Effects of seawall armoring on juvenile Pacific salmon diets in an urban estuarine embayment

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ABSTRACT: An important nursery function of estuaries is providing prey resources for juvenile fish. Shoreline armoring compromises epibenthic and terrestrial prey resources, but it is unclear how this affects fish feeding ecology, particularly in urban landscapes where armoring is common. In this study we sampled prey availability and diets from 3 species of juvenile Pacific salmon (*Oncorhynchus* spp.) in shallow habitats of an extensively armored urban estuary. We compared sites armored by intertidal seawalls with those at small, engineered beaches without armoring. Available prey was different between shoreline types: epibenthic copepods were more abundant and taxonomically diverse at beaches, and barnacles were more abundant at seawall sites. There was no effect of armoring on salmon stomach fullness. Armoring rarely influenced whether salmon selected for or against a prey taxon but did affect diet composition of small (<50 mm) chum salmon (*O. keta*), which consumed greater abundances of epibenthic copepods at beaches and planktonic copepods at seawall sites. At beaches, these fish selected for epibenthic copepods and against planktonic copepods. At seawall sites, they selected for both epibenthic and planktonic copepods. Armoring did not affect diets of other salmon species or larger chum salmon that had different diets than small chum salmon. Armoring effects on fish diets may depend on differences in prey selection among species and life history stages. Further research is necessary to assess effects of armoring on habitat quality because fish may consume alternative prey when armoring changes the prey field, but it is unclear whether there are energetic costs to the predator.

KEY WORDS: Shoreline development · Seawalls · Armoring · Diet composition · Juvenile salmon

INTRODUCTION

Estuarine shorelines interface a connected ecosystem comprised of terrestrial, pelagic, and benthic habitats (Polis et al. 1997, Sobocinski et al. 2010, Heerhartz et al. 2014). Fish use shallow estuarine waters as nurseries where these habitats produce abundant prey resources for juveniles (Simenstad et al. 1982b, Beck et al. 2001). Estuarine ecosystems are threatened by land-use change driven by human activities associated with population growth in coastal areas (Vasconcelos et al. 2007) and border many of the largest and fastest growing cities in the world (United Nations 2014). There is increasing interest in improving the biological functions of developed estuarine and coastal habitats, but inadequate information to inform shoreline management and design (Wilson et al. 2015). Despite the role of estuaries in providing feeding opportunities to juvenile fish and the development of estuarine shorelines worldwide, shoreline management is limited by a poor understanding of fish feeding ecology in urban habitats.

One of the major drivers of ecological change in estuaries is the use of shoreline armoring to minimize erosion caused by waves (Bulleri & Chapman 2010). Shoreline armoring protects economically desirable activities that are aggregated along shorelines and is particularly common along urban waterfronts. However, armoring can change the structure of shorelines

by preventing beach formation and replacing intertidal and backshore habitats with hard surfaces (Airoldi et al. 2005). Loss of fine sediment beaches reduces the environmental abundance of small epibenthic invertebrates in shallow ecosystems (Spalding & Jackson 2001, Dugan et al. 2008, Sobocinski et al. 2010, Morley et al. 2012, Toft et al. 2013), which can reduce epibenthic prey consumption by fish (Morley et al. 2012). Similarly, armoring that displaces backshore vegetation can reduce environmental diversity (Sobocinski et al. 2010) and fish consumption of terrestrial invertebrates (Toft et al. 2007). While evidence suggests that armoring compromises the connectivity of aquatic, benthic, and terrestrial habitats, the effects of armoring on the diets of fish have not been studied in an urban landscape where armoring is most common.

Among the species that are affected by armoring are juvenile Pacific salmon (*Oncorhynchus* spp.). Pacific salmon are anadromous fish that utilize estuarine habitats close to shore, including those modified by shoreline armoring, as they outmigrate from freshwater habitats (Toft et al. 2007, 2013, Munsch et al. 2014). Estuaries are important to many species and life history stages of Pacific salmon because juveniles use nearshore areas for foraging, predator refuge, and salinity acclimatization (Simenstad et al. 1982b, Groot & Margolis 1991, Quinn 2005). Juvenile salmon early in their estuarine residence feed on small invertebrate prey produced in epibenthic, terrestrial, and pelagic habitats (Toft et al. 2007, Duffy et al. 2010). Pacific salmon are culturally, ecologically, and economically significant species that have experienced widespread declines attributable in part to habitat loss (Nehlsen et al. 1991), resulting in the listing of many populations under the Endangered Species Act (USA).

Salmon use habitats modified by armoring during a life stage important to their overall survival. During their early estuarine and marine residence, juvenile salmon grow rapidly and experience high mortality rates inversely related to fish size (Parker 1962, Le-Brasseur & Parker 1964, Healey 1979, Healey 1982, Furnell & Brett 1986, Bradford 1995, Mortensen et al. 2000, Willette et al. 2001). Similar to many fish species, feeding is important to juvenile salmon because growth determines their ability to overcome gape-limited predation (Sogard 1997, Juanes et al. 2002, Duffy & Beauchamp 2008). Magnusson & Hilborn (2003) showed that the amount of estuarine habitat in pristine condition is positively correlated with survival of juvenile Chinook salmon (*O. tshawytscha*), but they did not identify the mechanisms behind this effect.

The aim of our study was to test the hypotheses that shoreline armoring affects environmental prey availability, juvenile salmon stomach fullness, and juvenile salmon diet composition within an urban landscape. Our sampling occurred close to shore along the urbanized waterfront of downtown Seattle, Washington (USA), a shoreline that is entirely armored with the exception of small man-made beaches. We compared (1) environmental prey and (2) diets of juvenile Chinook, chum (*O. keta*), and pink (*O. gorbuscha*) salmon in shallow habitats along shorelines armored by seawalls in the intertidal area with those at unarmored beaches, and examined relationships between prey availability and fish diets.

MATERIALS AND METHODS

Study system

Puget Sound is an inland sea that includes a deep, glacially formed fjord mixed with large river deltas and a multitude of smaller estuaries. Waters are cold temperate with salinity above 25 psu when not directly adjacent to freshwater input. Under natural conditions, beaches in Puget Sound are composed of fine sediment and are naturally maintained by erosion of glacial outwash and till from shoreline bluffs. Approximately one third of the 2144 km of shoreline along Puget Sound is armored, and the region has experienced widespread wetland loss and the replacement of bluff-backed beaches with armored waterfronts (Simenstad et al. 2011). Within Puget Sound, Elliott Bay is a highly urbanized 21 km^2 estuarine embayment located entirely within the City of Seattle, Washington (USA). There is no natural shoreline in Elliott Bay because of filling and dredging activities in the 20th Century (Klingle 2007). Seawall and riprap armoring is currently present along 99% of the shoreline in Elliott Bay and unarmored waterfronts are limited to engineered pocket beaches.

Elliott Bay is inhabited by juvenile Chinook, chum, and pink salmon, which are the numerically dominant fish species along the shorelines during the spring and summer months (Munsch et al. 2014). The juvenile chum and pink salmon in this system are typical of many systems, entering the estuary in the early spring shortly after emerging from the gravel. The Chinook salmon are 'ocean-type,' entering the estuary as sub-yearlings later in the season than chum and pink salmon. Coho salmon (*O. kisutch*) also utilize estuarine waters in Puget Sound, but we rarely observed this species. Juvenile Chinook salmon

entering Elliott Bay from the nearby Duwamish River are listed as threatened under the Endangered Species Act (National Marine Fisheries Service 1999).

Environmental prey and juvenile salmon diet sampling

Sampling occurred at 6 sites within Elliott Bay (Fig. 1) during high tides to allow for maximum inundation of shoreline habitat. The shorelines of 3 sites, referred to hereafter as 'seawall sites', were completely modified by riprap in front of a large vertical seawall that collectively replaced the intertidal area, occurring from the shallow subtidal area to 5.5 m above mean lower low water (MLLW). The shorelines of 3 additional sites, referred to hereafter as 'reference beaches', were pocket beaches composed of low-gradient mixed cobble and sand intertidal areas. Beaches were located at recreational areas where there was minimal anthropogenic structure in the water. We use the term 'shoreline type' to denote a site as either a seawall site or a reference beach. Site locations were chosen based on accessibility and logistical constraints. Accessible habitat along Elliott Bay is constrained by numerous piers extending into the bay and we selected seawall sites that were large enough to safely operate a boat between piers and where there was minimal vessel traffic. There is limited beach habitat in Elliott Bay and we chose the 3 beaches closest to the seawall that were large enough to allow nets to be deployed. Sites were sampled in haphazard order for each round of data collection. Due to the small size of sites, we were unable to randomize sampling locations within sites.

Environmental prey was sampled directly from the water during 3 sampling events that took place at each site during June–August 2012. For each sampling event, 2 types of nets were towed 5 m parallel to shore for 10 m. A neuston net was towed half-submerged at the surface (frame: 50 cm × 30 cm, mesh: 106 µm) and a plankton net (frame: 35 cm diameter, mesh: 106 µm) was towed at 1 m depth. These depths correspond with the depth distribution of juvenile salmon at these sites (Munsch et al. 2014). All inver-
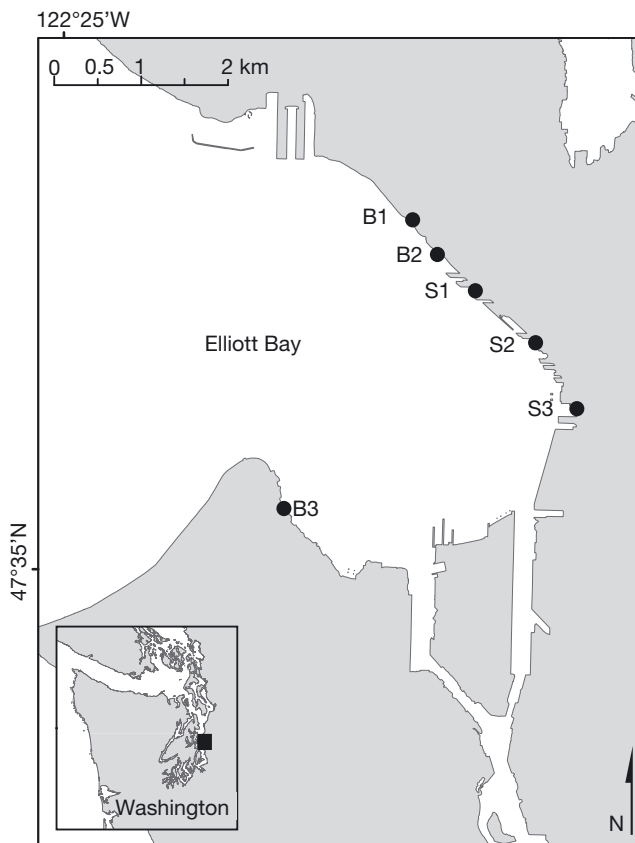

Fig. 1. Reference beaches (B1, B2, B3) and seawall sites (S1, S2, S3) within Elliott Bay, Washington (USA)

tebrates captured in nets were fixed in 10% buffered formaldehyde solution and the contents of each sample were identified and counted in the laboratory utilizing dissecting microscopes. Crustaceans were identified to genus or species and other taxa were identified to order or family.

Diets were sampled from juvenile salmon at the sites where prey were sampled. Diet sampling occurred during the annual outmigration of juvenile salmon, mainly from the adjacent Duwamish River, from March–August 2012 and March–April 2013 (Table 1). Diets were sampled by netting at each site during the daytime twice per month. Additional sampling occurred during the nighttime at each site once per month in April–July 2012. Daytime and nighttime sampling was defined by sunrise and sunset.

Table 1. Details of sampling methods, intensity per site, and timing over the study period. SDDN: snorkel diver deployed net

Month-year:	Mar 2012	Apr 2012	May 2012	Jun 2012	Jul 2012	Aug 2012	Mar 2013	Apr 2013
Daytime netting events	2	2	2	2	2	2	2	2
Nightime netting events	0	1	1	1	1	0	0	0
SDDN at seawall sites	No	No	No	No	No	No	Yes	Yes

Juvenile salmon were captured with nets that were appropriate for fishing shallow areas of the different shoreline types. A beach seine (37 m × 2 m, 0.64 cm mesh) designed to fish low-gradient intertidal areas in Puget Sound (Simenstad et al. 1991) was used to capture fish at reference beaches. In 2012, a Lampara net (37 m × 2 m, 0.64 cm mesh) was used to sample seawall sites because there was little or no intertidal area at seawall sites and this net is designed to enclose fish in the water column similar to a purse seine. In 2013, seawall sites were sampled using a snorkel diver deployed net (9.1 m × 1.2 m, 0.64 cm mesh) by having the divers swim a circular path with the net at the surface of the water to enclose juvenile salmon. This method allowed us to capture fish very close to the seawall where it was not possible to deploy the other net types. All nets were deployed from 4.5 m depth to as close to shore as practical. Small juvenile salmon at these sites occupy the top of the water column almost exclusively (Munsch et al. 2014) and all net types were designed to fish this stratum.

We sampled diets from age-0 Chinook, chum, and pink salmon. Diets of chum and pink salmon >60 mm fork length were sampled by gastric lavage. We also utilized gastric lavage to sample diets of all sizes of Chinook salmon, although this species rarely occurred in sizes <60 mm. This method flushes out 100% of fish stomach contents with no long-term adverse effects to the fish (Twomey & Giller 1990) and has been used in previous studies in the area (e.g. Toft et al. 2007). Stomach contents recovered by lavage were fixed in 10% buffered formaldehyde solution. Lavage is ineffective for fish <60 mm, so chum and pink salmon of this size were euthanized by an overdose of the anesthetic MS-222 and fixed in 10% buffered formaldehyde solution; then, the stomachs were removed and dissected in the laboratory. Fork length and mass measurements were taken of all fish that were sampled. In the laboratory, stomach contents were washed into a 106 μm sieve and identified similarly to environmental prey. Partially digested prey were identified as far as condition would allow. Prey were counted and weighed to the nearest 0.0001 g.

Analysis

Analysis was conducted using R version 3.1.1 (R Core Development Team 2014) and PERMANOVA+ for PRIMER-E (Anderson et al. 2008). In R, we utilized the 'Vegan' package (Oksanen et al. 2013) for ordination, and the 'glmmADMB' package (Skaug

et al. 2013) for linear mixed effects modeling. The PRIMER-E software with PERMANOVA+ add-on was utilized for permutational multivariate analysis of variance (PERMANOVA) because it allows for analysis of hierarchal designs. The glmmADMB package was selected to build models because it allows for (1) the incorporation of 2 random effects, (2) non-normal response variable distributions, and (3) zero inflation.

The juvenile salmon diet data was organized into 5 groups (hereafter: salmon groups) based on species, size, and diel sampling that were analyzed separately to isolate effects of shoreline type from variation attributable to other factors. We analyzed Chinook, chum, and pink salmon separately because we anticipated differences in size, timing, and prey selection among species (e.g. Quinn 2005, Toft et al. 2007). Chum and pink salmon were rarely captured at night, and those that were captured at night were excluded from analysis. For Chinook salmon, fish captured during the day were analyzed separately from those captured at night to account for potential diurnal variation in feeding. Chum salmon <50 mm length were analyzed separately from those ≥50 mm because chum salmon transition from epibenthic prey to planktonic prey at this length (Simenstad 1977, Simenstad & Salo 1982). We refer to these fish as small (<50 mm) and large (≥50 mm) chum salmon.

Data were standardized prior to multivariate analysis. For the environmental prey and each of the 5 salmon diet groups, prey taxa that occurred in less than 5% of samples were removed to reduce the influence of rare taxa (McGarigal et al. 2000). Next, the percent composition of each prey taxon per diet was calculated (prey taxa counts/total prey counts) and the data were arcsine square root transformed (e.g. McPeek et al. 2015). Bray-Curtis similarity matrices were utilized for all multivariate analyses (Bray & Curtis 1957).

We utilized nonmetric multidimensional scaling (NMDS) to compare—between shoreline types—the composition of prey in the environment and juvenile salmon diets. Prey taxa with significant gradients on ordinations were determined by bootstrapping, utilizing the 'envfit' function in the R package Vegan (permutations = 9999) and the corresponding vectors were plotted (Oksanen et al. 2013). Vector arrows indicated directions of increasing prey gradients and arrow lengths were proportional to the correlation of variables with ordination space.

We utilized PERMANOVA to test for significant differences in environmental prey and diet composition between shoreline types (Anderson et al. 2008).

For environmental prey comparisons, the factors were shoreline type (fixed; levels: seawall site, reference beach), net (fixed; levels: plankton [surface], neuston [1 m depth]), site (random; levels: S1, S2, S3, B1, B2, and B3), and the netting events that were unique to each site (random, levels: all combinations of sampling dates and sites). Netting event was nested within site and site was nested within shoreline type. Site was treated as a random effect to account for autocorrelation in samples taken from the same location over time. Netting event was also treated as a random effect to account for autocorrelation in samples taken at the same time and location. The same model structure was utilized for the analysis of diet data, except we considered only the single fixed effect of shoreline type.

We utilized generalized linear mixed effects models to test for the effect of shoreline type on environmental prey abundance, environmental prey taxa richness, stomach fullness, and prey abundance in the diets. Prey taxa richness was defined as the number of monophyletic prey taxa and stomach fullness was defined as the mass of the prey in a stomach divided by the mass of the individual fish. The fixed and random effects and their nesting structure for these models were the same as previously described for PERMANOVA tests. Unlike the multivariate analysis, the univariate analysis on prey abundances occurred on unstandardized data because we were interested in how shoreline armoring might decrease abundances of some taxa in diets while increasing others, which would not be detectable by proportional metrics.

Models were fit following the protocol by Zuur et al. (2009). In summary, we (1) selected a response variable distribution, (2) determined whether the model required treatment of zero inflation in the response variable, (3) if necessary, determined the optimal fixed structure via backwards selection beginning with the full model, and (4) validated the model.

Models of count data were initially constructed with negative binomial distributions, but if they could not be validated, we $\log_e$-transformed the count data and fit the models with Gaussian distributions (i.e. a linear mixed effects model; Zuur et al. 2009). Models of stomach fullness were constructed with Gaussian distributions on fourth-root transformed data to meet assumptions of normality. When appropriate, zero inflation was accounted for by specifying the 'zeroInflation = TRUE' argument within the glmmADMB function. Also, when appropriate, the optimal fixed structure was determined via a backwards selection process starting with the

full model and sequentially dropping the least significant term and comparing the fit to the previous model until all terms were significant or no terms remained (Zuur et al. 2009). For each step of the model-building process, candidate models were quantitatively compared to less parsimonious models via likelihood ratio tests utilizing the 'anova' function in base R and insignificant terms were dropped if the models showed no significant differences in their fit to the data. Models were validated when residuals plotted against fitted values and fixed effects exhibited a homogenous variance around a mean of zero.

Prey selectivity was estimated for each combination of prey taxa, juvenile salmon group, and shoreline type following the protocol of Gabriel (1978) to calculate the log of the odds ratio (LOR):

$$\text{LOR} = \ln\left(\frac{d_i(100 - e_i)}{e_i(100 - d_i)}\right) \quad (1)$$

where d_i and e_i are the mean percent composition of taxon i in the diet and the environment, respectively (e.g. Schabetsberger et al. 2003). This metric is symmetric around zero with positive values indicating positive selectivity and negative values indicating negative selectivity.

RESULTS

Prey in the environment

We quantified potential juvenile salmon prey in the environment from 17 neuston net and 17 plankton net tows. These samples included 65 500 individual invertebrates produced in epibenthic, planktonic, and terrestrial habitats (Table 2). The most abundant taxa were calanoid, cyclopoid, and harpacticoid copepods, and barnacle larvae (Fig. 2). Euphausiid larvae, gammarid amphipods, hyperiid amphipods, and polychaetes were less abundant, and crab larvae and insects were least abundant. Nearly all insects were captured in neuston nets. Many of these broader prey groupings were identified to finer taxonomic resolution and there was some variation in taxa richness within these prey groupings between shoreline types (Fig. 3).

The NMDS ordination of environmental prey composition indicated differences between shoreline types (Fig. 4). There was a significant positive gradient of barnacle larvae pointing towards samples collected from seawall sites and of harpacticoid copepods pointing towards samples collected from reference beaches. There was also a significant positive gradi-

ent of calanoid copepods in ordination space, but this pointed towards samples from samples taken from both shoreline types. PERMANOVA indicated significant differences in environmental prey composition between shoreline types (Table 3).

Table 2. Prey taxa in the environment and diets of juvenile salmon. Sources are epibenthic (E), planktonic (P), and terrestrial (T)

Taxon	Common name	Source
Aphididae	Aphids	T
Arachnida	Arachnids	T
Brachyura	Crabs	P
Calanoida	Calanoid copepods	P
Cirripedia	Barnacles	E/P[a]
Coleoptera	Beetles	T
Copepoda	Copepods	E/P
Crustacea	Crustaceans	P/T
Cyclopoida	Cyclopoid copepods	P
Diptera	True flies	T/E[a]
Euphausiacea	Krill	P
Gammaridea	Gammaridean amphipods	P
Harpacticoida	Harpacticoid copepods	E
Hemiptera	True bugs	T
Hymenoptera	Ants, bees, sawflies, wasps	T
Hyperiidea	Hyperiid amphipods	P
Insecta	Insects	T/E[a]
Larvacea	Larvaceans	P
Ostracoda	Seed shrimp	E
Polychaeta	Annelid worms	E/P[a]
Psocoptera	Booklice	T

[a]Source refers to a juvenile life stage of the prey taxa

We utilized the NMDS ordination of environmental prey composition to guide comparisons of finer environmental prey taxa abundances between shoreline types, and also compared the taxa richness of all broader prey taxa between shoreline types. We limited comparisons of finer environmental prey taxa abundances to taxa identified as significant in NMDS analysis to minimize chances of a Type I error caused by multiple comparisons. Linear mixed effects models indicated significantly greater abundances of harpacticoid copepods in the environment at reference beaches and greater abundances of barnacle larvae at seawall sites (Table 4). Of the major prey taxa for which many subtaxa were identified, there was significantly greater taxa richness of harpacticoid copepods at reference beaches and insects at seawall sites (Table 4). Plankton net samples were excluded in the analysis of insect taxa richness because nearly all insects were captured in neuston nets.

Juvenile salmon and their diets

A total of 459 juvenile salmon diets were analyzed (Table 5). Chum and pink salmon occurred earlier in the year and were smaller than Chinook salmon, and there was a trend of increasing length as the year progressed for all species (Fig. 5). There were no apparent differences in the size distribution of fish between shoreline types.
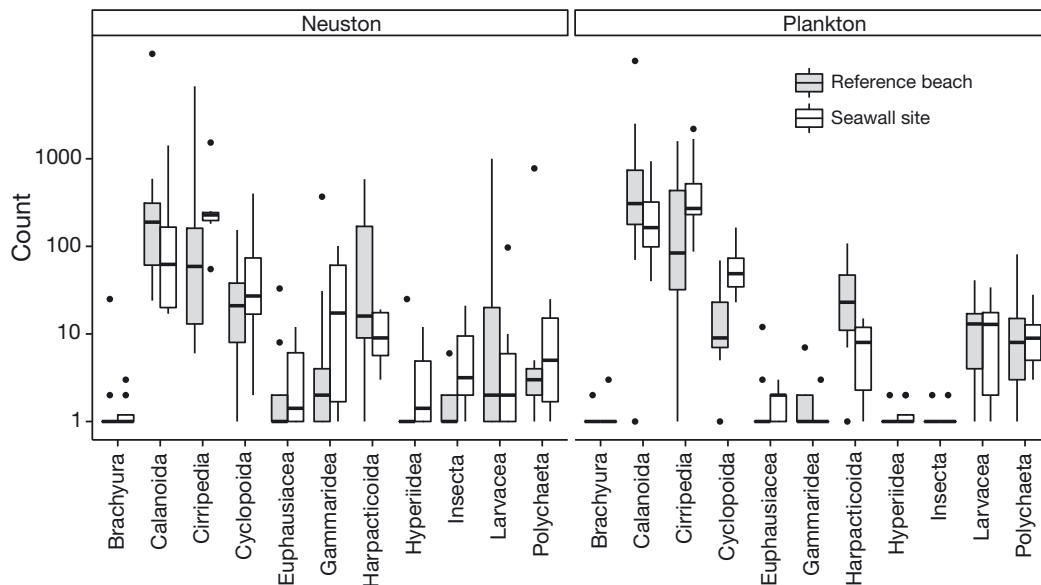

Fig. 2. Counts of prey in the environment as sampled by neuston and plankton nets. Counts are shown under $\log(x + 1)$ transformation. Upper and lower hinges: first and third quartiles; mid-line: median; whiskers: points within 1.5 × interquartile range; dots represent data outside of 1.5 × interquartile range

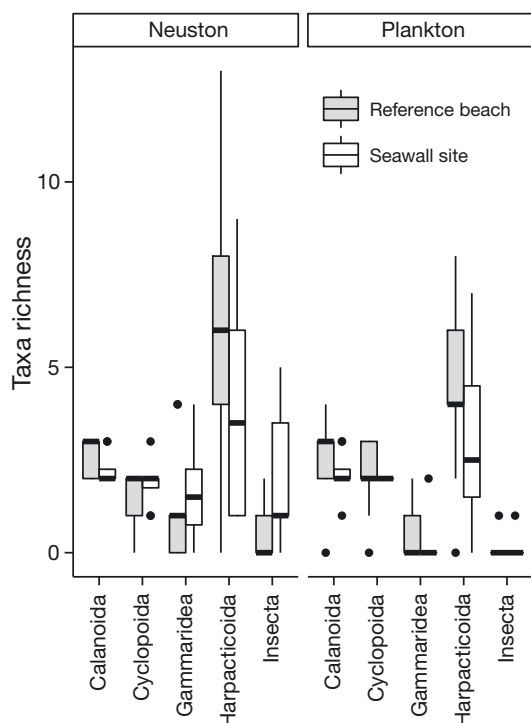Fig. 3. Taxa richness of prey in the environment as sampled by neuston and plankton nets. Box-plot definitions: see Fig. 2
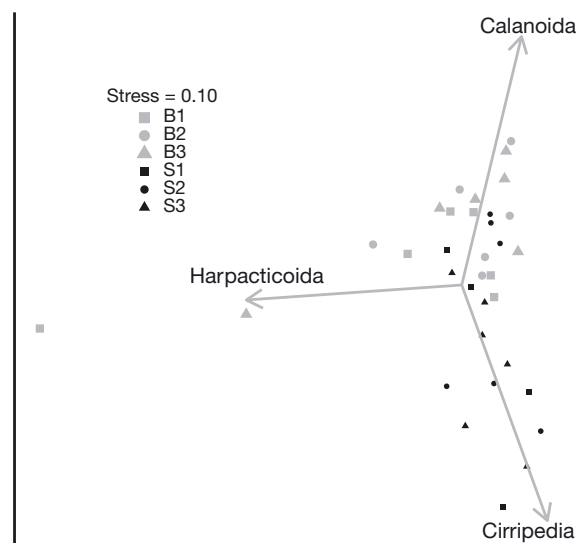

Fig. 4. Non-metric multidimensional scaling (NMDS) plots of prey composition in the environment of reference beaches (B1, B2, B3) and seawall sites (S1, S2, S3). Vectors indicate prey taxa with significant loadings on the axes

Table 3. Summary statistics of permutational multivariate analysis of variance (PERMANOVA) tests on differences in environmental prey composition according to the factors shoreline type (Sh), net (Ne), site (Si), and netting event (Ev). **Bold**: significant p-values ($\alpha = 0.05$)

Factor	df	SS	MS	Pseudo F	p
Sh	1	5708.4	5708.4	11.226	**0.0002**
Ne	1	923.11	923.11	2.3067	0.1141
Si(Sh)	4	1987.6	496.91	0.41259	0.9803
Sh × Ne	1	495.4	495.4	1.2379	0.3289
Ev(Si(Sh))	13	15654	1204.1	2.4341	**0.0066**
Si(Sh) × Ne	4	1592	398.01	0.80458	0.6637
Residual	9	4452.2	494.68		
Total	33	31811			

The stomachs of these juvenile salmon included 33 000 individual prey from epibenthic, planktonic, and terrestrial habitats. There were no significant differences between shoreline types in stomach fullness for any salmon group (Table 6). There was some variation in prey selectivity among salmon groups and between shoreline types, although in most cases shoreline type did not affect positive or negative selection for a prey taxa (Fig. 6). All groups of juvenile salmon positively selected insects and crab larvae and negatively selected barnacle larvae.

The diets of Chinook salmon comprised a variety of epibenthic, planktonic, and terrestrial prey taxa (Fig. 7). Brachyuran larvae and insects were particularly abundant prey in all sizes of Chinook salmon, with insects more abundant in smaller fish and brachyuran larvae more abundant in larger fish. Other common prey taxa included gammarid amphipods and polychaetes. Chinook salmon positively selected for gammarid and hyperiid amphipods, brachyuran larvae, and insects.

The NMDS of Chinook salmon diets did not show any separation between fish captured at different shoreline types during day or night (Fig. 8). Brachyuran larvae, gammarid amphipods, insects (comprised of Aphididae, Coleoptera, Diptera, Hemiptera, and Psocoptera), as well as several rarer taxa contributed to gradients that separated diets in ordination space (Fig. 8), but there were no patterns among these gradients relative to shoreline type. There was no significant effect of shoreline type on the diet composition of Chinook salmon during the day or night (PERMANOVA; Table 7).

Chum salmon <50 mm length fed on a mixture of epibenthic prey, such as harpacticoid copepods and polychaete annelids, and planktonic prey, such as euphausiids and calanoid and cyclopoid copepods (Fig. 7). Calanoid copepods were primarily in the genera *Calanus, Paracalanus*, and *Pseudocalanus*; cyclopoid copepods were entirely comprised of the genera *Corycaeus, Oncaea*, and *Oithona*; harpacticoid copepods were primarily in the genus *Harpacticus*. Small

Table 4. Summary statistics for linear mixed effects models (abundance) and generalized linear mixed effects models (richness) comparing environmental prey between shoreline types (baseline: reference beach) and net types (baseline: neuston net). Parameter estimates, standard errors, and p-values are reported for fixed effects, and variance and standard deviations are reported for random effects. Baseline refers to the level of the categorical fixed effect that the parameter provides comparison against

Response variable	Fixed effect	Parameter estimate	SE	p	Random effect	Variance	SD
Cirripedia abundance	Intercept	4.319	0.475	2×10^{-16}	Site	1.284×10^{-8}	1.133×10^{-4}
	Shoreline type	1.375	0.691	0.046	Netting event	1.776	1.333
Harpacticoida abundance	Intercept	3.207	0.384	2×10^{-16}	Site	1.99×10^{-8}	1.411×10^{-4}
	Shoreline type	−1.353	0.558	0.015	Netting event	0.8457	0.9196
Calanoida richness	Intercept	0.9505	0.1844	2.50×10^{-7}	Site	9.43×10^{-8}	3.07×10^{-4}
	Shoreline type	−0.1555	0.225	0.49	Netting event	3.56×10^{-9}	5.97×10^{-5}
	Net type	−0.0247	0.2229	0.91			
Cyclopoida richness	Intercept	0.5077	0.2222	0.022	Site	7.16×10^{-8}	2.68×10^{-4}
	Shoreline type	0.0553	0.2507	0.825	Netting event	1.16×10^{-7}	3.41×10^{-4}
	Net type	0.1881	0.2517	0.455			
Gammaridea richness	Intercept	0.6016	0.4380	0.170	Site	7.16×10^{-8}	2.68×10^{-4}
	Shoreline type	−0.0511	0.4235	0.904	Netting event	1.16×10^{-7}	3.41×10^{-4}
	Net type	−1.2203	0.4840	0.012			
Harpacticoida richness	Intercept	1.777	0.151	2×10^{-16}	Site	2.815×10^{-8}	1.678×10^{-4}
	Shoreline type	−0.474	0.229	0.038	Netting event	0.03581	0.1892
Insecta richness	Intercept	−0.95	0.566	0.093	Site	1.582×10^{-7}	3.977×10^{-4}
	Shoreline type	1.561	0.622	0.012	Netting event	0.2896	0.5382

Table 5. Sample sizes (n) of diets processed (total = 459) separated by juvenile salmon group

Species	Fork lengths	Day/Night	n
Chinook salmon	All	Day	173
	All	Night	81
Chum salmon	<50 mm	Day	73
	≥50 mm	Day	68
Pink salmon	All	Day	64

chum salmon positively selected for harpacticoid copepods at both shoreline types, but positively selected for the planktonic calanoid and cyclopoid copepods only at seawall sites (Fig. 6). They also positively selected for larvaceans only at seawall sites. Diets of chum salmon >50 mm in length were dominated by planktonic larvaceans, which these fish positively selected for at both shoreline types.

The NMDS of small chum salmon diets indicated separation in ordination space between fish captured at different shoreline types, although this plot should be interpreted cautiously because the stress was relatively high (Fig. 8). Orders of copepods, a prominent prey of small chum salmon, contributed to gradients in ordination space. There was an increasing gradient of harpacticoid copepods in the direction of diets from reference beaches and increasing gradients of calanoid and cyclopoid copepods in the direction

of diets from seawall sites. There was a significant effect of shoreline type on the diet composition of small chum salmon (PERMANOVA, Table 7).

The NMDS of large chum salmon diets showed qualitative separation in diets of fish captured at different shoreline types (Fig. 8). There was an increasing gradient of larvaceans, the primary prey of large chum salmon, in the direction of diets from both shoreline types. Calanoid copepods also contributed to the diets of large chum salmon and there was an increasing gradient of calanoid copepods in the direction of diets from fish captured at seawall sites (NMDS vectors; Fig. 8). There was no significant effect of shoreline type on the diet composition of large chum salmon (PERMANOVA; Table 7).

All sizes of pink salmon fed primarily on planktonic taxa (Fig. 7). The 2 smallest size classes of pink salmon fed primarily on larval euphausiids (30 mm size class) and calanoid copepods (50 mm size class). Like chum salmon, diets of larger pink salmon were dominated by larvaceans. In contrast to chum salmon, harpacticoid copepods were not abundant in the diets of pink salmon of any size. Pink salmon positively selected for larvaceans at both shoreline types, larval euphausiids at reference beaches, and calanoid copepods at seawall sites.

The NMDS of pink salmon diets showed an inconsistent separation of fish captured at different shoreline types (Fig. 8). There were gradients in ordination
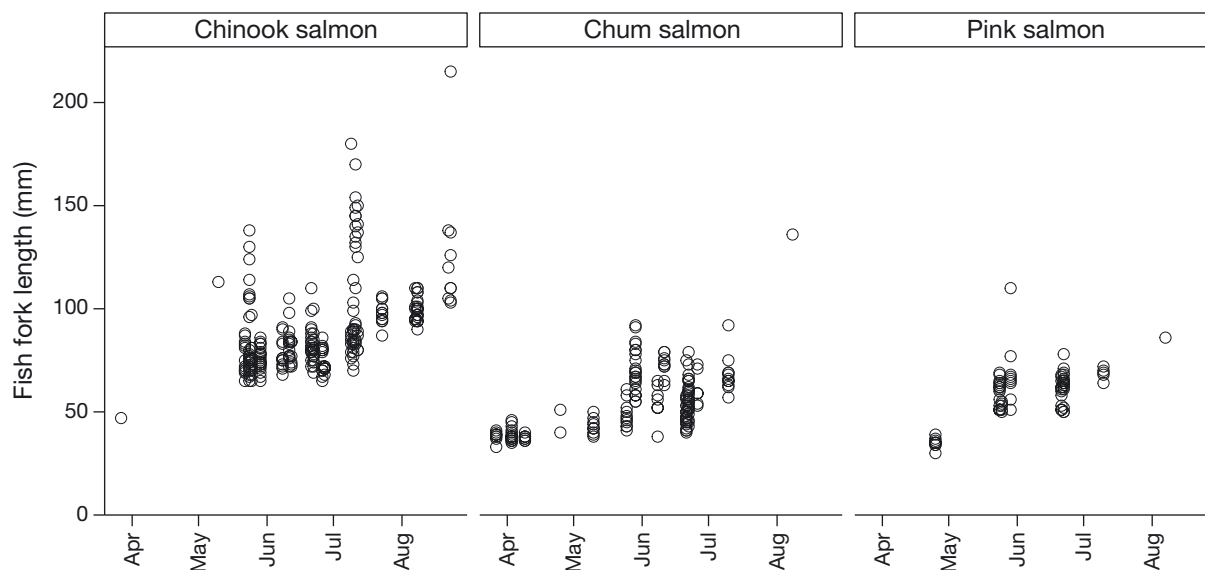
Fig. 5. Size and timing of Chinook, chum, and pink salmon. Diets of chum salmon before May were sampled in 2013; all other diets were sampled in 2012

Table 6. Summary statistics for linear mixed effects models comparing stomach fullness of salmon groups between shoreline types (baseline: reference beach). Parameter estimates, standard errors, and p-values are reported for fixed effects, and variance and standard deviations are reported for random effects

Salmon group	Fixed effect	Parameter estimate	SE	p	Random effect	Variance	SD
Chinook, day	Intercept	0.249	0.0113	2.00×10^{-16}	Site	2.06×10^{-9}	4.54×10^{-5}
	Shoreline type	0.0293	0.0194	0.13	Netting event	0.001317	0.03629
Chinook, night	Intercept	0.276	0.0162	2.00×10^{-16}	Site	2.06×10^{-9}	4.54×10^{-5}
	Shoreline type	0.0103	0.0219	0.64	Netting event	5.55×10^{-4}	0.02347
Chum, small	Intercept	0.2985	0.0125	2.00×10^{-16}	Site	2.06×10^{-9}	4.54×10^{-5}
	Shoreline type	−0.0075	0.0159	0.62	Netting event	2.06×10^{-9}	4.54×10^{-5}
Chum, large	Intercept	0.2442	0.019	2.00×10^{-16}	Site	2.06×10^{-9}	4.50×10^{-5}
	Shoreline type	0.0246	0.0298	0.41	Netting event	0.001827	0.04275
Pink	Intercept	0.2525	0.02955	2.00×10^{-16}	Site	0.002122	0.04607
	Shoreline type	0.00726	0.04335	0.87	Netting event	7.84×10^{-4}	0.028

space of many taxa that were abundant in pink salmon diets, but they were not related to shoreline type. There was no significant effect of shoreline type on the diet composition of pink salmon (PERMANOVA; Table 7).

Post-hoc analysis of small chum salmon

Small chum salmon were analyzed post-hoc because PERMANOVA indicated a significant effect of shoreline type on the composition of their diets. For this analysis, we quantitatively compared the abundance of copepods in both the diets of small chum salmon and in the environment. We analyzed effects on cope-

pod taxa because they were the most abundant prey in the diets of small chum salmon and statistically significant vectors on NMDS ordinations suggested an effect of shoreline type on their abundances in diets. The taxa analyzed were harpacticoid copepods, which are mainly epibenthic, and calanoid and cyclopoid copepods, which are mainly planktonic.

Three linear mixed effects models quantified the effect of shoreline type on the abundance in the diets of small chum salmon of (1) epibenthic copepods, (2) planktonic copepods, and (3) total copepods. In the first 2 models, harpacticoid copepods were analyzed separately from calanoid and cyclopoid copepods because of the *a priori* hypothesis that shoreline armoring would reduce epibenthic invertebrate availability
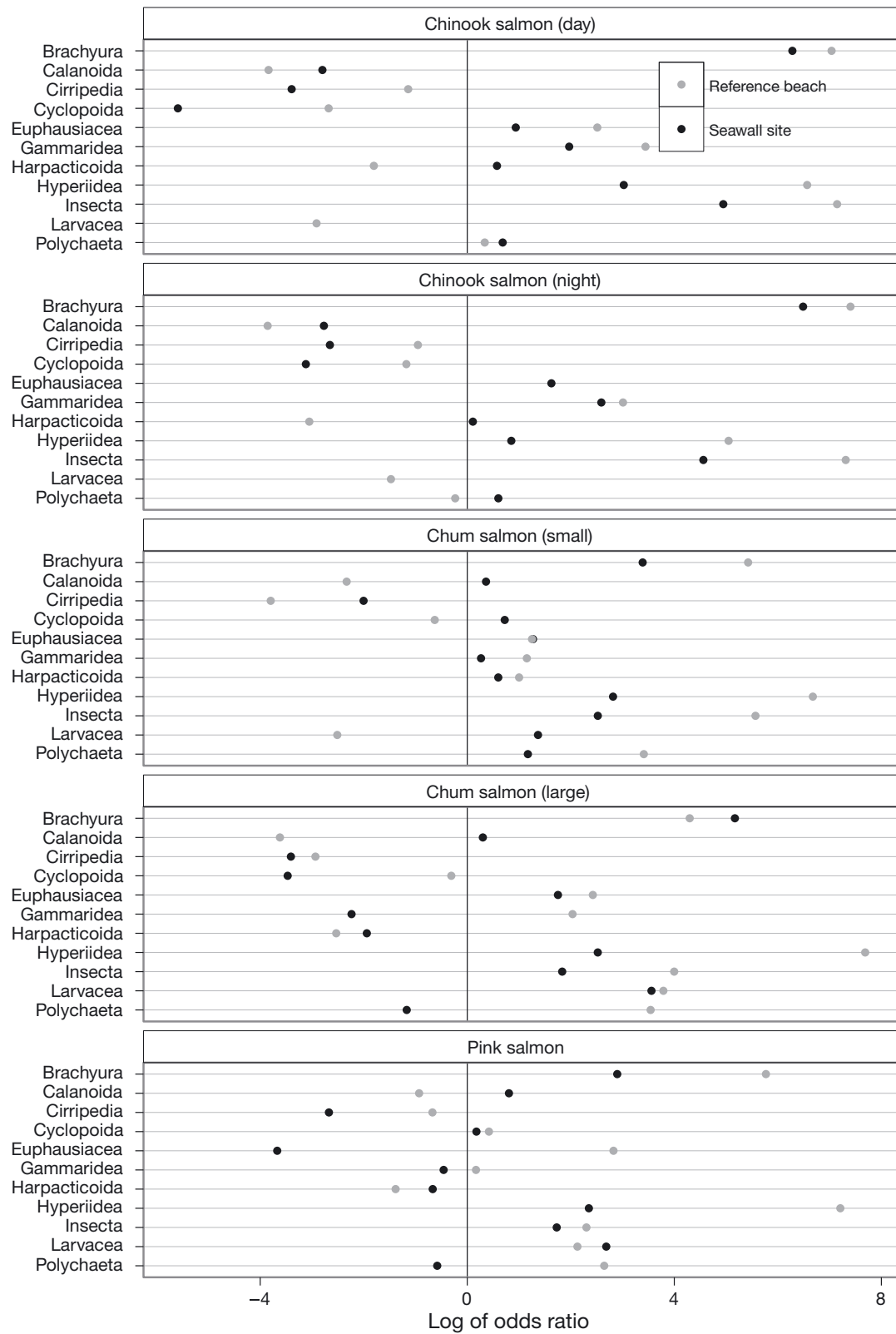
Fig. 6. Selection of prey taxa by 5 salmon groups (Chinook, day; Chinook, night; chum, small; chum, large; pink) separated by 2 shoreline types (reference beaches, seawall sites), quantified by the log of the odds ratio. Positive and negative values indicate positive and negative prey selection, respectively
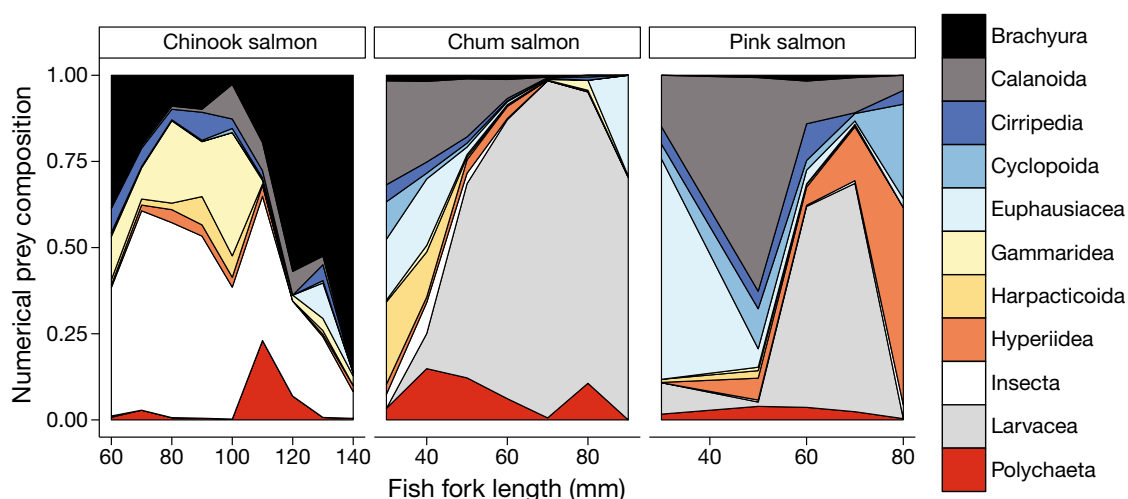
Fig. 7. Numerical composition of prey for Chinook, chum, and pink salmon, binned by 10 mm length increments

Table 7. Summary statistics of PERMANOVA tests on differences in diet composition of the salmon groups according to the factors shoreline type (Sh), site (Si), and netting event (Ev)

Salmon group Factor	df	SS	MS	Pseudo F	p
Chinook, day					
Sh	1	1941.6	1941.6	0.46215	0.8788
Si(Sh)	4	18448	4611.9	0.98872	0.486
Ev(Si(Sh))	31	31	1.99×10^5	6433.7	0.0001
Residual	131	2.90×10^5	2212.2	2.9083	
Total	167	5.23×10^5			
Chinook, night					
Sh	1	4060.7	4060.7	0.89803	0.4947
Si(Sh)	4	19389	4847.2	0.88172	0.5934
Ev(Si(Sh))	10	63942	6394.2	2.7466	0.0001
Residual	64	2328	2328		
Total	79	2.47×10^5			
Chum, small					
Sh	1	7048.2	7048.2	2.8898	0.0174
Si(Sh)	4	9392.9	2348.2	0.44034	0.9875
Ev(Si(Sh))	9	76462	8495.8	6.1573	0.0001
Residual	56	77269	1379.8		
Total	70	2.02×10^5			
Chum, large					
Sh	1	6445.3	6445.3	2.235	0.1262
Si(Sh)	4	14705	3676.4	0.87362	0.534
Ev(Si(Sh))	8	36161	4520.1	2.4329	0.0008
Residual	53	98467	1857.9		
Total	66	1.87×10^5			
Pink					
Sh	1	4225.6	4225.6	0.62525	0.7218
Si(Sh)	4	31518	7879.5	1.6094	0.0904
Ev(Si(Sh))	7	35806	5115.2	4.7639	0.0001
Residual	51	54761	1073.8		
Total	63	1.29×10^5			

(e.g. Morley et al. 2012) and not have an effect on planktonic invertebrates.

Linear mixed-effects models indicated a significant effect of shoreline type on the abundance of epibenthic (harpacticoid) and planktonic (calanoid and cyclopoid) copepods in diets of small chum salmon and the environment (Table 8, Fig. 9). Abundances of epibenthic copepods were significantly greater in diets from reference beaches while abundances of planktonic copepods were significantly greater in diets from seawall sites. There was no significant effect of shoreline type on the total abundance of copepods in diets. There was also no significant effect of shoreline type on the abundance of planktonic copepods in the environment, although there were significantly greater abundances of planktonic copepods captured in plankton nets compared to neuston nets (Table 8; environmental epibenthic copepod abundances analyzed in Table 4).

DISCUSSION

Here, we show that the feeding ecology of juvenile salmon in shallow water habitats can be influenced by shoreline armoring within an urban landscape. Shoreline armoring affected the composition of prey in the environment and the prey selectivity and diet composition of small chum salmon. There were no significant effects of armoring on the diets or stomach fullness values of other salmon groups.

Our study contributes to a growing recognition that shoreline infrastructure changes the feeding ecology of fish in shallow habitats. Morley et al. (2012) found that riprap armoring along the Duwamish River estu- ary affected the diet composition of chum salmon, and that epibenthic invertebrates were significantly less abundant at armored sites. The Duwamish River flows into Elliott Bay where our study sites are
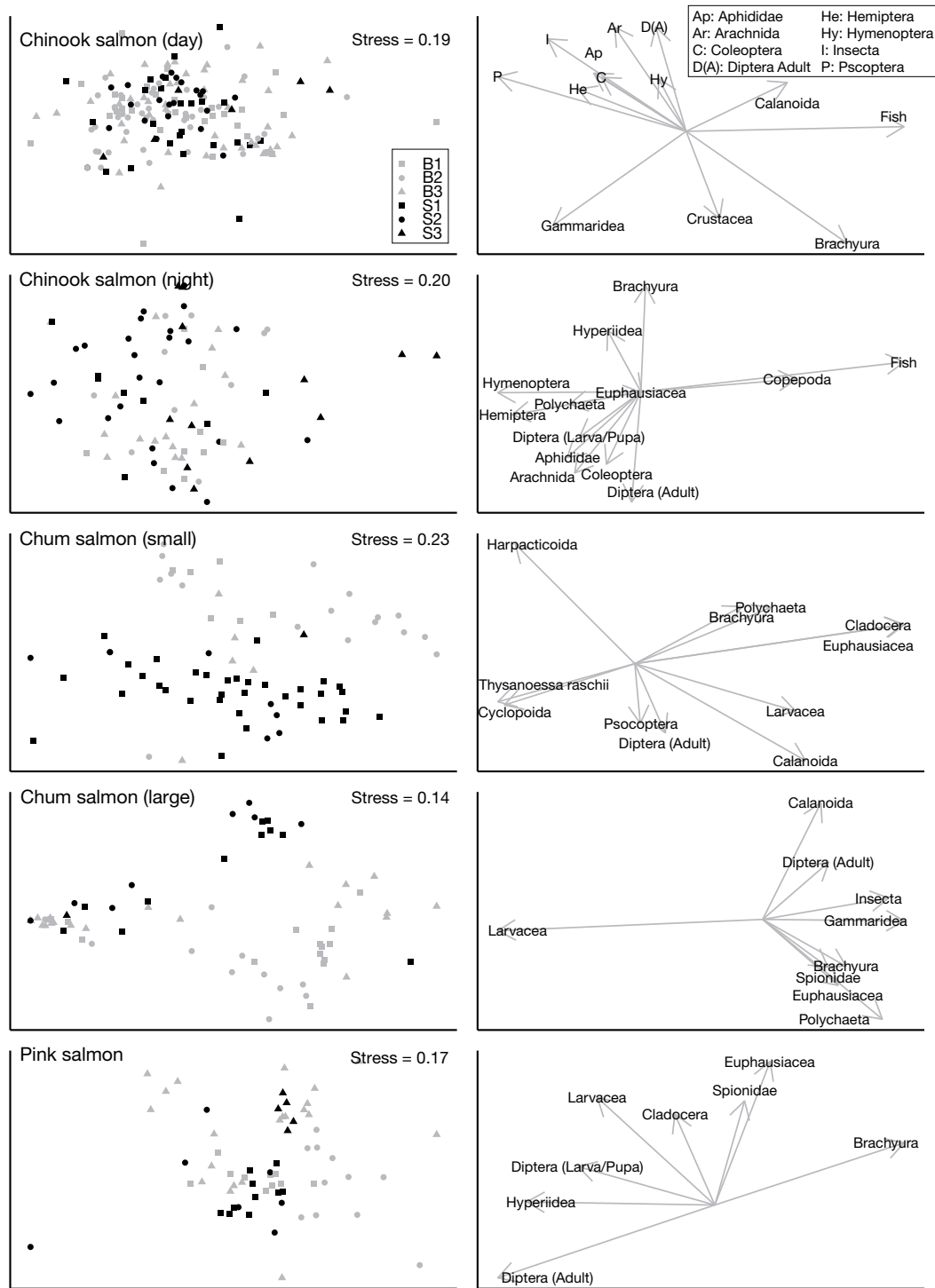

Fig. 8. NMDS of prey composition for each salmon group at reference beaches (B1, B2, B3) and seawall sites (S1, S2, S3). Vectors indicate prey taxa with significant loadings on the axes

Table 8. Summary statistics of linear mixed effects models quantifying copepods in the diets of small chum salmon (Diet) and in the environment. Baseline values for shoreline type and net type are reference beach and neuston net, respectively. Parameter estimates, standard errors, and p-values are reported for fixed effects, and variance and standard deviations are reported for random effects

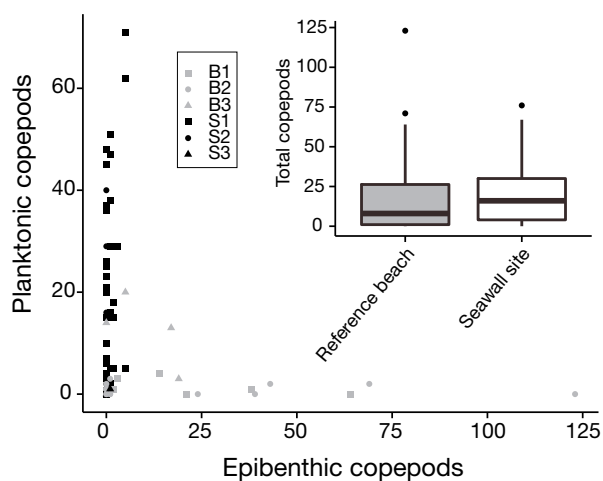| Response variable	Fixed effect	Parameter estimate	SE	p	Random effect	Variance	SD
Diet							
Epibenthic copepods	Intercept	1.96	0.413	2.10×10^{-6}	Site	1.83×10^{-8}	1.25×10^{-4}
	Shoreline type	−1.504	0.52	0.0038	Netting event	0.770	0.878
Planktonic copepods	Intercept	1.098	0.382	0.004	Site	6.25×10^{-9}	7.91×10^{-5}
	Shoreline type	1.37	0.492	0.0053	Netting event	0.716	0.846
Total copepods	Intercept	2.368	0.4444	9.90×10^{-8}	Site	2.08×10^{-9}	4.56×10^{-5}
	Shoreline type	0.165	0.574	0.77	Netting event	1.04	1.022
Environment							
Planktonic copepods	Intercept	5.17	0.367	2.00×10^{-16}	Site	1.56×10^{-9}	1.25×10^{-4}
	Net type	0.763	2.39	0.017	Netting event	1.47	1.21

Fig. 9. Number of planktonic and epibenthic copepods in the diets of small chum salmon. Inset = total number of copepods in the diets of small chum salmon. Box-plot definitions: see Fig. 2

effects are evident in different ecosystem types, fish species, and regions, and suggest that shoreline infrastructure can change the feeding ecology of fish along many developed waterfronts.

While it is clear that shoreline armoring causes ecological changes, additional research is necessary to determine effects on habitat quality. The alternative prey that fish consume in modified habitats could create energetic costs to the predator that are not clear from diet analysis alone, for example if the prey that occur there are more cryptic or evasive (Gerking 1994). In our study, small chum salmon consumed more planktonic copepods when armoring compromised environmental abundances of epibenthic copepods that these fish select for under more natural conditions (Feller & Kaczynski 1975, Healey 1979, Sibert 1979, Webb 1991). However, harpacticoid copepods may comprise more desirable prey because they are brightly pigmented and associate with substrata where they are presumably less evasive than the planktonic copepods. Indeed, some species of calanoid copepods evade predation from chum salmon more effectively than harpacticoid copepods under laboratory conditions (Simenstad et al. 1982a). Juvenile chum salmon balance metabolic costs of maintenance and migration with food intake and growth (Wissmar & Simenstad 1988), and preferentially consume prey that are less evasive (Eggers 1982), suggesting that the energetic costs of consuming alternative prey along armored shorelines could impair habitat value there. The effects of armoring on habitat value will be better understood if studies take into account the energetic consequences of detecting, capturing, and consuming alternative prey (e.g. Giacomini et al. 2013, Van Deurs et al. 2015).

located, suggesting that chum salmon may experience altered feeding conditions across a broader armored landscape than that which we studied. Our results are also consistent with Doi et al. (2010), who determined that armoring reduced benthic prey consumption by largemouth bass (*Micropterus salmoides*) in lakes. More broadly, Toft et al. (2007) and Francis & Schindler (2009) found that armoring reduced the consumption of terrestrial prey by fish in estuarine and lacustrine systems, respectively. Furthermore, effects have been found from other infrastructure types; for example, Duffy-Anderson & Able (1999, 2001) found that fish enclosed in areas shaded by a large pier consumed less prey and experienced negative growth rates compared to fish in sunlit areas. Taken together, these studies indicate that armoring

Effects of shoreline armoring are potentially mediated by prey selection behaviors that vary among fish species and life history states. Variable prey selection among fish species is common in many ecosystems, including coastal areas (Ross 1986). Ontogeny also influences the diets of many fish (Gerking 1994), including juvenile salmon (Simenstad et al. 1982b, Groot & Margolis 1991, Duffy et al. 2010). As a result, different species and life stages of fish within a community may feed on prey produced in habitats (e.g. terrestrial, planktonic, epibenthic) that are affected by shoreline armoring differently or not at all (e.g. Morley et al. 2012, Sobocinski et al. 2010). Our results reflect this in that we found that armoring affected the diets of fish that fed on epibenthic prey but did not affect those that fed primarily on plankton. Doi et al. (2010) similarly found that armoring affected the diets of smallmouth bass but not bluegill sunfish (*Lepomis macrochirus*), although their findings were supported by isotopic data rather than analysis of diet contents. Armoring may also have variable effects on pink salmon diets based on ontogeny because, like chum salmon, they feed more on epibenthic prey when they are small (Kaczynski et al. 1973). However, we could not address this in our study because the pink salmon we captured were large.

Fish mobility and the spatial scale of our sampling may have influenced some of our results regarding insects in the environment and in juvenile Chinook salmon diets. Armoring can reduce terrestrial prey diversity (Sobocinski et al. 2010) and consumption by juvenile Chinook salmon (Toft et al. 2007), but we found that armoring was associated with higher insect taxa richness in the environment and had no overall effect on Chinook salmon diets. However, the studies of Sobocinski et al. (2010) and Toft et al. (2007) were conducted at relatively broad scales, including relatively natural reference beaches, while our unarmored sites were small man-made beaches within the larger landscape of an urban bay. Much of the insect prey in Chinook salmon diets in our study consisted of dipteran flies that can utilize armored habitat such as riprap (Toft et al. 2013), and vegetation-oriented insects such as Homoptera were rarely observed. Also, Chinook salmon were the largest and most mobile of the salmon we collected, and they may not have occupied the shoreline types long enough for us to detect some of the site-associated effects such as those seen by Toft et al. (2007), who used nets to enclose fish at armored and unarmored shorelines. Taxa such as the insects caught in the neuston nets and consumed by Chinook salmon can be widely dispersed via water currents (e.g. export from the nearby Duwamish River) and wind (Brodeur 1989). A landscape scale approach (Pittman et al. 2011) may be an appropriate alternative means for assessing effects of armoring on the diets of fish that consume prey with potentially large dispersal ranges. For example, Duffy et al. (2010) found a greater contribution of insects to the diets of Chinook salmon captured in the less developed northern region of Puget Sound as compared to the more developed central and southern regions.

Mobility of the juvenile salmon with regard to the arrangement of our sample sites should also be considered. Prey in the diets of salmon may have been integrated from a range of shallow habitats that the salmon encountered before they were captured. Seawall sites occurred along a long continuous seawall, while reference sites were small pocket beaches interspersed in an armored shoreline. Furthermore, juvenile salmon avoid areas under large piers that bounded the shorelines of our seawall sites (Munsch et al. 2014), which may have increased their residence times at seawall sites compared to reference beaches. Thus, the diets of fish captured at seawall sites may have reflected more site fidelity than those from fish captured at the reference beaches. If this was the case, diet differences related to shoreline type may be greater than indicated by our study. Fish captured at the reference beach B3 may have experienced a different sequence of prey fields than those captured at beaches B1 and B2 on the other side of Elliott Bay, as suggested by our finding that diets from fish captured at B1 and B2 were more similar to each other than to those from B3. We were unable to randomize site selection or arrangement in this study because of logistical challenges associated with the constraints of access and availability in the urban setting. Sampling a wider array of beaches, including those directly adjacent to the seawall, or enclosing fish at a number of seawall and beach sites prior to diet sampling may allow a more accurate evaluation of the effects of armoring on juvenile salmon diets.

Our study addresses the challenge to understand ecological effects of man-made nearshore environments so that more ecologically beneficial shorelines can be designed (Wilson et al. 2015). In circumstances where the removal of armored shorelines is not practical (e.g. Toft et al. 2013, 2014), constructed beaches can protect shorelines from erosion while providing some structural elements similar to natural conditions that provide fish habitat (Speybroeck et al. 2006). Engineered beaches have been considered ecologically preferable to armoring, but few quanti-

tative studies have evaluated their benefits to fish (Hartig et al. 2011). Built beaches in urban areas can directly benefit society, for example by providing opportunities for recreation and engaging nature (Standish et al. 2013), and superior protection from flooding associated with sea level rise compared to conventional armoring (Temmerman et al. 2013). Toft et al. (2013) showed that replacing an armored shoreline with a beach (B2 in our study) can produce greater abundances and taxa richness of epibenthic prey. Our results suggest that this increased production of epibenthic prey is reflected in the diets of juvenile chum salmon, although the epibenthic contribution was not as great as seen in less modified landscapes (e.g. Feller & Kaczynski 1975, Healey 1979). Thus, built beaches may be effective in restoring some of the lost functions of degraded shorelines, and warrant further consideration as a management tool.

Estuarine and coastal development has occurred on a global scale and impacted the natural resources provided by aquatic habitats (Lotze et al. 2006). Despite the widespread and predictable introduction of shoreline infrastructure into shallow waters, our understanding of the broader ecological consequences is incomplete (Bulleri & Chapman 2010). Some fish and other consumer taxa may be resilient to change, for example through plasticity of feeding behavior, and ecological change alone may not indicate a change of habitat value. Research that directly addresses the ecological fitness consequences of changes caused by shoreline development will be particularly informative to those responsible for managing coastal and estuarine habitats.

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