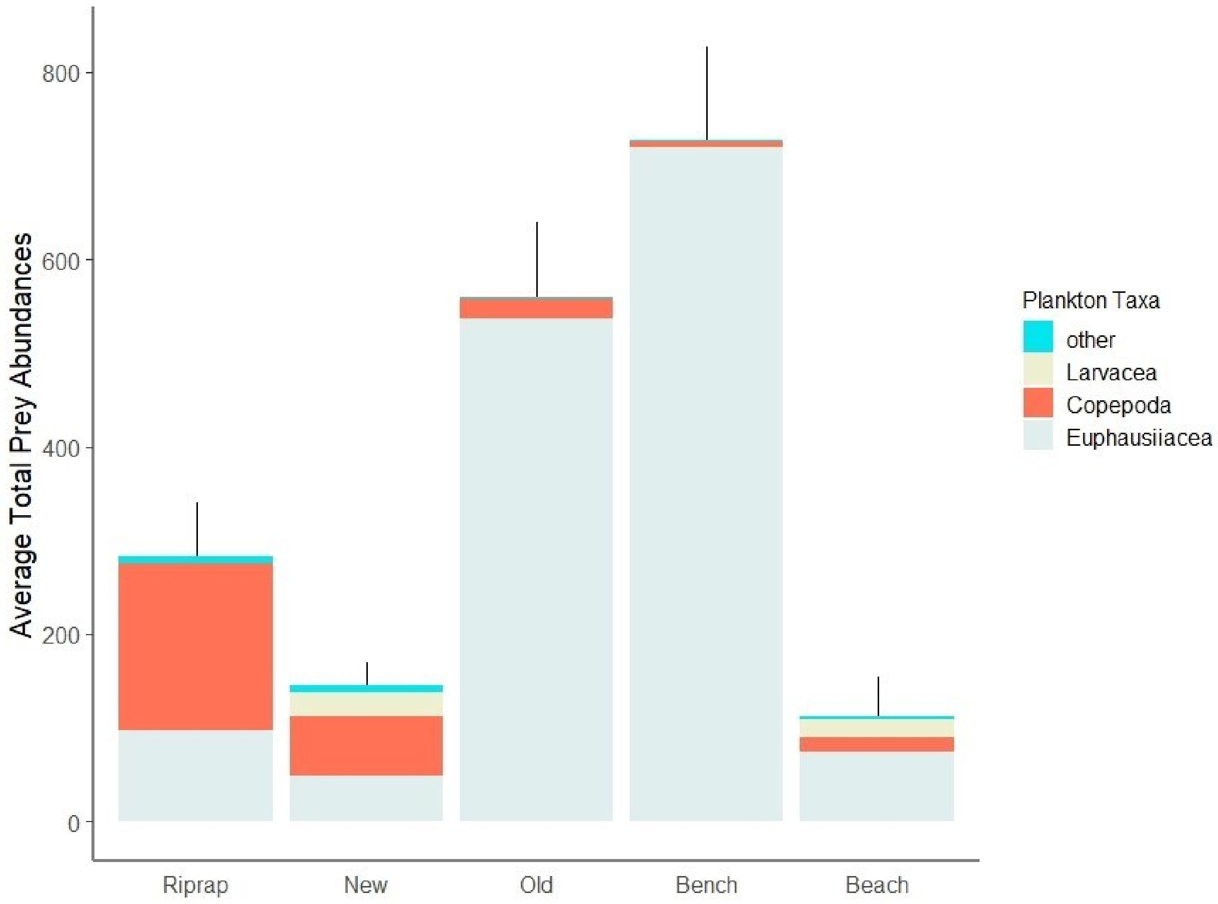

Figure 19. Average total prey abundance of planktonic prey in the entire gut of juvenile chum salmon from both Events among the five shoreline sites. Prey are ordered from bottom to top by increasing total abundance from all sites combined.

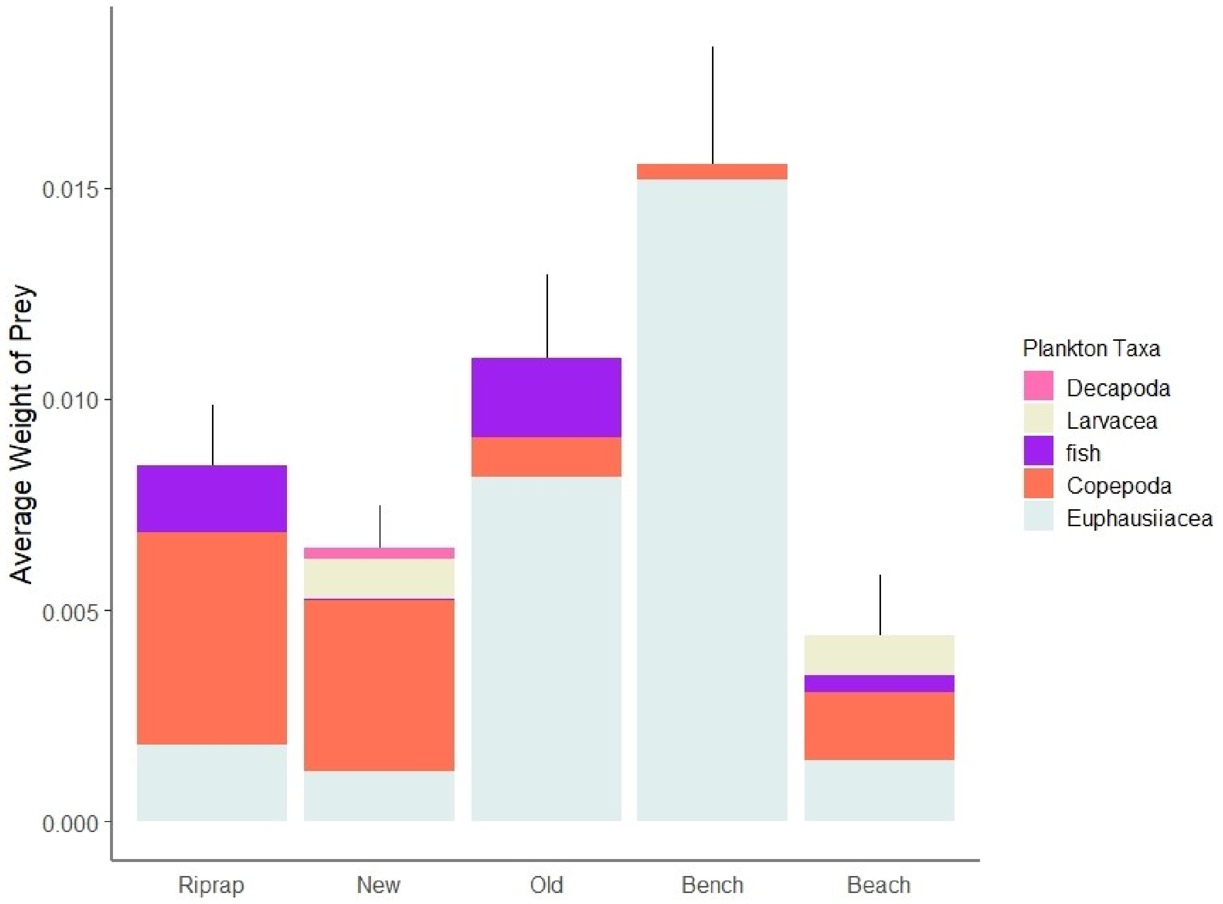

Figure 20. Average total prey by weight (grams) of planktonic prey in the entire gut of juvenile chum salmon from both Events among the five shoreline sites. Prey are ordered from bottom to top by increasing total weight from all sites combined.

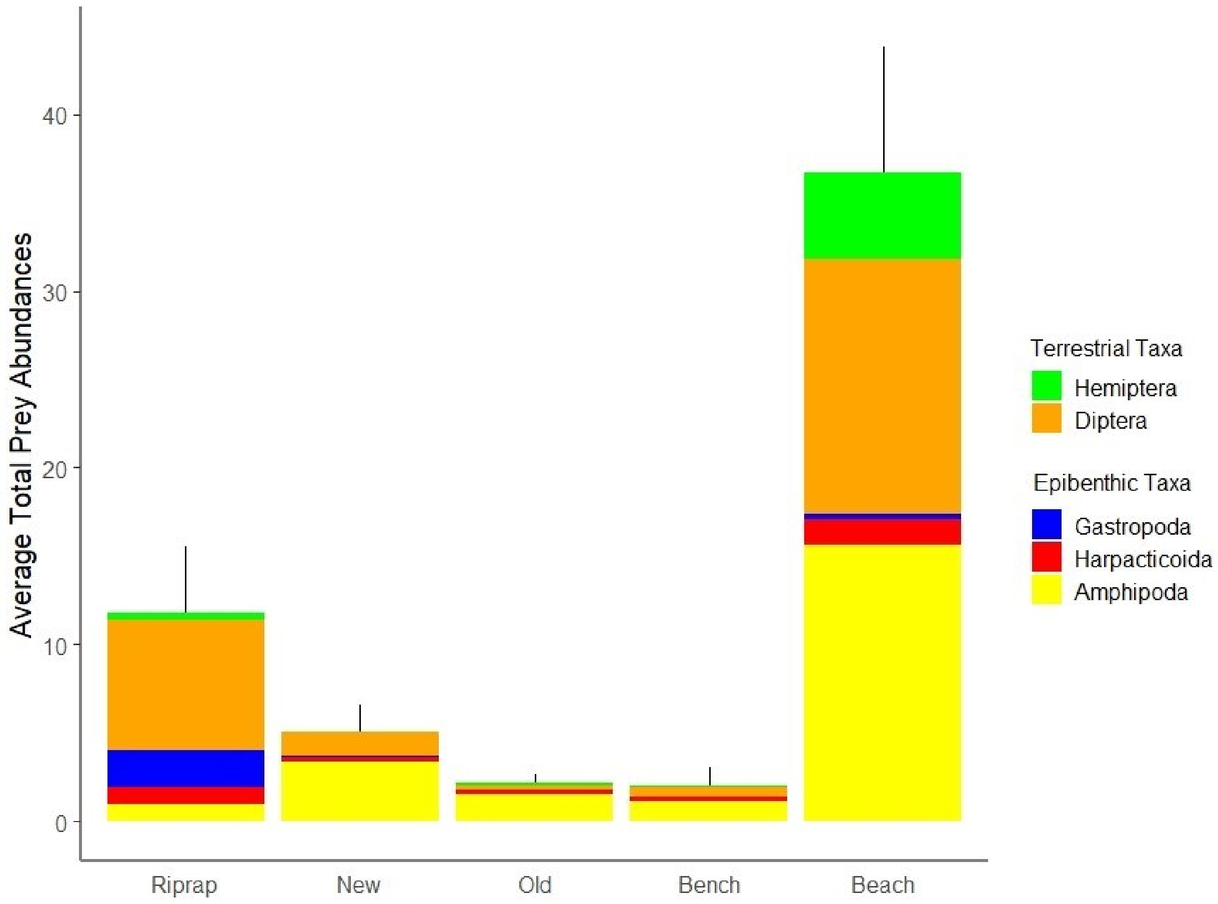

Figure 21. Average total prey abundances of terrestrial and epibenthic prey in the entire gut of juvenile chum salmon from both events among the five shoreline sites. Prey are ordered from bottom to top by type and increasing total abundance from all sites combined.

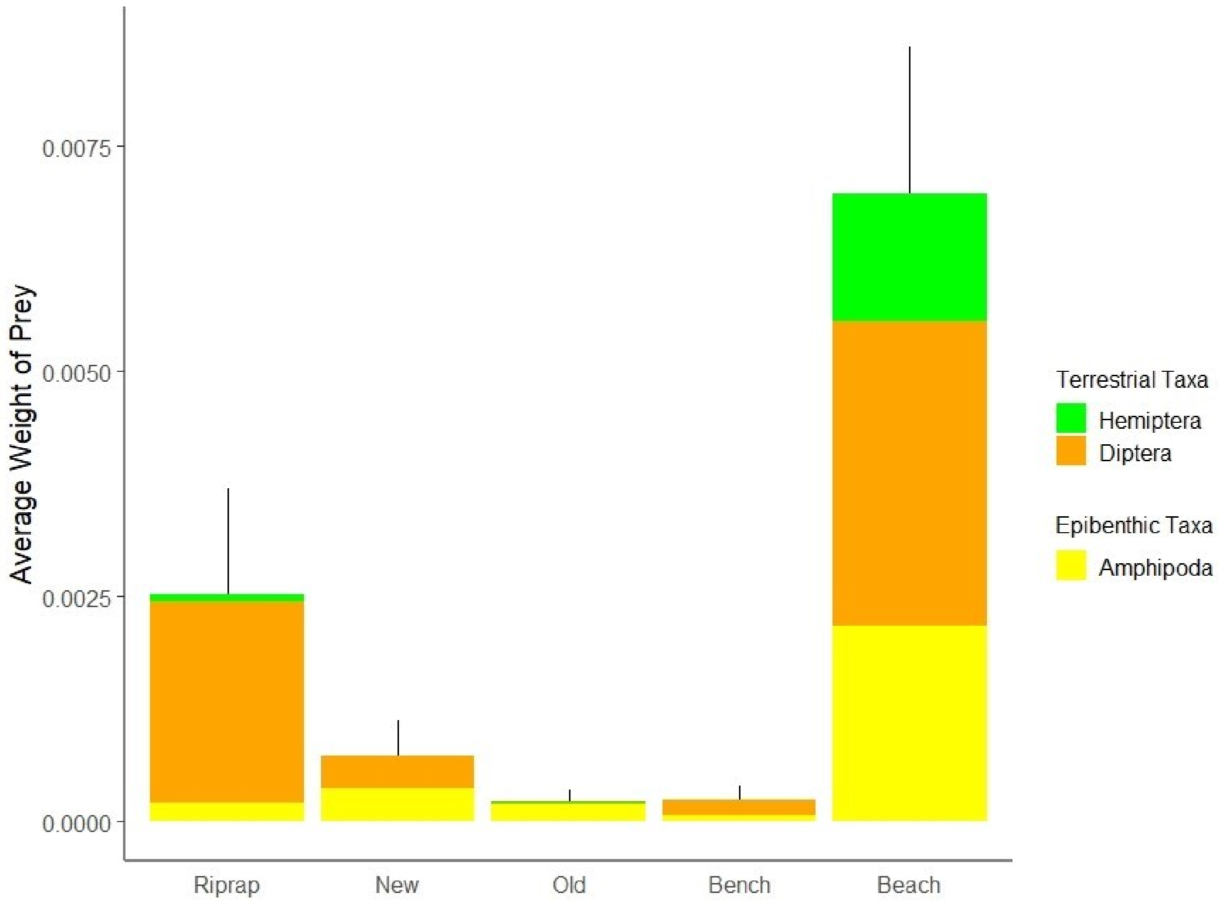

Figure 22. Average total prey by weight (grams) of terrestrial and epibenthic prey in the entire gut of juvenile chum salmon from both events among the five shoreline sites. Prey are ordered from bottom to top by type and increasing total weight from all sites combined.

Site Comparisons of Diet Composition

There was a significant effect of site and a significant interaction of site and event ($P<0.05$) on the composition of prey by count and weight in the entire gut (Table 4) (PERMANOVA). The NMDS ordination of prey counts and vector ordination indicated that the prey in diets were primarily characterized by either planktonic copepods (New) or euphausiids (Old and Bench), or a combination of epibenthic, terrestrial and other planktonic prey (Riprap and Beach) (Figure 23). Fish diets from Riprap and New were associated with planktonic calanoid and cyclopoid copepods, polychaete larvae, and decapod larvae. Diets from Old and

Bench clustered together and were generally associated with planktonic euphausiid larvae. Insects, epibenthic amphipods, and fish larvae were associated with fish diets from Beach. There were differences in the taxa that drove separation between the first gut partition and the entire gut, but those differences were among taxa within the same prey group; for example, planktonic larvaceans were significant drivers of differences in the first gut partition while planktonic copepods and decapods were significant drivers in the entire gut.

Table 4. Summary statistics from a PERMANOVA of juvenile chum salmon prey count and weight data from the five shoreline sites (Bench, New, Old, Beach, and Riprap) and two sampling events.

Data Type	Source	Df	MS	Pseudo-F	R^2	P (perm)
Counts	Site	4	1.35	12.2	0.349	**<0.001**
	Event	1	0.89	8.1	0.058	**<0.001**
	Site x Event	3	0.85	7.7	0.166	**<0.001**
	Residuals	68	0.11		0.428	
Weights	Site	4	1.48	9.5	0.307	**<0.001**
	Event	1	0.99	6.4	0.051	**<0.001**
	Site x Event	3	1.01	6.5	0.157	**<0.001**
	Residuals	68	0.16		0.485	

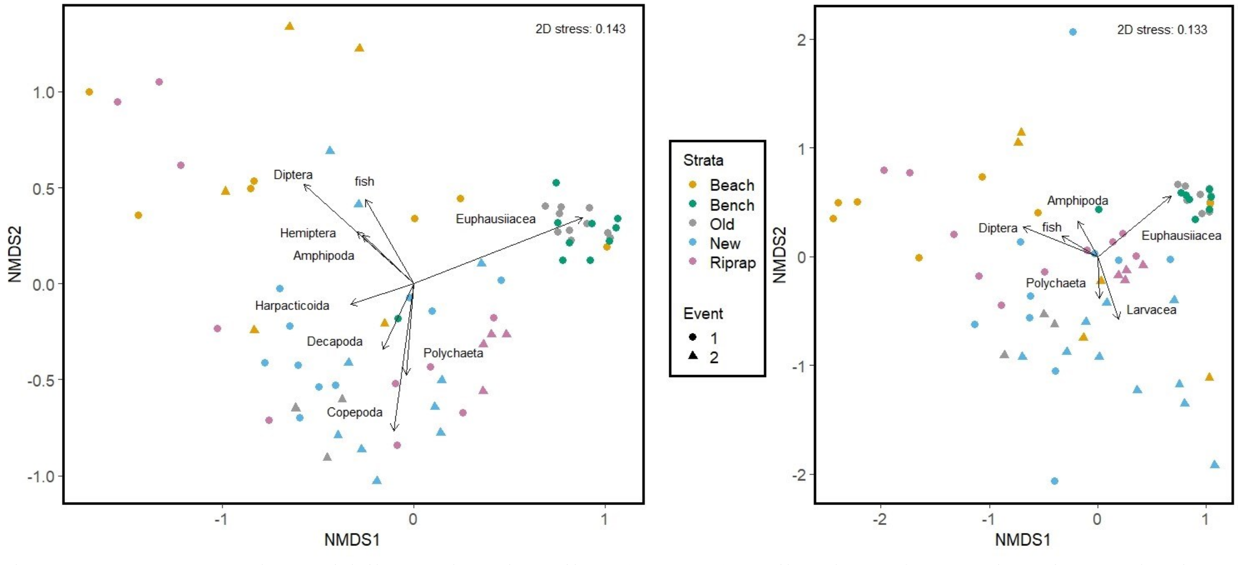

Figure 23. Non-metric multidimensional scaling (NMDS) ordination of prey abundances in the entire gut (Left) and first partition (Right) of juvenile chum salmon from the five shoreline sites.

Points on the ordination are individual fish and arrows are fitted vectors of prey taxa. Only taxa that were significant (P>0.05) are shown.

The NMDS ordination of prey weight data in the entire gut similarly showed that the four southern sites were associated with planktonic prey taxa while Beach was associated with all prey groups (Figure 24). Fish from New, Old, and Bench were generally associated with planktonic prey and fish from Beach were associated with terrestrial and epibenthic prey more so than fish from the other sites.

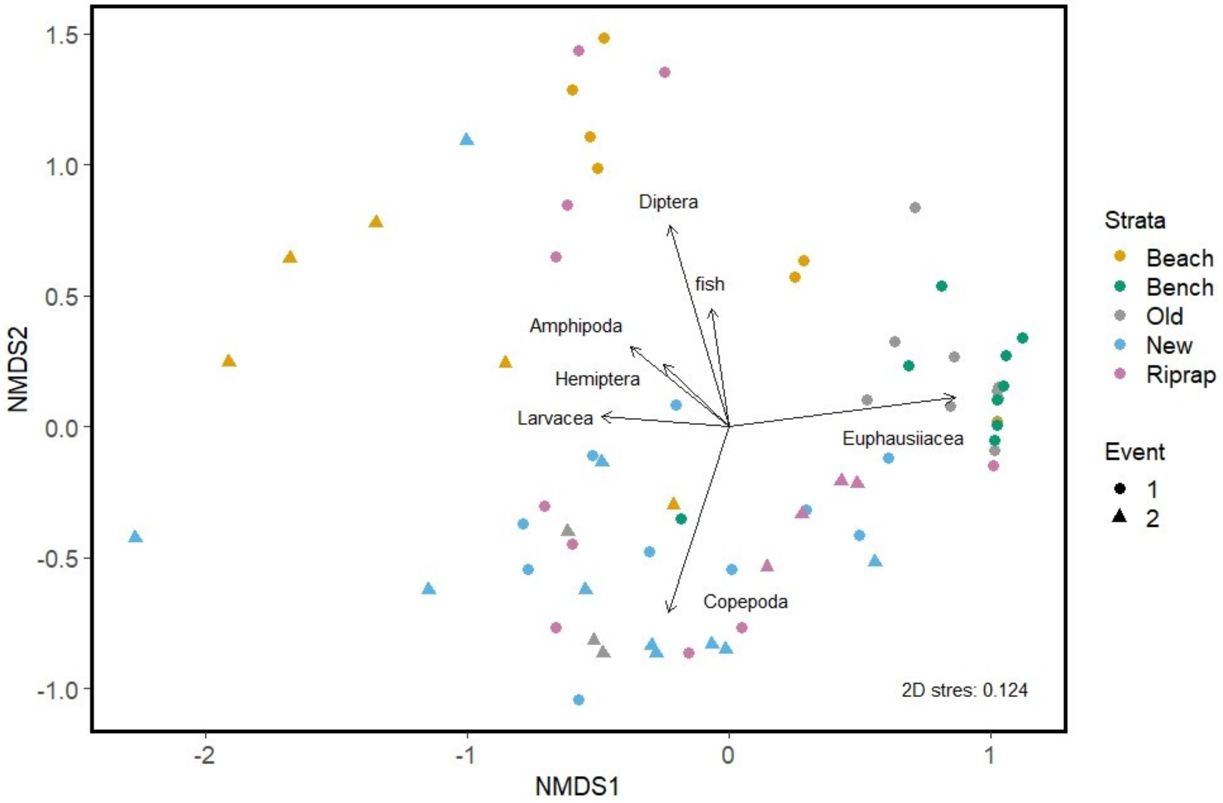

Figure 24. Non-metric multidimensional scaling (NMDS) ordination of prey by weight in the entire gut of juvenile chum salmon from the five shoreline sites. Points on the ordination are individual fish and arrows are fitted vectors of prey taxa. Only taxa that were significant (P>0.05) are shown.

Site Comparisons of Ecological Group (Entire Gut)

Plankton Prey

There were significant differences among sites and an interaction of site and event of plankton prey by count and weight in juvenile chum salmon diets, (two-way ANOVA) (Table 5). Subsequent PWC tests showed that in Event 1, higher abundances and a greater biomass of planktonic prey were found in the diets of juvenile chum salmon collected at Bench than New, Beach, and Riprap, and more were found in diets from Old than from Beach and Riprap (Figure 19). Plankton also contributed to a larger portion of the diets by weight at Bench than New and Beach, and at Old than Beach in Event 1 (Figure 20).

Table 5. Summary statistics from two-way ANOVAs of invertebrate prey counts by source in juvenile chum salmon diets according to the factors site and event. Significant p-values (<0.05) are bold.

Data Type	Taxa group	Factor	df	SS	MS	F-value	p
Counts	Plankton	Site	4	2684.9	671.2	19.264	**< 0.001**
		Event	1	0.0	0.0	0.000	0.999
		Site x Event	3	813.9	271.3	7.786	**< 0.001**
		Residuals	60	2090.7	34.8		
	Epibenthic	Site	4	8.963	2.241	7.653	**< 0.001**
		Event	1	0.846	0.846	2.888	0.094
		Site x Event	3	4.128	1.376	4.700	**0.005**
		Residuals	60	17.567	0.293		
	Terrestrial	Site	4	16.117	4.029	10.982	**< 0.001**
		Event	1	0.318	0.318	0.867	0.356
		Site x Event	3	2.642	0.881	2.400	0.077
		Residuals	60	22.014	0.367		
Weights	Plankton	Site	4	0.274	0.007	6.930	**< 0.001**
		Event	1	$8.00\text{x}10^{-5}$	$7.60\text{x}10^{-5}$	0.077	0.783
		Site x Event	3	0.009	0.003	2.900	**0.042**
		Residuals	60	0.059	0.001		
	Epibenthic	Site	4	0.260	0.065	7.481	**< 0.001**
		Event	1	0.007	0.007	0.780	0.381
		Site x Event	3	0.064	0.021	2.446	0.072
		Residuals	60	0.521	0.009		
	Terrestrial	Site	4	0.574	0.143	10.819	**< 0.001**
		Event	1	0.039	0.039	2.904	0.094
		Site x Event	3	0.083	0.028	2.078	0.113
		Residuals	60	0.795	0.013		

Epibenthic and Terrestrial Prey

Epibenthic prey abundances in chum salmon diets were significantly different for site and the interaction with event, and epibenthic prey weights were significant by site only (Table 5). In Event 1, juvenile chum salmon consumed higher numbers of epibenthic prey at Beach and Riprap than Old and Bench (Figure 21), and in Event 2, more were consumed at Beach had than New and Riprap. Epibenthic prey contributed to a larger portion of the diets of fish from Beach than all other sites (Figure 22).

There were significant differences by site in the abundances and weights of terrestrial prey in chum salmon diets. PWC tests showed those fish had consumed significantly more terrestrial prey at Beach than all other sites (Figure 21, Figure 22).

Discussion

Prey Sources

In this study, I investigated how four armored shorelines and an unarmored reference pocket beach were reflected in the diets of small (< 50 mm) juvenile chum salmon. I was specifically interested in how diets differed among the eco-engineered seawall at New, the flat, vertical, unenhanced seawall at Old, and the most natural shoreline at Beach. Epibenthic and terrestrial prey contributed to the diets of juvenile chum salmon at Beach but fish consumed mostly planktonic prey at New and Old. Preferred epibenthic prey were likely available at New (Chapter 2) suggesting fish were unable to access them.

More epibenthic prey by count and weight were consumed at Beach, the site with habitat most similar to natural salmon habitat, than at New, Old, and Bench and there were not significant differences in epibenthic prey consumption between the eco-engineered seawall (New) and the un-enhanced seawall (Old). Harpacticoids contributed to these site differences, but most was due to consumption of the amphipod *Calliopius* spp. (Figure 19, Figure 20) a common prey of juvenile chum salmon that can be abundant along unaltered Puget Sound shorelines (Simenstad et al. 1980) but relatively rare on altered shorelines (especially compared to the related species *P. pratti*) (Toft 2013, Cordell et al. 2017a). *Calliopius* spp. were rare along the eco-engineered shoreline (Chapter 2) in 2018 and may have been rare at New in 2019 and unavailable to out-migrating juvenile chum salmon contributing to the near absence in those diets. *Calliopius* spp. were also rare or absent in the diets from the other armored sites (Old, Bench, and Riprap), also likely due to low site abundances and shoreline accessibility (Munsch et al. 2014, Munsch et al. 2015, Cordell et al. 2017b, Sawyer et al. 2020).

Harpacticoids tend to dominate the diets of small juvenile chum salmon in estuarine waters throughout the Pacific Rim (Harris and Hartt 1977, Healy 1979, Simenstad et al. 1982, Cordell 1986, D'Amours 1987, Webb 1991, Massa 1995, Mayama and Ishida 2003) and only a few taxa (species in the *Harpacticus uniremis* group, *Tisbe* spp., and *Zaus* spp.) are typically selected. Harpacticoids were rare in this study and were mostly observed in the diets of fish from Beach and Riprap. Preferred harpacticoid prey were abundant in the environment at Beach (Toft et al. 2013) so their presence in the diets was expected, but I also predicted they would be abundant in the diets from Bench because they were in higher densities at Bench than Beach previously (Toft et al. 2013). The armoring at Bench may interfere with shallow water feeding.

Our multivariate findings that juvenile chum salmon consumed more euphausiids at Old and Bench and more varied planktonic taxa at the other sites may be due to several factors. Juvenile chum salmon generally consumed more plankton at Old and Bench than at New and

Beach. Although significantly fewer plankton were consumed in Event 1 than 2 at Old, this difference was due to a transition from euphausiid eggs and larvae to calanoid and cyclopoid copepods. Euphausiid eggs and larvae were smaller per individual than copepods in our samples, so greater numbers were likely required to satiate the fish but were less able to avoid predation and can be encountered in high densities. Calanoid copepods were relatively large adults in our samples thus likely more mobile and capable of evasion than the smaller euphausiids (Keister et al. 2017). It is unknown if there are energetic costs when fish select between these two taxa, but both share similar caloric density (Davis 1993). Juvenile chum salmon may not select for one of these taxa over the other, rather they may consume what is immediately available and a reflection of copepod and euphausiid temporal and spatial variability. We did not collect zooplankton to investigate this trend.

More terrestrial prey were consumed at Beach (and Riprap though not significant) than New, Old, and Bench. These were mostly hemipteran insects and various life stages of chironomids (Diptera). Hemipteran insects and chironomids are common in juvenile salmon diets feeding in shallow shorelines especially when backed by emergent or riparian vegetation (Congleton 1979, Simenstad et al. 1982, Shreffler et al. 1992, Massa 1995, Cordell et al. 1999). Previous monitoring of Beach and Bench showed that total insect and hemipteran insects densities captured in fallout traps were higher at the enhanced sites than the remaining armored sites following construction of the enhancements (2007 and 2009) (Toft et al. 2013). Chironomids contributed substantially to the fish diets from Beach, but also unexpectedly to diets from Riprap, possibly because chironomid adults may have dispersed from other locations and chironomids of any life stage may have drifted downstream from the adjacent Duwamish River. Also, although abundances tend to be higher around riparian and emergent vegetation, chironomids are diverse, and some species may not depend on terrestrial vegetation (Armitage et al. 1995). Hemiptera (mostly aphids) contributed to the diets from Beach but were rare in the diets from Bench (even though they were equally abundant in previous years (Toft et al. 2013, Cordell et al. 2017a)) which may be due to the design of these sites. The seawall and riprap shoreline at Bench interrupt the land-water connection which may prevent or reduce hemipteran insects from dispersing to the water, but the shallow sloping shoreline at Beach allows the water at high tide to reach further inland and closer to the vegetation increasing the chance that Hemiptera produced there may land on the water and become available to juvenile salmon.

Juvenile Salmon Eco-engineered Habitat

The eco-engineered seawall, elevated seafloor bench, and overhead LPS sidewalk at New and along the southern section of the Seattle waterfront was designed to improve fish passage and increase prey availability. Along the original seawall (Old), juvenile salmon were observed between-piers in the nearshore area (within three meters of the seawall where the bench was built) in significantly higher abundances than the under-pier nearshore and offshore areas (greater than three meters from the seawall) (Munsch et al. 2014). This distribution shifted following construction of the eco-engineered seawall as relative fish densities increased under-piers along the nearshore (Sawyer et al. 2020, Accola et al. 2022), suggesting the increased light under piers was at least partially effective at encouraging juvenile salmon migration under piers. However, there was also an apparent, though not significant, shift between-piers from nearshore to offshore in overall abundances (Sawyer et al. 2020). This was surprising given the increased use of under-pier habitat but is likely attributed to the overhead cantilevered LPS sidewalk. Although the LPS sidewalk increased nearshore light penetration under-piers, overall light levels decreased along the nearshore between-piers (Sawyer et al. 2020) because the original seawall was not covered at all or was covered by a much shorter overhead ledge. This shading likely influenced the redistribution of salmon offshore when between piers and may have diverted salmon away from epibenthic prey available at New and along the eco-engineered seawall and bench.

Tidal height also interacts with near-shore shading and influences juvenile salmon distribution. Sawyer et al (2020) observed that offshore between-pier juvenile salmon densities increased at high tide and nearshore under-pier densities increased at low tide at the eco-engineered seawall, and Munsch et al. (2014) observed a similar shift from shaded under-pier areas at low tide to unshaded areas at high tide at the original seawall. Light penetrates further below piers at lower tides due to the relative movement of the shade line cast by piers granting juvenile salmon expanded access, but the angle and depth changes throughout the day with the relative position of the Sun. The west facing shoreline is shaded in the morning, but shade recedes throughout the day and by afternoon, the seawall and eco-engineered habitats can receive full sun. Juvenile salmon may be unable to access epibenthic prey available along the eco-engineered seawall and bench through the first part of a day or at high tides in the afternoons and evenings driving them to feed offshore on neritic planktonic prey.

Riprap armored shorelines like Bench can alter epibenthic communities and juvenile salmon prey abundances but may not impact juvenile salmon feeding rates, in fact a larger proportion of juvenile chum salmon were observed feeding at Bench than at Beach in 2007 and 2009 (Toft et al. 2013); however, diets were not collected from Bench so it is not known if the types of prey consumed differed. We found a low proportion of epibenthic prey in the diets of fish from Riprap and Bench in our study, suggesting even though feeding rates may not be affected by riprap armoring, reduced epibenthic and or terrestrial prey densities may drive juvenile chum salmon to consume planktonic prey. Feeding and other behaviors have recently been used as metrics of restoration success. My results emphasize the need to consider what prey fish are accessing, not just that they are engaged in feeding.

Study Considerations

We identified multiple sampling factors that may have influenced our results. At each of the sites we attempted to focus our sampling on fish utilizing nearshore habitat, as along the eco-engineered bench at New, but high fish mobility limited our ability to ensure we collected fish that had occupied specific nearshore habitats. However, our findings in the context of fish behavior surveys at New, Old, Bench, and Beach (behavior surveys were not conducted at Riprap) (Sawyer et al. 2020, Accola et al. 2022) suggest we captured the feeding habits of fish at those sites.

Juvenile chum salmon typically remain in shallow water and feed on epibenthic prey until they reach at least 50 mm FL (Feller & Kaczynski 1975, Simenstad et al. 1982), but some studies have observed chum salmon of this size consuming planktonic prey even along un-altered shorelines (Simenstad et al. 1980, Bollens et al. 2010). It is not clear what drives this, but by June in the Puget Sound region most of the relatively few remaining small juvenile chum salmon have transitioned to offshore feeding. We sampled in May, and it is possible the fish we captured had already transitioned offshore and therefore would not be expected to consume epibenthic prey from the eco-engineered seawall at New. It is possible that the heavily urbanized Elliott Bay may not be very productive of epibenthic prey driving fish to feed planktonically earlier than may be expected.

We did not observe a significant difference in the proportion of epibenthic or terrestrial prey consumed along the eco-engineered seawall relative to the un-enhanced seawall, but the observed changes in behavior, shoreline distribution, and under-pier use (Sawyer et al. 2020, Accola et al. 2022) suggest the eco-engineering has enhanced juvenile salmon habitat. Shading appears to have a strong influence on juvenile chum salmon behavior and the interaction of several factors (time of day, tidal height, shade line location, and overall light intensity) likely impact juvenile salmon use of the eco-engineered shoreline, driving variation in the diets of juvenile chum salmon.

Future studies comparing the impacts of the eco-engineered habitat on small juvenile chum salmon diets to other shorelines in close proximity should consider a larger sample size focused on the most recently consumed prey in the guts, collect fish during March through early May when confidence is highest that they would be feeding in shallow water (if in unaltered habitat), and either control or measure light intensity and tidal position in tandem with fish collection.

Recent studies of shoreline armoring removal and restoration, and living shoreline installation, suggest various ecological functions develop at different rates (Gittman et al. 2015 & Toft et al. 2021). Though I did not find evidence of increased consumption of preferred prey, the Seattle seawall and adjacent eco-engineering may continue to develop and provide increased function to juvenile salmon. Temporal development of eco-engineered shorelines has not been documented and shorelines that have been softened or restored can take several years to develop and reach desired goals (Borja et al. 2010, Toft et al. 2021). The eco-engineering may continue to develop as habitat along with the distribution and feeding behaviors of juvenile salmon migrating along the eco-engineered seawall, therefore repeated monitoring is needed to determine the long-term effects of this eco-engineering and contribute to our knowledge of the ecological development along eco-engineered shorelines.

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Chapter 4. Summary

We investigated the effect of eco-engineering along the Seattle seawall designed to benefit juvenile salmon and their epibenthic invertebrate prey and found that the eco-engineering along the southern reach of the Seattle seawall provides habitat for epibenthic invertebrates and supports similar densities on the outside-pier strata to densities at an un-armored pocket beach. The preferred epibenthic invertebrate prey of juvenile salmon also appear to benefit from the eco-engineered enhancements, but juvenile chum salmon are not accessing these prey. We attribute this to shading by the cantilevered LPS sidewalk which may drive juvenile salmon away from the eco-engineering and the source of epibenthic prey (Sawyer et al 2020). However, the eco-engineered Seattle seawall has improved conditions for juvenile salmon out-migrating along the Seattle waterfront by allowing for travel under piers.

Our results and other studies indicate juvenile salmon behavior is influenced considerably by light availability (Ono and Simenstad 2014, Munsch et al. 2014, Sawyer et al. 2020, Accola et al. 2022), likely because they are visual predators and to avoid predation. Although the LPS sidewalk may limit prey production and juvenile salmon access to prey when between piers, it allows enough light to penetrate under piers to encourage under-pier juvenile salmon migration and avoid deep water migration around piers (Sawyer et al 2020, Accola et al. 2022). Removing the overhead LPS sidewalk in the between pier sections or replacing them with a more translucent surface could potentially increase epibenthic invertebrate production, encourage juvenile salmon nearshore feeding, and promote expanded under-pier travel by juvenile salmon. A pier at the northernmost end of the eco-engineered seawall, Pier 62, was replaced, and metal grating was used instead of the LPS sidewalk. The grating appears to allow greater light penetration below the pier relative to the LPS sidewalk although the grating is wider from the seawall to the waterward extent (unpublished). The three eco-engineered features were tested for their impacts to juvenile salmon (Cordell et al 2017a) but were not tested together prior to construction of the new Seattle seawall. It may be valuable to test complete designs of eco-engineered armoring when possible, to illuminate conflicting aspects of enhancements.

Salmon populations in the PNW have declined substantially since European settlement, and although some have rebounded, they continue to face multiple barriers to large-scale recovery. In Puget Sound, a history of habitat degradation and loss due in part to stormwater runoff and industrial pollution, logging, draining of wetlands, and human development has contributed to these declines. Salmon not only play a critical role in the ecology of Puget Sound but are vital to regional economies and are part of the spiritual and cultural identity of indigenous communities. This broad significance has made salmon recovery central to ecosystem restoration in the region. Restoration of shallow-nearshore estuarine habitats is often focused specifically on juvenile Puget Sound Chinook salmon, in waters they reside, due to their threatened status under the ESA. However, other salmon species, especially chum, may benefit from restoration of these habitats because of their association with similar nearshore shallow water habitat and early marine residency. Epibenthic harpacticoids and amphipods are the preferred prey of small juvenile chum and Chinook salmon in estuaries but are also important prey to some juvenile pink salmon and other forage fish species (Simenstad et al. 1988) and as consumers of primary production, are a critical link in the local food web. Maintaining habitats that support these species therefore is essential to the health of the Puget Sound ecosystem and local human communities.

Complete removal of armoring can rehabilitate shoreline habitats and directly benefit juvenile salmon (Toft et al. 2013) and although untested, removal of overwater structures should likewise. However, sea level rise, an increasing human population, and our dependence on the services they provide preclude removal of many of these structures and will likely accelerate shoreline armoring. Alternatively, modifying shorelines structures following an eco-engineering framework may address both needs. Small juvenile chum salmon have been shown to consume the same epibenthic prey (*H. uniremis*, *Tisbe* spp., and *Zaus* spp.) in nearshore marine habitats throughout the Pacific Rim (Healy 1979, Simenstad et al. 1982, Cordell 1986, Mayama & Ishida 2003, Chebanova et al. 2015) and as in the Puget Sound, armoring can drive consumption of neritic prey (Irie 1987, Feist 1991). Our findings therefore should be considered in any shoreline modification projects where juvenile chum salmon reside.

Juvenile chum salmon consumed epibenthic prey at the restored OSP pocket beach (Beach) in this and previous studies (Toft et al. 2013), highlighting the value of even small pockets of shallow habitat in urban areas. The construction of pocket beaches, placement of sub-tidal habitat benches, and eco-engineering seawalls can provide benefits through increased epibenthic densities and juvenile salmon prey, but invertebrate densities can vary greatly from year to year thus long-term monitoring is necessary to determine the stability and success of restoration efforts. It may be unproductive to view any of these habitat enhancements as “better” than another and instead whether an enhancement has achieved realistic objectives within the context and constraints of the surrounding environment. For example, the urban pier and ferry pier study (Cordell et al. 2017b) suggests there may be limits to what can be expected from habitat enhancements around dense urban piers versus isolated piers. Monitoring of similar eco-engineering along varying densities of piers could improve our understanding of these limitations. Softening shorelines by planting terrestrial vegetation or transitioning to living shorelines, shifting seawalls landward, and when softening is not feasible, developing eco-engineered designs may provide intermediate benefits to juvenile salmon (Toft et al. 2007, Cordell et al 2017a, Sawyer et al. 2020, Accola et al. 2022, Toft et al. 2021).

Studies in other systems have observed ecological benefits from eco-engineered shorelines at smaller scales (Chapman and Underwood 2011), and the potential of eco-engineered armoring to provide ecosystem goods and services to humans (Heery et al. 2020). Unfortunately, extensive hard armoring without eco-engineered features continues to be built (Bugnot et al. 2021). Given the need for shoreline protective structures in the face of sea level rise and length of time these structures are predicted to last before needing replacement, it is important for coastal agencies to consider the long-term ecological impacts of coastal defenses prior to development and consider eco-engineered designs to prevent or reduce those impacts.

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Appendix

Supplementary Figures

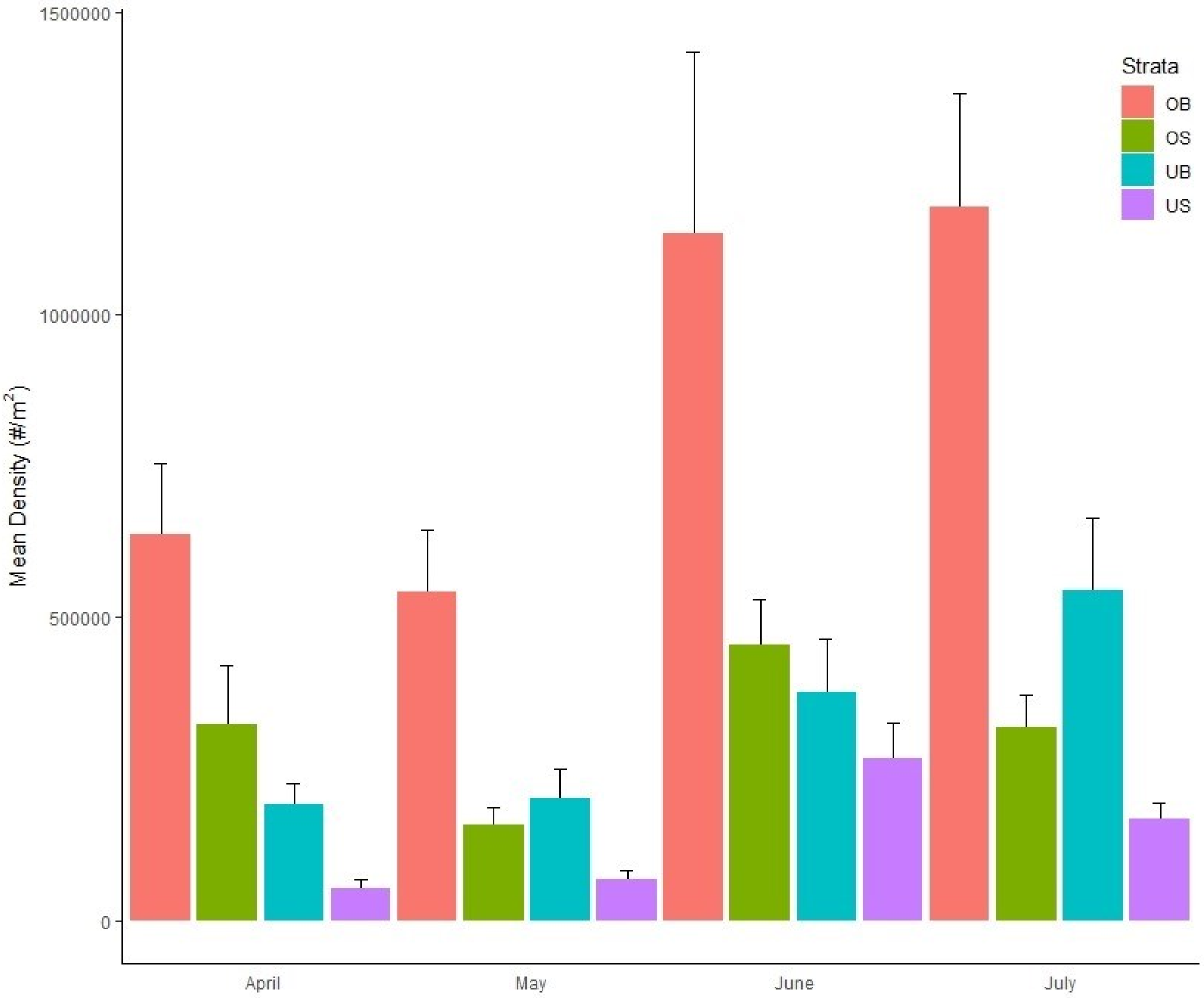

Figure 25. Mean density of epibenthic invertebrates by month and strata. Error bars are standard error.

Supplementary Tables

Table 6. List of all epibenthic invertebrate taxa collected.

Taxa Identified	Group
Acari	Acari
Halacaridae	
Stephos sp.	Calanoida
Caprella sp.	Caprellidea
Cirripedia cyprid	Cirripedia
Cumella vulgaris	Cumacea
Cyclopinidae	Cyclopoida
Cyclopoida copepodids	
Cyclopoida, unidentified	
Euryte sp.	

Heptacarpus sp.	Decapoda
Hippolytidae	
Paguridae	
Chironomidae larvae	Diptera
Foraminifera	Foraminifera
Ampithoidae	Gammaridea
Aoroides sp.	
Calliopius sp.	
Corophiidae juveniles	
Eochelidium sp.	
Eogammarus confervicolus	
Gammaridea juveniles	
Hyalidae	
Ischyrocerus sp.	
Jassa sp.	
Melitidae	
Monocorophium insidiosum	
Monocorophium sp.	
Paracalliopiella pratti	
Pleustidae	
Pontogeneia rostrata	
Acrenhydrosoma sp.	Harpacticoida
Alteutha sp. 1	
Alteutha sp. 2	
Ameira longipes	
Ameira sp.	
Ameiridae unidentified	
Amenophia sp.	
Amonardia normani	
Amonardia perturbata	
Amphiascoides spp.	
Amphiascopsis cinctus	
Dactylopodella sp.	
Dactylopusia crassipes	
Dactylopusia paratisboides	
Dactylopusia sp. A	
Dactylopusia vulgaris	
Danielssenia typica	
Diarthrodes cf. *nobilis*	
Diarthrodes spp.	
Diosaccus sp.	
Diosaccus spinatus	
Echinolaophonte sp.	
Ectinosoma melaniceps	

Ectinosomatidae	
Harpacticoida copepodids	
Harpacticoida unidentified	
Harpacticus obscurus group	
Harpacticus uniremis	
Harpacticus uniremis group	
Heterolaophonte longisetigera	
Heterolaophonte sp. A	
Heterolaophonte sp. B	
Heterolaophonte variabilis	
Laophonte cornuta	
Laophonte elongata	
Laophontidae copepodids	
Laophontidae unidentified	
Laophontodes hedgepethi	
Mesochra sp.	
Miraciidae unidentified	
Nitokra sp.	
Paradactylopodia spp.	
Paralaophonte pacifica	
Paralaophonte perplexa group	
Parastenhelia hornelli	
Parastenhelia spinosa	
Parathalestris californica	
Parathalestris sp. A	
Parathalestris verrucosa	
Peltidiidae	
Pseudonychocamptus sp.	
Rhynchothalestris helgolandica	
Robertsonia sp.	
Sarsamphiascus minutus	
Sarsamphiascus sp.	
Sarsamphiascus undosus	
Scutellidium sp.	
Stenhelia peniculata	
Tachidius triangularis	
Tegastidae	
Thalestridae unidentified	
Thalestris sp.	
Tisbe spp.	
Xouthous purpurocincta	
Zaus sp.	
Hydrozoa	Hydrozoa
Epicaridea	Isopoda

Limnoria sp.	
Munna sp.	
Munnidae	
Uromunna ubiquita	
Oligochaeta	Oligochaeta
Euphilomedes producta	Ostracoda
Ostracoda	
Poecilostomatoida	Poecilostomatoida
Nerillidae	Polychaeta
Polychaeta	
Syllidae	
Siphonostomatoida	Siphonostomatoida
Turbellaria	Turbellaria

Table 7. Unscaled vectors, R^2 values, and p-values of taxa included in the NMDS ordination. All taxa with p-values (<0.05) are in bold. Only taxa with R^2 values greater than 0.28 are displayed on the NMDS ordination and are also in bold.

Taxa	MDS1	MDS2	R^2	Pr(>r)
Alteutha sp. 1	0.5738	0.8190	0.0590	**0.001**
Ameira longipes	0.6139	0.7894	**0.3925**	**0.001**
Ameira spp.	0.9352	0.3542	0.2127	**0.001**
Ameiridae unidentified	0.8479	-0.5301	0.0092	0.221
Amonardia normani	0.7670	0.6416	0.2062	**0.001**
Amonardia perturbata	1.0000	0.0012	**0.3335**	**0.001**
Amphiascoides spp.	0.9113	0.4117	0.1647	**0.001**
Amphiascopsis cinctus	0.9811	-0.1937	0.0851	**0.001**
Aoroides spp.	0.7071	0.7071	0.0545	**0.001**
Calliopius spp.	0.6751	-0.7377	0.0569	**0.001**
Chironomidae larvae	0.3174	-0.9483	0.1575	**0.001**
Cirripedia cyprid	-0.9762	0.2167	0.2011	**0.001**
Cyclopinidae	0.9975	0.0703	0.1108	**0.001**
Cyclopoida unidentified	0.8611	0.5084	0.0509	**0.002**
Dactylopusia crassipes	0.3028	-0.9530	0.0707	**0.001**
Dactylopusia sp. A	0.2331	-0.9725	**0.3174**	**0.001**
Dactylopusia vulgaris	0.9721	0.2344	**0.2871**	**0.001**
Danielssenia typica	0.9613	-0.2754	0.0417	**0.003**
Diarthrodes spp.	1.0000	-0.0093	**0.4213**	**0.001**
Diosaccus spinatus	0.7968	-0.6042	0.0876	**0.001**
Echinolaophonte spp.	0.9123	0.4096	0.1097	**0.001**
Ectinosomatidae	0.9539	0.3000	**0.5459**	**0.001**
Epicaridea	0.9886	-0.1504	0.0354	**0.005**
Euryte spp.	0.9996	0.0283	0.0471	**0.001**
Foraminifera	0.9960	-0.0896	0.2167	**0.001**

Halacaridae	0.7059	-0.7083	0.0850	**0.001**
Harpacticoida copepodids	0.9965	0.0831	**0.3163**	**0.001**
Harpacticoida unidentified	0.0239	0.9997	0.0005	0.923
Harpacticus obscurus group	0.9030	-0.4296	**0.3990**	**0.001**
Harpacticus uniremis group	0.0667	-0.9978	**0.4658**	**0.001**
Heterolaophonte longisetigera	0.6472	-0.7623	0.2556	**0.001**
Heterolaophonte sp. A	0.6633	-0.7483	0.1225	**0.001**
Heterolaophonte sp. B	-0.2071	-0.9783	0.0018	0.755
Laophonte cornuta	0.9724	0.2332	0.0136	0.114
Laophonte elongata	0.7067	0.7075	0.1845	**0.001**
Laophontidae copepodids	0.9906	-0.1368	0.1780	**0.001**
Laophontidae unidentified	0.9639	0.2661	0.0766	**0.001**
Mesochra spp.	0.9565	-0.2918	**0.4386**	**0.001**
Miraciidae unidentified	0.9828	0.1848	0.0772	**0.001**
Monocorophium spp.	0.9676	-0.2526	0.0213	**0.031**
Nerillidae	0.7300	0.6834	0.0471	**0.002**
Nitokra spp.	0.9943	0.1067	0.0783	**0.001**
Ostracoda	0.9768	0.2141	0.1351	**0.001**
Paracalliopiella pratti	0.5823	-0.8130	0.0441	**0.002**
Paradactylopodia spp.	0.8717	0.4901	**0.3768**	**0.001**
Paralaophonte pacifica	0.9303	0.3669	0.2500	**0.001**
Paralaophonte perplexa group	0.9841	-0.1777	0.1767	**0.001**
Parastenhelia spinosa	0.6551	-0.7555	0.0973	**0.001**
Parathalestris californica	0.5945	-0.8041	0.0307	**0.014**
Parathalestris sp. A	0.9910	0.1341	0.0372	**0.002**
Pleustidae	0.5861	0.8103	0.0094	0.210
Polychaeta	0.9993	0.0363	0.0218	**0.032**
*Pontogeneia rostra*ta	0.9508	-0.3098	0.0347	**0.005**
Pseudonychocamptus spp.	0.1259	0.9920	0.0086	0.243
Rhynchothalestris helgolandica	0.9208	-0.3899	0.1138	**0.001**
Robertsonia spp.	0.9643	-0.2648	0.0270	**0.019**
Sarsamphiascus minutus	0.9524	0.3049	**0.2870**	**0.001**
Sarsamphiascus spp.	0.7508	0.6605	0.0226	**0.041**
Scutellidium spp.	0.5942	-0.8043	0.0327	**0.007**
Stenhelia peniculata	0.8582	0.5133	0.0434	**0.002**
Tegastidae	0.7685	0.6399	0.2545	**0.001**
Thalestridae unidentified	-0.2062	0.9785	0.0019	0.722
Tisbe spp.	0.9413	-0.3375	**0.4079**	**0.001**
Turbellaria	0.9941	0.1089	0.0628	**0.001**
Zaus spp.	0.6652	-0.7467	0.1174	**0.001**

Table 8. Summary statistics from post-hoc TukeyHSD tests following significant two-way ANOVAs on differences of epibenthic invertebrate taxa according to the factors of seawall strata

and month. TukeyHSD was only used when there was a non-significant interaction. Ectinosomatidae and Paradactylopodia data were only analyzed in June and July. Significant p-values (<0.05) are bold.

	Taxa Richness	Total Density	Group 1
OS x OB	**<0.05**	**<0.05**	0.13
UB x OB	**<0.05**	**<0.05**	**<0.05**
US x OB	**<0.05**	**<0.05**	**<0.05**
UB x OS	**<0.05**	0.99	**<0.05**
US x OS	0.07	**<0.05**	**<0.05**
US x UB	**<0.05**	**<0.05**	**0.08**
Apr x May	0.99	0.78	**0.02**
Apr x Jun	**<0.05**	**<0.05**	**0.01**
Apr x Jul	**<0.05**	**<0.05**	0.99
May x Jun	**<0.05**	**<0.05**	**<0.05**
May x Jul	**<0.05**	**<0.05**	**0.01**
Jun x Jul	**<0.05**	0.99	**0.02**

Table 9. Summary statistics from pairwise comparison (PWC) tests of invertebrate prey counts by source in juvenile chum salmon diets by site within each event. Significant p-values (<0.05) are bold. When two-way interactions were non-significant, multiple PWC tests with a Bonferroni adjustment were used if main effects were significant. If a significant interaction (p<0.05) was detected, simple PWC tests were used. Dashes (--) are displayed when main effects and all PWCs were not significant. Fish were not collected from Bench in Event 2 therefore PWC therefore those could not be performed (gray cells).

	Planktonic		Epibenthic		Terrestrial	
	Event 1	Event 2	Event 1	Event 2	Event 1	Event 2
Bench : New	**3.64x10^{-7}**		0.916		1	
Bench : Old	1		1		1	
Bench : Beach	**8.56x10^{-7}**		**0.030**		**6.23x10^{-5}**	
Bench : Riprap	**5.26x10^{-5}**		**0.016**		0.765	
New : Old	**3.16x10^{-7}**	--	1	1	1	--
New : Beach	1	--	1	**1.32x10^{-4}**	**1.17x10^{-6}**	--
New : Riprap	1	--	1	1	0.227	--
Old : Beach	**7.53x10^{-7}**	--	**0.036**	0.065	**2.36x10^{-4}**	--
Old : Riprap	**4.60x10^{-5}**	--	**0.020**	1	1	--
Beach : Riprap	1	--	1	**6.75x10^{-4}**	**0.009**	--