Fish Ecology Along Modified Shorelines

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Abstract

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Waterfronts are busy places. Ancient civilizations often formed along the water where people benefited from aquatic resources and trade. People have continued to develop waterfronts, and these areas are now major components of the global economy. They support not only international trade, but a diversity of local industries such as tourism and transportation. Waterfront development is occurring globally as the human population grows and increasingly locates in coastal settings.

People have modified shorelines to support societal functions of waterfronts. These modifications have eliminated, restructured, and shaded shallow waters, which is concerning because many species of fish use shallow areas along shore, often during juvenile stages. Fish and their associated nearshore ecosystems often contribute to the value of waterfronts to people because they are culturally and economically significant. Thus, people and fish share waterfronts, and people will benefit by protecting nearshore ecosystems and the fish habitats that they support.

In this dissertation, I examined effects of shoreline modifications (e.g., seawalls, piers) on fish and elucidated their natural history. The first three chapters are parts of a study that assessed fish habitat in Elliott Bay, WA. Our findings informed habitat rehabilitation along its urbanized shoreline as part of a seawall reconstruction. My participation in this study and the literature I read to prepare for my General Examination interested me in the behavior and habitat use of nearshore fish in Puget Sound. Therefore, in the fourth and fifth chapters, I assembled and analyzed data on fish behavior collected by the Wetland Ecosystem Team over the past decade throughout Puget Sound, WA. Following this work, I was interested in understanding how shoreline modifications affect fish habitats globally. I therefore wrote the sixth chapter to synthesize the current primary literature examining effects of shoreline modifications on estuarine fish and discuss how we can improve fish habitats along shore within constraints of human uses.

In Chapter One, I quantified effects of seawalls and piers on fish assemblages and juvenile salmon feeding behavior in Elliott Bay. I found that (1) the composition of fish assemblages varied between (a) sites modified by seawalls and piers and (b) built beaches without piers, (2) fish abundances were lower in shaded areas under piers relative to sunlit areas, which also affected assemblage composition under piers, and (3) feeding behavior of juvenile Pacific salmon (*Oncorhynchus* spp.) was lower under piers relative to sunlit areas. In Chapter Two, I compared subtidal fish and crab assemblages between sites modified by intertidal seawalls and built beaches. I found that (1) the composition of fish assemblages varied between seawall sites and beaches and (2) species that selected for a substrate type (e.g., sand, rocks) often contributed to compositional differences. In Chapter Three, I compared the diets of juvenile Pacific salmon between seawall shorelines and reference beaches in Elliott Bay, WA. I found that (1) epibenthic copepods were less abundant along seawall shorelines and (2) small (<50 mm) chum salmon (*O. keta*) consumed less epibenthic copepods and more planktonic copepods along seawall shorelines. In Chapter Four, I quantified context-dependent behaviors of shallow water fish assemblages in Puget Sound. I found (1) smaller fish occupied shallower depths where predators were less abundant, (2) smaller fish schooled in larger groups, (3) pelagic fish schooled in larger groups in deeper water, (4) demersal fish schooled in larger groups when occupying the water column, (5) species partitioned habitats by depth and season, and (6) smaller fish were proportionally less abundant along deep shorelines created by intertidal armoring. In Chapter Five, I quantified the diurnal feeding behavior of juvenile Pacific salmon in Puget Sound, WA. I found that (1) juvenile salmon fed often and throughout the day, (2) their feeding intensity declined from dawn to late afternoon, and (3) this trend in behavior was not evident from examining diets alone. In Chapter Six, I synthesized a global understanding of effects of shoreline infrastructure on shallow fish assemblages and recommended how to research, manage, and rehabilitate shallow habitats along modified waterfronts.

Overall, this dissertation suggests that built shorelines affect the ecology of fish, and that effects are primarily negative. It also suggests that we can protect nearshore ecosystems, but to do so requires that we understand their natural histories and appreciate their habitat functions and processes. Shoreline modifications are common worldwide, and the literature suggests that they affect the ecology of many nearshore systems. Many of these changes appear to affect basic habitat and fish attributes such as shelter, food availability, and vision. Thus, the findings in this dissertation may be generalizable elsewhere, or can at least provide a starting point for ecologists working in other systems. The fundamental challenge for managers and ecologists is to balance the protection of shallow fish habitats with the utility of waterfronts to people. I hope that my dissertation can guide efforts to reach this goal.

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Dedication

To my family. Thank you for raising me near the water and showing me the fish that live in it.

General Introduction

People have long benefited from aquatic resources and have developed waterfront land. While waterfront infrastructure dates to brick-lined docks in Lothal (2300 BCE; Schwartz 1980) and a seawall along Alexandria (332 BCE; Rao 1965), we have only recently considered its ecological consequences. At present, half of the human population lives within 60 km of shore and three-quarters of the world's largest cities are on the water (UNEP 2014). Shoreline infrastructure is often used to aggregate and accommodate economically desirable activities along the water. As a consequence, intertidal areas have been modified or eliminated by shoreline infrastructure worldwide (Perkins et al. 2015). As the human population increases and sea levels rise, infrastructure will continue to replace natural shorelines (Bulleri and Chapman 2010). Thus, shoreline infrastructure is common along much of the world's waterfronts and in many locations nearshore ecosystems are centuries removed from natural states.

Nearshore waters often support ecologically, culturally, and economically important ecosystems. Coastal areas provide ecosystem services that are annually valued in the hundreds of billions of US dollars (Costanza et al. 1997). Fish provide some of these services relating to biological control (e.g., trophic-dynamic regulations of populations), habitat, food, recreation, and culture (Costanza et al. 1997). Ecotones at the interface of land and sea are often productive and their waters support high densities and diversities of fish (Beck et al. 2001). These shallow areas are of conservation concern because they may contribute disproportionately great numbers of juvenile fish to adult populations (e.g., Beck et al. 2001, Dahlgren et al. 2006, Sheaves et al. 2006, Layman et al. 2006). Many shallow waters facilitate the growth and survival of juvenile fish, and their potentially complex role in fish production and ecosystem function has only recently been appreciated (Sheaves et al. 2014, Nagelkerken et al. 2015). Thus, nearshore ecosystems are among the most degraded on earth and important to fish as well as society. This should concern the many people that rely on fish for identity, food, or employment because habitat degradation threatens fish populations (e.g., U.S. Fish and Wildlife Service 1973, Nehlsen et al. 1991, National Research Council 1996, Magnusson and Hilborn 2003, Feyrer et al. 2007, NOAA 2007).

Despite implications of shoreline management on the sustainability of fisheries, fish ecology and waterfront management in developed landscapes are emerging areas of research. Managers can design shorelines that are beneficial to fish within constraints of developed shorelines; however, they must understand ecological effects of shoreline infrastructure and how to mitigate negative effects. This requires a detailed understanding of habitat use that goes beyond abundance metrics and assesses habitat capacity, opportunity, and realized function (Simenstad and Cordell 2000). That is, can fish access appropriate environments and is there direct indication that fish benefit from accessing a given habitat? It also requires an understanding of fishes' natural history (Able 2016): what behaviors or traits of fish suggest that shoreline modifications will degrade their habitats?

In this dissertation, I examine the ecology of fish in the developed estuary Puget Sound. Much of this work examines effects of shoreline modifications, and is supplemented by descriptions of natural history, defined as "The fundamental properties of organisms—what they are, how and where they live, and the biotic and abiotic interactions that link them to communities and ecosystems" (Tewksbury et al. 2014). Chapters One, Two, and Three examine the assemblage composition, behavior, and diets of fish in Elliott Bay, WA, an urban estuarine embayment comprised of a mosaic of artificial shallow environments. In these chapters we compare the ecology of fish in artificial environments, including along built beaches and armored shorelines, and under large piers. Chapters Four and Five have greater focus on natural history, and examine context dependent behavior of fish in Puget Sound. Chapter Four examines the fine-scale habitat use and behavior of fish, exploring how behaviors such as habitat selection and schooling vary at different points in the fishes' development. These observations have implications for avoiding predation, utilizing shallow areas as nurseries, and partitioning habitats in space and time. Chapter Five examines the diurnal feeding behavior of juvenile Pacific salmon, providing an unprecedented real-time, fine temporal-scale chronology of when and how often these fish feed. Chapter Six coalesces lessons from our group's involvement with habitat improvements in downtown Seattle and synthesizes a global understanding of effects of shoreline modifications on estuarine fish. I discuss what we know about effects of shoreline infrastructure on fish, how we can improve research and management, and how we can facilitate efforts to improve habitats.

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Chapter One: Effects of Seawalls and Piers on Fish Assemblages and Juvenile Salmon Feeding Behavior

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Abstract

Shoreline modifications, such as seawall armoring and piers, are ubiquitous along developed waterfronts worldwide, and recent research suggests that their ecological effects are primarily negative. We utilized snorkel surveys to quantify the effects of seawalls and piers on fish in nearshore habitats of an urbanized estuary in Puget Sound, Washington. We observed 17 species of fish and 4 species of crab during April–August 2012 at sites modified by seawalls and piers and at reference beach sites with minimal anthropogenic structures. Species assemblages at modified sites were significantly different from those at reference beaches. At modified sites, fish distribution and assemblage structure varied with proximity to the shade cast by piers; overall fish abundances were reduced under piers, and the greatest abundances were observed at high tides in areas directly adjacent to piers. Juvenile Pacific salmon Oncorhynchus spp. were the dominant fish species, and piers reduced their presence and feeding, indicating that areas under piers provide less-valuable habitat to salmon species. Piers may interrupt movements of juvenile salmon when they use shallow waters along shorelines to migrate from freshwater to marine habitats, as juvenile salmon tend to avoid shade under piers, especially at high tides. Our results show that shoreline modifications can alter species assemblage structure, thus potentially creating novel combinations and abundances of species, and can reduce habitat function for species that utilize these and similar habitats elsewhere.

Introduction

The aggregation, expansion, and maintenance of residential, commercial, and tourism activities in estuarine and coastal waterfront landscapes have transformed these areas on a global scale (Bulleri and Chapman 2010). Most of these activities are accompanied by shoreline modifications, such as armoring (e.g., seawalls and riprap) and overwater structures (e.g., piers and floating docks) that provide the economically important functions of erosion protection and waterfront access. Waterfront development is likely to continue as human populations grow and locate disproportionally in coastal, urban locations (Grimm et al. 2008) and as climate change and rises in sea level occur (Bulleri and Chapman 2010). Estuaries are especially vulnerable to change, as 22 of the world's 32 largest cities are located on estuaries (Ross 1995). Despite the widespread use of shoreline modifications along developed waterfronts, ecological effects of the modifications have only recently been studied, and many of the results indicate negative effects on indigenous species (reviewed by Bulleri and Chapman 2010).

Recent research suggests that shoreline armoring drives ecological change. Shoreline armoring, which is the use of hard structures to absorb wave energy and prevent erosion, can alter the physical environment of shallow waters by truncating the intertidal area (Chapman and Bulleri 2003) and hardening the substrate (Airoldi et al. 2005). Armoring can reduce the production and input of terrestrial invertebrates (i.e., fish prey) into aquatic ecosystems (Peterson et al. 2000; Chapman 2003; Cruz Motta et al. 2003; Romanuk and Levings 2003; Moschella et al. 2005; Sobocinski et al. 2010), which may lead to reduced consumption of terrestrial prey by fish (Toft et al. 2007). Introducing novel structures to aquatic habitats can also attract atypical and nonnative organisms (Glasby 1998; Davis et al. 2002; Glasby et al. 2007; Strayer et al. 2012). Most of the research investigating the effects of shoreline armoring on fish is recent; such studies have used scuba (Clynick 2006; Clynick et al. 2008), snorkeling (Toft et al. 2007, 2013), enclosure nets (Toft et al. 2007), beach seines (Bilkovic and Roggero 2008), and electrofishing (Strayer et al. 2012), and the resulting data suggest that land development and changes to shoreline structure influence the composition of nearshore fish species. Seawalls, which are vertical slabs of hard, typically featureless surfaces, are a common type of shoreline armoring, but their effects on fish are not well understood (however, see Toft et al. 2013).

Overwater structures, such as piers and floating docks, constitute another type of shoreline modification that causes ecological change by reducing light and introducing pilings to shallow waters. In the Hudson River estuary, a series of studies demonstrated that overwater structures can negatively impact fish: acoustic surveys showed that a large pier reduced pelagic fish abundances (Able et al. 2013); piers changed the composition of invertebrate (fish prey) species, with reduced abundances of larger species (Duffy-Anderson and Able 2001); and cage experiments suggested that shading of habitat by piers caused a reduction in growth opportunities by limiting prey detection and consumption by demersal fishes (Duffy-Anderson and Able 1999, 2001). In Puget Sound, Washington, shallow-water areas that were located directly adjacent to areas shaded by overwater structures were shown to have high densities of fish, whereas pier pilings were often utilized by crabs (Toft et al. 2007), indicating that overwater structures influenced fish and crab distributions.

The objective of our study was to quantify the effect of seawalls and piers on nearshore fish and crab communities in an urbanized estuary (Elliott Bay, Seattle, Washington) by comparing their distribution and species assemblage structure (1) between highly modified sites and reference beaches and (2) among stations within modified sites, with stations being defined based on their proximity to piers. Juvenile Pacific salmon Oncorhynchus spp. were the focus of this study, and our analysis quantified their ability to access and feed in modified nearshore habitats. We were interested in effects on juvenile salmon because they are among the dominant fish species in our study area during the spring and summer months; they have cultural, ecological, and economic significance (discussed in detail by Quinn 2005); they rely on nearshore habitat early in their life history (Simenstad et al. 1982); and the Chinook Salmon O. tshawytscha in our study area are currently listed as threatened under the Endangered Species Act.

Pacific salmon are anadromous species that enter estuarine or marine environments as juveniles, exhibiting a strong initial tendency to stay in shallow waters, which they use for feeding, predator refuge, and salinity acclimatization (Simenstad et al. 1982). In developed areas, this tendency places the juvenile salmon close to shoreline modifications (Toft et al. 2007), including armoring that reduces the production of their invertebrate prey (Sobocinski et al. 2010). Juvenile salmon are active visual predators, capturing individual prey in the water column and from the substrate (Quinn 2005). Laboratory experiments have suggested that light levels affect prey detection by juvenile salmon (Ali 1959), but the effects of shade on salmon have otherwise received little attention.

Methods

Study system.—Puget Sound is an inland sea with cold temperate waters and salinity above 25 psu in areas that are not directly adjacent to riverine input. Puget Sound experiences mixed semidiurnal tides, including a daily cycle of two approximately equal high-water levels and two unequal low-water levels. Natural beaches in Puget Sound are composed of mixed sand and gravel sediments sustained by coastal bluff erosion (Shipman 2010). Within Puget Sound, the Duwamish River delta and Elliott Bay (Figure 1) are characterized by severe wetland loss and the replacement of bluff-backed beaches with armored shorelines (Simenstad et al. 2011). Elliott Bay is a 21-km2 estuarine embayment that is highly urbanized, occurring entirely within the City of Seattle. About 99% of the shoreline is armored by seawalls and riprap, and numerous overwater structures extend into the bay (Simenstad et al. 2011).

Six shallow-water sites within Elliott Bay were monitored (Figure 1). Three of the sites (hereafter, “seawall sites”; S1–S3) were directly adjacent to urban infrastructure and were completely modified by seawalls that effectively removed the intertidal zone. Each seawall site included one large wooden pier (~4.3 m above mean lower low water [MLLW]) that was over 60 m wide and extended over 100 m into the bay. The shorelines of three reference beaches (R1–R3) were composed of sloping, heterogeneous sand and cobble that formed an intertidal zone (R2 is described in detail by Toft et al. 2013). Reference beaches were located within city parks where there were no intertidal seawalls or piers.

Physical data.—Tidal height data relative to MLLW was retrieved from Tides and Currents (National Oceanic and Atmospheric Administration; NOAA 2013). For each fish survey, snorkelers measured the position of pier shade relative to overhead pier structure (which varied with the position of the sun and with tidal height), water depth, and horizontal underwater visibility by using a tape measure. Efforts were made to snorkel during conditions of at least 2.5-m underwater visibility; transects that did not meet this requirement were excluded from analysis to minimize the effects of turbidity on fish count efficiency and on the ability to detect the fish's behavioral responses to observers (Toft et al. 2007, 2013).

Representative light levels were measured relative to the pier at one of the seawall sites (S2) once per month during April–July 2013. A Li-Cor Spherical Underwater Quantum Sensor was used to measure 15-s averages of photosynthetically active radiation (PAR; i.e., 400–700-nm wavelength) above the surface and at underwater depths of 0.0, 0.5, 1.0, 1.5, and 2.0 m. These measurements occurred approximately 1 m away from the seawall in ambient light and under the pier at distances of 3, 15, and 24 m from the pier edge. Measurements occurred during ebbing tides.

Fish and crab observations.—Snorkeling, a visual survey method, was used to monitor fish because (1) it allowed for accurate fish identification and behavioral information (e.g., feeding activity) to be collected (Toft et al. 2007, 2013); (2) it allowed the entire water column to be surveyed, including in areas under piers and close to urban infrastructure, where other sampling methods are impractical; (3) visual surveys do not confound catch efficiency and species composition as occurs in net surveys that sample habitats of different substrate types (Rozas and Minello 1997); and (4) it was well suited for use in observing our focal species, which mostly occupy the middle or upper portion of the water column.

In total, 192 snorkel surveys occurred during April–August 2012, coinciding with the peak of juvenile salmon migration (Toft et al. 2007). Surveys occurred during daylight at each site approximately once per week. An equal number of surveys took place at each site during high and low tides at heights (mean ± SE) of 2.5 ± 0.06 and 0.77 ± 0.07 m MLLW, respectively. For each data collection event, two observers simultaneously swam surface transects that were 3 and 10 m from and parallel to shore (Figure 2). At high tides, the water depths (mean ± SE) along the transects were 2.3 ± 1.0 m (3 m from shore) and 3.6 ± 1.6 m (10 m from shore); at low tides, the depths were 1.4 ± 0.6 and 2.4 ± 0.8 m. Observers swam slowly to minimize behavioral responses in fish and to allow for their vision to adjust to lower-light conditions when surveying shaded areas under piers. Eight observers who were trained in the identification of local fish and crab species participated in the surveys. To standardize data collection and minimize interobserver effects, particular attention was given to instructing observers on the identification of juvenile salmon species and how to estimate large counts of fish. We assumed that each sampling event comprised an independent observation of fish because surveys were separated on average by 1 week, which encompassed several tidal cycles, and they targeted mostly mobile and often migrating species in relatively small sites.

Observers recorded the finest identifiable taxon, group size, and water column position (surface, middle, or bottom) of fish and crabs. For juvenile salmon, observers recorded the presence or absence of feeding activity, which was characterized by conspicuous darting motions. Feeding at the surface or substrate was indicated by individuals accelerating toward and contacting these areas. Feeding in the water column was indicated by individuals changing their orientation and darting toward a presumed prey item in the water. When salmon were not feeding, their movements were horizontal and often unified in a shoal. Juvenile salmon (along with other fish and crabs) were typically observed several meters away from snorkelers and rarely responded to observer presence, but those that accelerated away from observers in a distinct fleeing behavior (Toft et al. 2007) were excluded from behavioral analyses.

Sites were constrained by urban infrastructure, which limited the amount of continuous shoreline that could be surveyed, and we chose to sample the maximum amount of habitat available at each site. Transect lengths at reference beaches were limited by the amount of unarmored beach shoreline at each site and were 75 m (R1 and R3) and 35 m (R2). Transect lengths at seawall sites were constrained by the amount of continuous, unshaded shoreline bounded by piers that were unevenly spaced along the seawall. Seawall site transects were established to measure the effects of one pier on fish distributions while minimizing the effects of the adjacent pier (Figure 2), which resulted in seawall site transect lengths of 63 m at S1, 39 m at S2, and 69 m at S3. The widths of all transects were quantified by horizontal underwater visibility (Toft et al. 2007, 2013).

At seawall sites, the fine-scale positions of fish and crabs along transect lines were recorded by using landmarks along the shoreline. Observations along seawall sites were also categorized into three pre-assigned sections (pier, corner, and open) that were defined by their locations relative to the piers. The length of each section constituted one-third of the transect length. The pier section was defined as the area underneath the pier; the corner section was the middle portion of the transect and started at the edge of the pier; and the open section was farthest from the pier and started at the end of the corner section (Figure 2). Open sections at each site were therefore located an equivalent distance from the piers on either side, regardless of the uneven pier spacing along the seawall. Because of the variable position of shade lines, borders of pier and corner sections were defined by the structural presence of piers rather than based on the shade cast by piers; this ensured equal sampling intensity among sections. Surveys always occurred in the same order (open, corner, and pier), which allowed observers to swim directly from a boat to the beginning of the transect with minimal site disturbance. Transects at reference beaches were not delineated into sections because no artificial structures were present in the water column.

Observations of juvenile Chum Salmon O. keta and Pink Salmon O. gorbuscha were consolidated into the category “Chum/Pink Salmon” because these species were difficult to distinguish underwater and because they overlapped in size and in timing of peak abundances. Juvenile Coho Salmon O. kisutch, which look similar to Chinook Salmon when observed during snorkeling and which occasionally shoal with Chinook Salmon, were present in this system but are relatively rare (Toft el al. 2007); therefore, a small percentage of Chinook Salmon observations may have included Coho Salmon.

Analysis.—Statistical analysis was conducted in R version 2.15.2 (R Development Core Team 2012) utilizing the BIOSTATS collection of R functions (McGarigal 2011) and the Vegan package (Oksanen et al. 2013). The two main analyses compared observations (1) between seawall sites and reference beaches and (2) among sections within seawall sites (Figure 3). Density data were used for comparisons between seawall sites and reference beaches to standardize data from transects of unequal length. Density data were also used for comparisons of species assemblage structure among sections within seawall sites. Fish density was calculated as fish count/(transect length × transect width). Another metric (hereafter referred to as an "encounter") was defined as an observation of an independently swimming shoal or a single fish; this metric treated all observations equally regardless of shoal size. Thus, for each observation, two types of data were recorded: the total number of fish observed (a number from 1 to 1,000) and the encounter (always counting as one, regardless of shoal size). The encounter metric is useful because shoaling behavior is not well understood in the context of habitat selection, and a large group of fish may not be more indicative of habitat use than a single fish (Able et al. 2013).

Multivariate analysis was conducted in Vegan (Oaksanen et al. 2013). Nonmetric multidimensional scaling was used to visualize differences in assemblage structure (1) between seawall sites and reference beaches and (2) among pier, corner, and open sections within seawall sites separately for high- and low-tide data, excluding species that were observed in less than 5% of the surveys. Data from high and low tides were analyzed separately because of an a priori hypothesis that fish distributions among seawall site sections were affected by light levels, which are lowest under piers during high tides that limit penetration of horizontal ambient light. Species with statistically significant loadings on the axes were identified by permutation and visualized by vectors with the function envfit. To aid in interpretation, ellipses containing 1 SD of two-dimensional point spreads around their means were overlaid onto plots by using the function ordiellipse. We tested for differences in species assemblage structure by using the function adonis, which is a permutational multivariate ANOVA (PERMANOVA). The PERMANOVA tests were performed on Bray–Curtis dissimilarity matrices calculated from loge transformed density data, excluding species that were observed in less than 5% of surveys (Bray and Curtis 1957; Anderson 2001; McArdle and Anderson 2001). In comparisons between seawall sites and reference beaches, factors included shoreline type (seawall site or reference beach; fixed), position (3 or 10 m from shore; fixed), site nested within shoreline type (S1, S2, S3, R1, R2, or R3; random), and interactions. In comparisons among pier, corner, and open sections within seawall sites, factors included section (pier, corner, or open; fixed), position (3 or 10 m from shore; fixed), and their interactions; sites (S1, S2, or S3; random) were treated as a blocking factor by constraining the permutations by site (Oaksanen et al. 2013). All factors were incorporated into PERMANOVA models, but we only present statistics for the main effects of shoreline or section type.

To test for differences in single-species densities between seawall sites and reference beaches, ANOVA tests were conducted on loge transformed data using the same factors used for the PERMANOVA tests. To test for uneven distribution of fish among sections within seawall sites, a chi-square test was performed on count data separately for high and low tides. Our design ensured that even amounts of area (m^2) were sampled among pier, corner, and open sections; therefore, we used the chi-square test to evaluate the null hypotheses that (1) one-third of the total number of fish observed would occur in each section; and (2) one-third of the total number of encounters would occur in each section. The chi-square test was also used to compare feeding versus nonfeeding behavior in juvenile salmon (1) between seawall sites and reference beaches and (2) among pier, corner, and open sections within seawall sites (Toft et al. 2013). When the chi-square test was significant for data with more than two groupings, the data were subdivided to isolate significantly different groupings (Zar 2010). For chi-square analyses of salmon feeding behavior among sections within seawall sites, data were pooled for all salmonid species, including unidentified salmon, to allow for more robust comparisons while separating high- and low-tide data. Salmon feeding behavior at seawall sites was also analyzed by using a binomial test to evaluate the a priori hypothesis that proportions of salmon exhibiting feeding behavior would be lowest in pier sections (probability = 0.333) for each combination of tide and identified salmon species (Zar 2010).

Results

Approximately 35,000 individuals representing 17 fish species and 4 crab species were observed (Table 1). Juvenile Chum/Pink Salmon (56% of total fish) and Shiner Perch (17% of total fish) were the numerically dominant fish species. Juvenile Chum/Pink Salmon, juvenile Chinook Salmon, Kelp Perch, red rock crabs, Striped Seaperch, Shiner Perch, and Tubesnouts were the most common species and were observed in greater than 5% of surveys. Pacific Sand Lances were rarely observed, but three shoals in the corner sections of seawall sites totaled 3,500 fish. Large predators were rare; the most common of these was the Lingcod (0.006% of total fish). It is important to note that our snorkeling methods were appropriate for observing the common species (those occurring in > 5% of surveys) but were not as effective for observing some of the rarer species (e.g., small demersal fish) listed in Table 1. We provide Table 1 to generally describe the fish and crab community, although our main focus is on the common species.

Table 1. Mean ± SE density of fish and crabs per 1,000 m^2 in the pier, corner, and open sections within seawall sites and reference beaches (beach) at high (H) and low (L) tides.

Group	Species	Scientific Name	Pier (H)	Corner (H)	Open (H)	Beach (H)	Pier (L)	Corner (L)	Open (L)	Beach (L)
Juvenile Salmon	Chinook Salmon	*Oncorhynchus tshawytscha*	45.3±39.6	25.6±13.6	23.9±11.6	5.6±2.3		42.2±40.0	3.4±2.0	3.5±3.2
	Chum/Pink Salmon	*O. keta / O. gorbuscha*	563.2 ± 454.3	1460.6±708.2	1018.5±736.8	328.3±140.6	250.0±188.2	267.7±134.3	312.6±260.5	296.1±150.8
	Unidentified Juvenile Salmon	*Oncorhynchus spp.*		70.3±66.8		6.551363	1.5	33.5±24.4	90.5±75.5	39.7±32.4
Forage Fish	Pacific Sand Lance	*Ammodytes hexapterus*		615.8±488.8				17.8		0.3
	Pacific Herring	*Clupea pallasii*						8.9		54.8±53.8
	Surf Smelt	*Hypomesus pretiosus*					0.2	24.8		10.4
	unidentified forage fish							18.8		
Surfperches	Kelp Perch	*Brachyistius frenatus*	2.7±2.0	14.5±7.0	1.1±0.8	0.2±0.2	2.0±1.1	2.6±1.1	0.4	0.7±0.3
	Pile Perch	*Rhacochilus vacca*		1.2	3.3±2.3	0.7±0.6	0.5			0.5±0.3
	Striped Seaperch	*Embiotoca lateralis*	6.1±4.1	4.9±2.6	4.2±2.6	3.4±1.3	5.9±3.1	0.4	3.2±2.2	16.4±13.8
	Shiner Perch	*Cymatogaster aggregata*		504.3±304.9	225.4±97.7	12.0±5.6	0.9	175.3±167.8	251.1±147.2	105.9±64.9
	unidentified perch		0.8	0.2		<0.1				2.5±2.3
Crabs	Dungeness Crab	*Metacarcinus magister*					0.3	0.4	0.2	
	Northern Kelp Crab	*Pugettia producta*	0.2	1.2±0.7	0.3	<0.1	0.4	0.5	0.2	
	Red Rock Crab	*Cancer productus*	6.5±2.0	4.0±1.4	1.6±0.8	0.6±0.3	0.5	2.7±1.7	1.6±0.7	0.3±0.1
	shore crab	*Hemigrapsus spp.*				<0.1				0.2±0.1
Demersal Fish	Lingcod	*Ophiodon elongatus*	0.2	0.2						
	Penpoint Gunnel	*Apodichthys flavidus*				0.1±0.1				
	Rock Sole	*Lepidopsetta bilineata*				<0.1				
	Sculpin	*Cottidae*				0.1±0.1	0.4	0.3		0.1
	Spotted Ratfish	*Hydrolagus colliei*				0.2				0.1
	unidentified gunnel	*Pholidae*				0.1±0.1				0.1
Other Fish	Pacific Lamprey	*Entosphenus tridentatus*			0.2					
	larval fish					1.4				0.2
	ThreeSpine Stickleback	*Gasterosteus aculeatus*						0.5		
	Tubesnout	*Aulorhynchus flavidus*	82.3±32.0	90.0±62.8	190.6±167.5	<0.1	51.6±21.6	124.3±61.9	33.8±24.9	13.9±9.7
	unknown species			36.8±25.3		0.1		0.4		2.3±2.1

Juvenile Chinook Salmon and Chum/Pink Salmon were observed at the surface and middle of the water column; Kelp Perch, Shiner Perch, and Striped Seaperch were most often observed in the middle of the water column; and Tubesnouts and red rock crabs were demersal (Table 2). Red rock crabs were not exclusively found at the bottom of the water column because they climbed structures such as pier pilings.

Table 2. Depth distribution of common species. Surface/middle indicates a shoal of fish that included individuals at the surface and middle of the water column.

Species	Total Encounters	Surface	Surface/Middle	Middle	Bottom
Chinook Salmon	81	27.16%	1.23%	70.37%	1.23%
Chum/Pink Salmon	108	60.19%	7.41%	32.41%	0.00%
Kelp Perch	45	6.67%	0.00%	73.33%	20.00%
Red Rock Crab	66	3.03%	0.00%	24.24%	72.73%
Shiner Perch	101	2.97%	0.99%	80.20%	15.84%
Striped Seaperch	83	0.00%	0.00%	50.60%	49.40%
Tubesnout	77	0.00%	0.00%	57.14%	42.86%

Comparison of Seawall Sites and Reference Beaches

Community assemblage structure.—Ordination of species assemblage structures at high tides showed that red rock crab and Tubesnout species vectors were correlated with seawall site ellipse, whereas Chum/Pink Salmon and Striped Seaperch species vectors were to a lesser degree correlated with reference beach ellipse (Figure 4). Patterns at low tides were less clear; however, Kelp Perch, red rock crab, and Tubesnout species vectors were correlated with the seawall site ellipse, while Chinook Salmon and Chum/Pink Salmon species vectors were slightly more correlated with the reference beach ellipse (Figure 4). The PERMANOVA tests indicated that fish and crab assemblage structures at seawall sites were significantly different than those at reference beaches at high tides (PERMANOVA: $F_{1, 59} = 4.43$, $P < 0.01$) and low tides ($F_{1, 59} = 2.0$, $P = 0.03$).

Fish distribution.—Seawall sites and reference beaches did not significantly differ in densities of Chinook Salmon (ANOVA, high tide: F1, 80 = 3.04, P = 0.09; low tide: F1, 81 = 0.69, P = 0.41; Figure 5) or Chum/Pink Salmon (high tide: F1, 80 = 0.97, P = 0.15; low tide: F1, 81 = 0.01, P = 0.92; Figure 5). Of the seven species that were observed in over 5% of surveys, only the red rock crab exhibited densities that were significantly different depending on shoreline type, occurring in greater abundance at seawall sites than at reference beaches at high tides (ANOVA: $F_{1, 80} = 12.10$, $P < 0.01$) and low tides ($F_{1, 81} = 4.40$, $P = 0.04$).

Juvenile salmon feeding behavior.—There was no significant difference in the feeding behavior of juvenile Chinook Salmon between seawall sites and reference beaches at high tides ($\chi 2 = 0.04$, df = 1, P = 0.84) or low tides ($\chi 2 = 0.68$, df = 1, P = 0.41). Feeding behavior of Chum/Pink Salmon was significantly greater at seawall sites than reference beaches at high tides ($\chi 2 = 4.19$, df = 1, P = 0.04) but not at low tides ($\chi 2 = 0.03$, df = 1, P = 0.86).

Comparison of Sections within Seawall Sites

Effect of the S2 pier on light.—Light measurements taken relative to the pier at S2 indicated that this pier caused a substantial decrease in PAR in the air and at the depths occupied by most fish (Table 3). The level of PAR was inversely related to the distance from the pier edge and to water depth.

Table 3. Average ± SE photosynthetically active radiation (μmol photons m^{-2} s^{-1}) at ambient levels and under the pier along the seawall at 3, 15, and 24 m from the pier edge, measured in the air and at water depths from the surface to 2.0 m.

Depth (m)	Ambient	3 m	15 m	24 m
Air	1028.2 ± 446.6	43.8 ± 7.2	12.6 ± 4.5	4.9 ± 1.5
0 (Subsurface)	763.3 ± 424.4	20.4 ± 6.7	2.4 ± 0.5	0.7 ± 0.1
0.5	645.4 ± 384.7	18.8 ± 7.1	2.3 ± 0.5	0.7 ± 0.2
1	446 ± 261.5	17.1 ± 6.8	2 ± 0.5	0.6 ± 0.2
1.5	370.1 ± 222.0	16.1 ± 7.1	1.3 ± 0.3	0.3
2	328.5 ± 189.8	17.4 ± 9.1		

Community assemblage structure.—Ordination of species assemblage structures at high tide showed that corner and open sections had similar species compositions; Chum/Pink Salmon, Shiner Perch, and Tubesnout species vectors were correlated with the ellipses of these sections, whereas the red rock crab species vector was correlated with pier section ellipse (Figure 4). Patterns were less clear for low tides. To a lesser degree than at high tide, Striped Seaperch and red rock crab species vectors were correlated with open and corner section ellipses, the Chum/Pink Salmon species vector was correlated with corner and pier section ellipses, and Tubesnout species vector was correlated with the pier section ellipse (Figure 4). Within seawall sites, species assemblages were significantly different among sections at high tide (PERMANOVA: $F_{2, 74} = 1.87$, $P = 0.02$) but not at low tide ($F_{2, 65} = 1.20$, $P = 0.52$).

Fish and crab distribution.—Within seawall sites, fish and crab abundances varied based on proximity to the pier structures (Figure 6) and in relation to the shade cast from piers (Figure 7). Overall fish abundances were lower in pier sections, and fish were consistently observed to be directly adjacent to shade and were less often observed in shaded areas (Figure 7). Overall fish abundances were lower under piers and highest in corner sections during high tides (Figure 6). Differences in fish distribution between tidal stages and among sections were attributable mainly to differences in juvenile salmon distribution. During high tides, total fish counts were over five times greater in corner sections than in pier sections. Chinook Salmon were significantly more abundant in corner sections during high tides ($\chi2 = 11.7$, df = 1, $P < 0.01$), and Chum/Pink Salmon were significantly less abundant in pier sections ($\chi2 = 1{,}001$, df = 1, $P < 0.01$) and more abundant in corner sections than in open sections ($\chi2 = 383$, df = 1, $P < 0.01$; Figure 6). The number of Chinook Salmon encounter events was significantly lower in pier sections at high tide ($\chi2 = 6.5$, df = 1, $P = 0.04$); Chum/Pink Salmon encounters showed no patterns among sections at high tide ($\chi2 = 1.0$, df = 2, $P = 0.60$; Figure 6).

Effects of piers on juvenile salmon distributions were different at low tides than at high tides, although overall fish counts remained lowest under piers. During low tides, Chinook Salmon were more abundant in corner sections ($\chi2 = 274$, df = 1, $P < 0.01$) and significantly less abundant in pier sections than in open sections ($\chi2 = 13$, df = 1, $P < 0.01$; Figure 6). Chum/Pink Salmon abundances at low tides were significantly greater in areas under piers than in other sections ($\chi2 = 46$, df = 1, $P < 0.01$) and were greater in corner sections than in open sections ($\chi2 = 5.1$, df = 1, $P = 0.02$; Figure 6). Shoals of Chum/Pink Salmon were also observed farther into shaded areas at low tides than at high tides (Figure 7). Chinook Salmon were never encountered in pier sections at low tide, and encounters were significantly greater in corner and open sections ($\chi2 = 12$, df = 1, $P < 0.01$). Chum/Pink Salmon encounters were not significantly different among sections during low tides ($\chi2 = 1.1$, df = 2, P = 0.56; Figure 6).

The distribution of red rock crabs differed from fish distributions. At high tides, abundances were greatest in pier and corner sections ($\chi2 = 6.0$, df = 1, P = 0.02; Figure 6). Red rock crabs were less abundant overall at low tides, and distributions were not significantly different among sections ($\chi2 = 2.9$, df = 1, P = 0.23). Red rock crabs were rarely seen in groups; total counts and the number of encounter events were equivalent. Unlike other species, red rock crabs were commonly observed to occur several meters away from sunlit areas (Figure 7).

Juvenile salmon feeding behavior.—At high tides, the feeding behavior of juvenile salmon (all species combined) was greater in open and corner sections than in pier sections ($\chi2 = 3.57$, df = 1, P = 0.059; Figure 8). Differences in juvenile salmon feeding prevalence among sections at low tides were not significant ($\chi2 = 2.58$, df = 2, P = 0.27; Figure 8). However, feeding behavior was consistently lower under piers for each combination of salmon species and tide, excluding Chinook Salmon at low tide because they were never observed in pier sections (binomial test: P = 0.037; Figure 8).

Discussion

Our results demonstrate that the presence of seawalls and piers causes measurable change in the fish assemblages of Elliott Bay, Washington. The present findings expand on a recent but geographically diverse literature, including studies conducted in Australia

(Clynick et al. 2008), Italy (Clynick 2006), Puget Sound (Toft et al. 2007), and the Hudson River (Strayer et al. 2012). These studies collectively suggest that the fish assemblages at many developed waterfronts are different from historical assemblages. There are few natural analogs to featureless, vertical concrete shorelines or to large shaded areas created by piers; the effects at the intersection of these two types of modification are particularly unique. At high tides, corner sections at seawall sites were inhabited by relatively abundant fish communities that differed in assemblage structure from those observed in adjacent areas, especially pier sections, where fish were rare and crabs were relatively common. This finding is consistent with the hypothesis proposed by Hobbs et al. (2006) that human-induced changes to the abiotic environment can create novel ecosystems—those with species combinations and relative abundances that did not occur historically. We assumed that fish were distributed relative to the amount of habitat between adjacent piers, which varied among seawall sites. The fine-scale positions of fish relative to pier shade (standardized by transect length) suggest that this is accurate. However, if the fish aggregated next to piers according to their absolute distance rather than relative distance from the piers, we may have underestimated aggregation effects in the corner sections because these sections were longer at the larger sites (13 m [S2] versus 21 m [S1] and 23 m [S3]) and included areas that were farther away from piers.

Our results from three replicate piers suggest that the piers exerted negative impacts on fish in Elliott Bay, especially at high tides. These findings were supported separately by fish count and fish encounter metrics and by fine-scale fish distributions relative to shade, all of which showed that most fish species avoided areas under piers at high tide. When tides were lower and horizontal ambient light penetrated under the piers, fish distribution patterns became less distinct and species assemblages were not significantly different, suggesting that habitat use was driven by the shade cast by the piers rather than resulting from a structural effect of the piers. Red rock crabs were an exception, as they were commonly observed on pier pilings. Shaded areas under piers may mimic nighttime conditions, when red rock crabs become more abundant in intertidal areas and feed by using chemosensory cues to locate prey (Robles et al. 1989). Mobile species, such as Shiner Perch and juvenile salmon, tended to avoid areas that were shaded by piers; in contrast, Tubesnouts, which are often stationary in the water column, were common under the edges of piers, including the shaded areas. A plausible explanation for this result is that fish with high swimming speeds may avoid shaded areas rather than experience reduced visual acuity resulting from rapid changes in light intensity (Ali 1959). Kelp Perch, which use bull kelp Nereocystis luetkeana for cover, were rarely observed in the shaded areas where kelp did not grow, thus indicating that shade also reduces habitat quality for fish that interact with algae.

Our findings of reduced fish abundances under piers are consistent with those of Able et al. (2013), who found reduced pelagic fish abundances under a large pier in the Hudson River estuary, suggesting that these effects occur in other systems. Unlike the Hudson River estuary study (Able et al. 2013), we did not find higher predator abundances in areas under piers, but predators were rare overall at the depths and habitats that we sampled, and the effects of piers on predators at greater depths are a potential topic for further investigation in our region. Results of our study and the study by Duffy-Anderson and Able (1999 and 2001) suggest that piers can also impair the value of shallow-water habitats by reducing the feeding ability of fish. Many fish species are primarily visual predators, and a reduction in light levels may adversely affect the ability of these predators to detect prey, especially by reducing the backlighting of prey at the surface.

We recognized the possibility that the use of visual surveys could result in underestimation of fish counts or encounters in shaded areas under piers due to low light levels. Our surveys minimized this risk by targeting fish species that occurred in close proximity to observers at the surface of the water column, often in large schools. Observers also swam slowly enough for their eyesight to adjust to shaded conditions as they entered areas under the piers. These areas were not completely dark because the water level was below the piers even during high tides, and some (although reduced) horizontal ambient light could penetrate.

Our results contribute to growing evidence that piers impair the value of nearshore habitat for juvenile salmon. Simenstad and Cordell (2000) proposed a framework for assessing habitat by utilizing metrics that address a habitat's capability to provide (1) opportunity, (2) capacity, and (3) realized function for juvenile salmon. In this scenario, opportunities for salmon to access habitat and to benefit from the habitat's capacity can be inferred by measuring the extent of tidal flooding, the presence of important geomorphic features, and the proximity to anthropogenic stressors (e.g., pier shade). The capacity of the accessible habitat can be evaluated by examining prey availability and water temperatures, salinities, and other conditions that promote prey production and refuge from predators. The realized function, resulting from opportunity and capacity, can be measured through habitat-specific residence time, feeding, growth, and survival. In our study, pier shading was an anthropogenic stressor that reduced the ability of juvenile salmon to access habitat (i.e., reduced opportunity) and caused a reduction in feeding under piers (i.e., a reduction in realized function).

Previous research has shown that shoreline armoring may impair salmon habitat capacity by directly reducing prey production (Sobocinski et al. 2010) and altering substrate temperatures that support prey production (Morley et al. 2012). However, we did not find reductions in salmon abundance or feeding intensity related to seawall presence, and detection of these effects may require more intensive sampling than we conducted. We found that the prevalence of feeding behavior among Chum/Pink Salmon was significantly higher at seawall sites than at reference beaches during high tides, when their movements under piers were most restricted. Research on the movements and feeding behavior of juvenile salmon in this system has shown that swimming directionality and feeding are related: salmon tend to either (1) swim in a sinuous path and feed or (2) swim directionally and rarely feed (S. M. Heerhartz, University of Washington and J. D. Toft, unpublished data). It is possible that piers interrupt alongshore movements of salmon, causing them to switch from directional movements without feeding to more sinuous movements accompanied by an increase in feeding intensity. Alternatively, salmon in highly modified habitats may compensate for lower-quality prey by feeding more often. The effects of piers and seawalls on juvenile salmon feeding are likely to occur by different mechanisms (e.g., piers impair prey detection, while seawalls impair prey availability), and our visual survey methods may have been more effective at measuring pier effects than seawall effects. Sampling of salmon diets and available prey fields in nearshore habitats that are modified by seawalls would provide a more detailed understanding of how shoreline armoring affects the capacity and realized function of shorelines for juvenile salmon and other fishes.

Results of our study and the study by Toft et al. (2007) indicate that piers could delay the out-migration of juvenile salmon because (1) juveniles stay in shallow waters early in their life history as they migrate from freshwater and estuarine habitats to marine habitats (Toft et al. 2007), (2) piers are common along waterfronts and extend into waters deeper than those used by juvenile salmon early in their life history (Simenstad et al. 2011), and (3) juvenile salmon avoid the shaded areas created by piers and thus do not cross under piers from one lighted area to another but instead aggregate adjacent to the piers. Our observations of Chum/Pink Salmon occurring farther into shaded areas under piers at low tide may also indicate that out-migrating juvenile salmon wait in corner sections until low tides allow a greater amount of light to penetrate the areas under piers. If piers delay the out-migration of juvenile salmon, this may have negative impacts on their survival by retaining the fish in suboptimal habitats, delaying their access to ephemeral prey resources in more natural habitats (Webb 1991, 1992; Cooney et al. 1995), and increasing their vulnerability to predation (Willette et al. 1999). Although our study provides indirect evidence that piers cause migration delays, methods such as mark–recapture, acoustic tagging, and visual observations that follow salmon would permit direct testing of pier effects on salmon movements.

In our study, fish were surveyed along transects at the surface of the water and close to shore. This strategy was effective at quantifying juvenile salmon and several other fish species across a variety of shoreline conditions, but other observation methods could evaluate how seawalls and piers affect additional fish species. For example, surveying fish at greater depths would extend our results to more resident and benthic species. Toft et al. (2007) found that shoreline armoring reduces flatfish densities in Puget Sound; we also found fewer flatfish at seawall sites relative to reference beaches, but we could not fully evaluate seawall effects on flatfishes because they were rarely observed.

The physical transformation of urban waterfronts is largely irreversible, and the prospect of restoration to prehistorical conditions is impractical. Enhancement of the shoreline by applying habitat improvements is often the only option for improving ecological functions (Toft et al. 2013). As land and seascapes are increasingly transformed, a shift in management toward a more practical approach of assessing and enhancing the functional attributes of new ecosystems—rather than investing resources in trying to restore permanently altered systems—may be warranted (Seastedt et al. 2008). One option to mitigate the effects of shading by overwater structures is to incorporate light-penetrating surfaces, such as glass blocks or grating in pier surfaces. For example, in Elliott Bay, juvenile salmon occur within a few meters of shore, and light-penetrating surfaces are presently being installed that could allow for more natural feeding and movement alongshore. Preliminary research on light-penetrating surfaces has shown that they can reduce shade intensity (Gayaldo and Nelson 2006), but larger-scale evaluations and studies in the context of fish habitat have not occurred. Light mitigation is only one of many enhancements that may increase the functions of highly modified nearshore ecosystems (other examples are reviewed by Chapman and Underwood 2011), and development of these enhancements is a promising area for future research.

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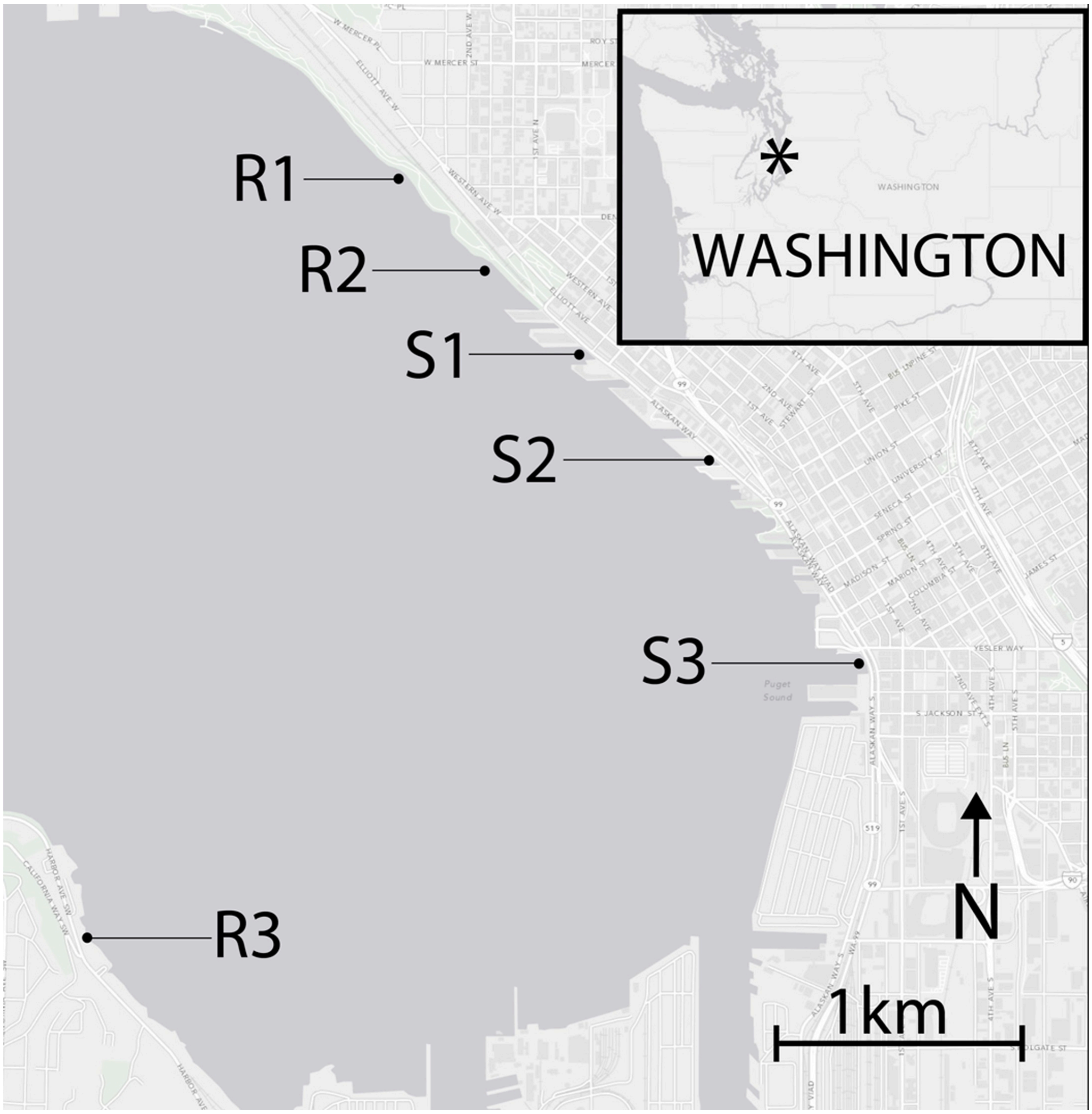

Figure 1. 1. Locations of sampling sites within Elliott Bay, Washington. Sites included three replicate seawall sites (S1–S3) and three reference beaches (R1–R3).

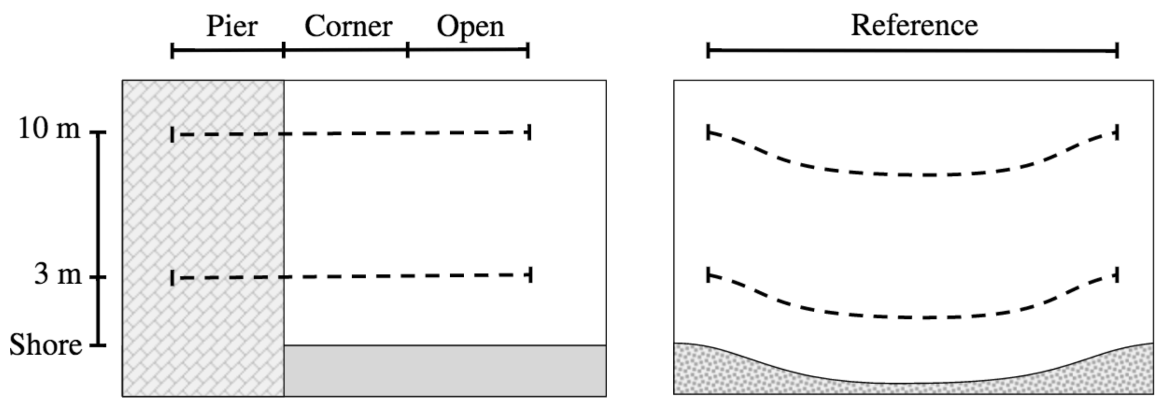

Figure 2. Overhead view of seawall sites and reference beaches in Elliott Bay. Snorkel transect paths are indicated by dashed lines. Section delineations of seawall sites relative to piers are shown, and each section is equal to one-third of the total transect distance (d).

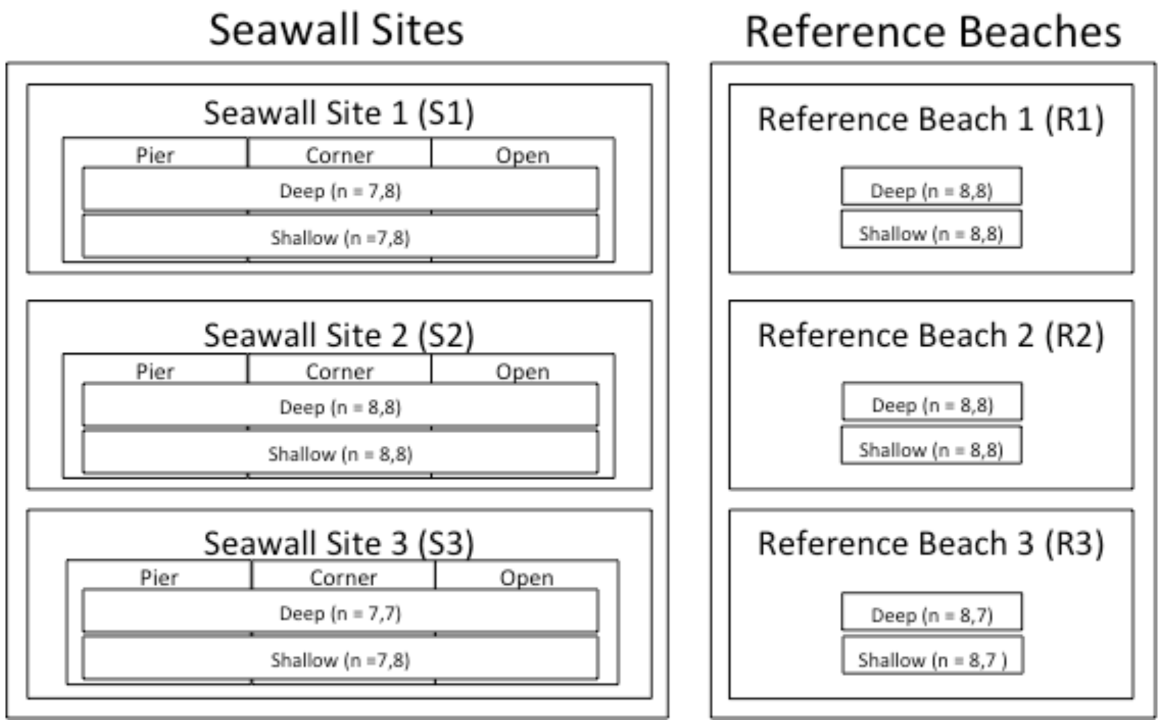

Figure 3. Organization of the data, including the following factors: shoreline type (seawall site versus reference beach; fixed), site (S1, S2, S3, R1, R2, and R3; random, nested within shoreline type), section (pier, corner, or open; fixed), and transect depth (shallow [3 m from shore] or deep [10 m from shore]; fixed). Sample size (n) indicates the number of surveys that occurred at high tide and low tide, respectively.

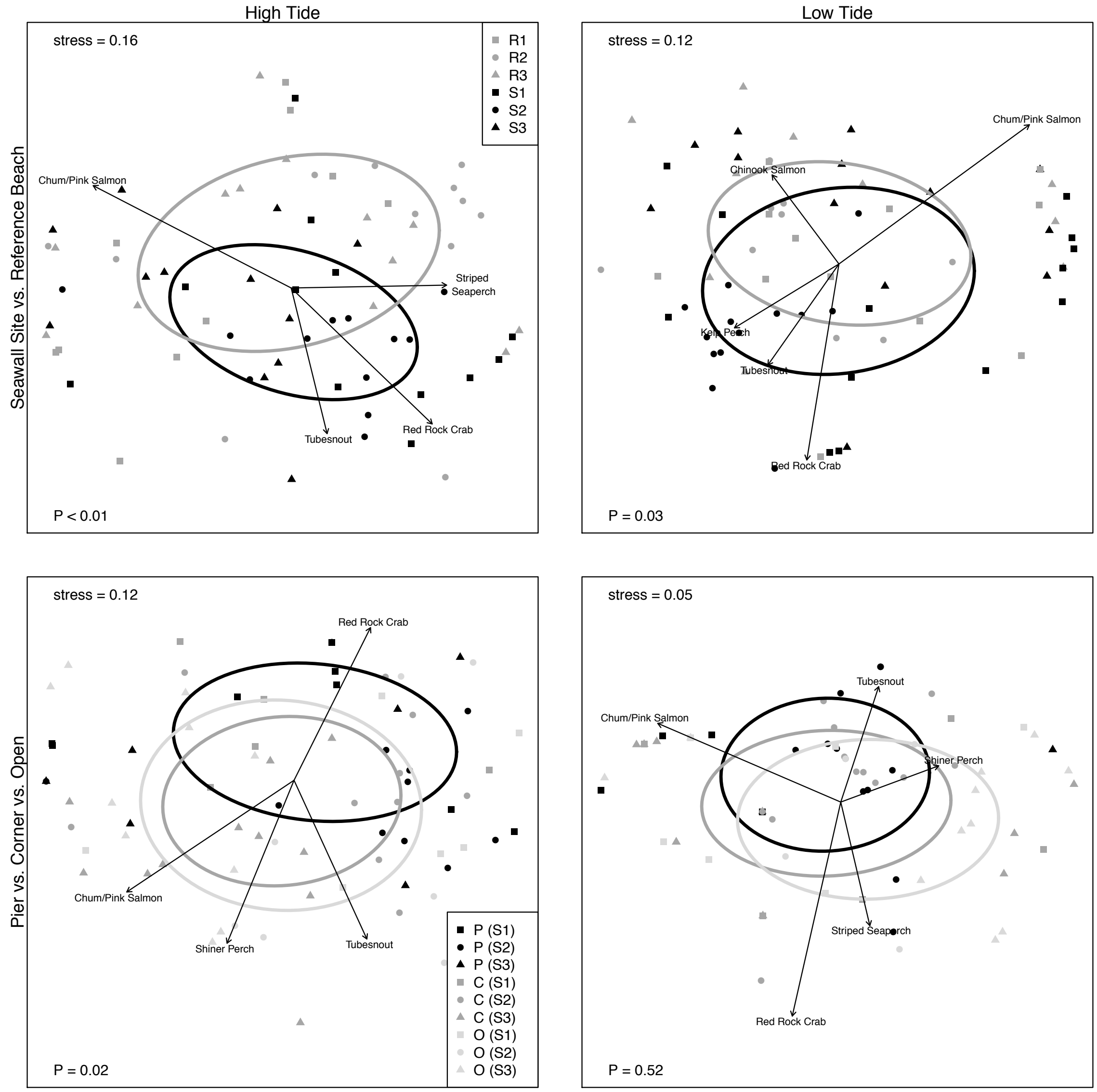

Figure 4. Nonmetric multidimensional scaling ordination of species assemblage structures, comparing seawall sites (S1–S3) to reference beaches (R1–R3) and comparing pier (P), corner (C), and open (O) sections for high- and low-tide data. Ellipses show 1 SD of two-dimensional point spreads around the mean; P-values refer to results from permutational multivariate ANOVA.

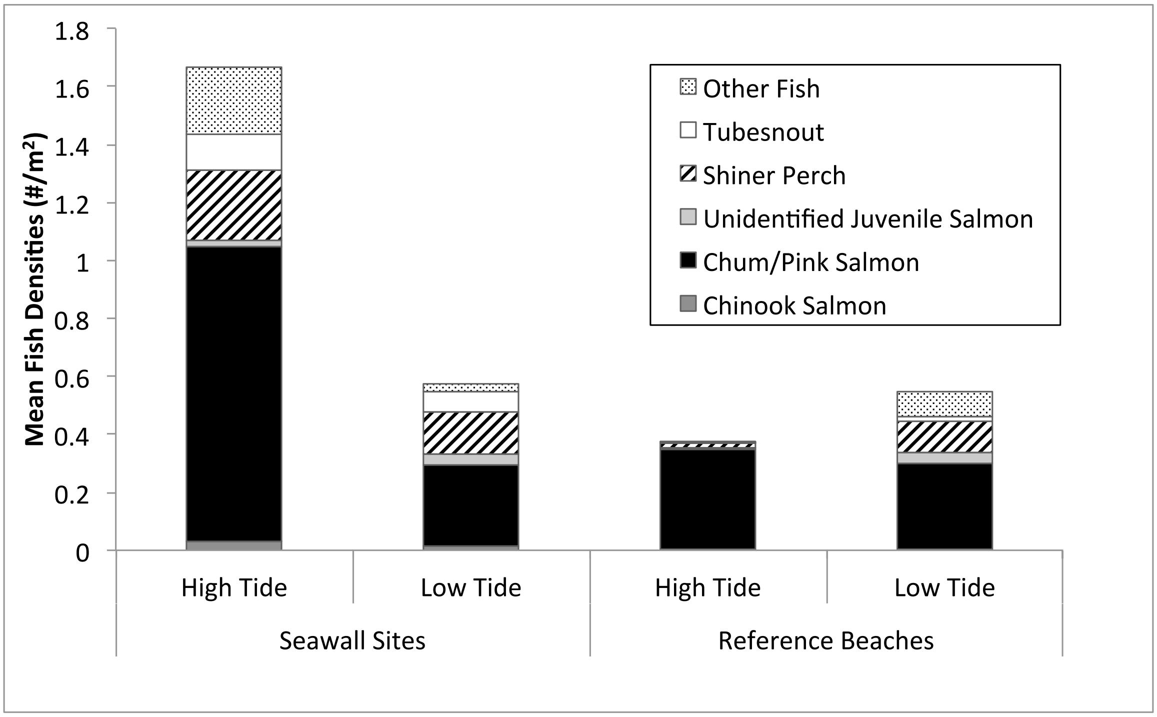

Figure 5. Mean densities of fish observed at seawall sites and reference beaches in Elliott Bay during high and low tide.

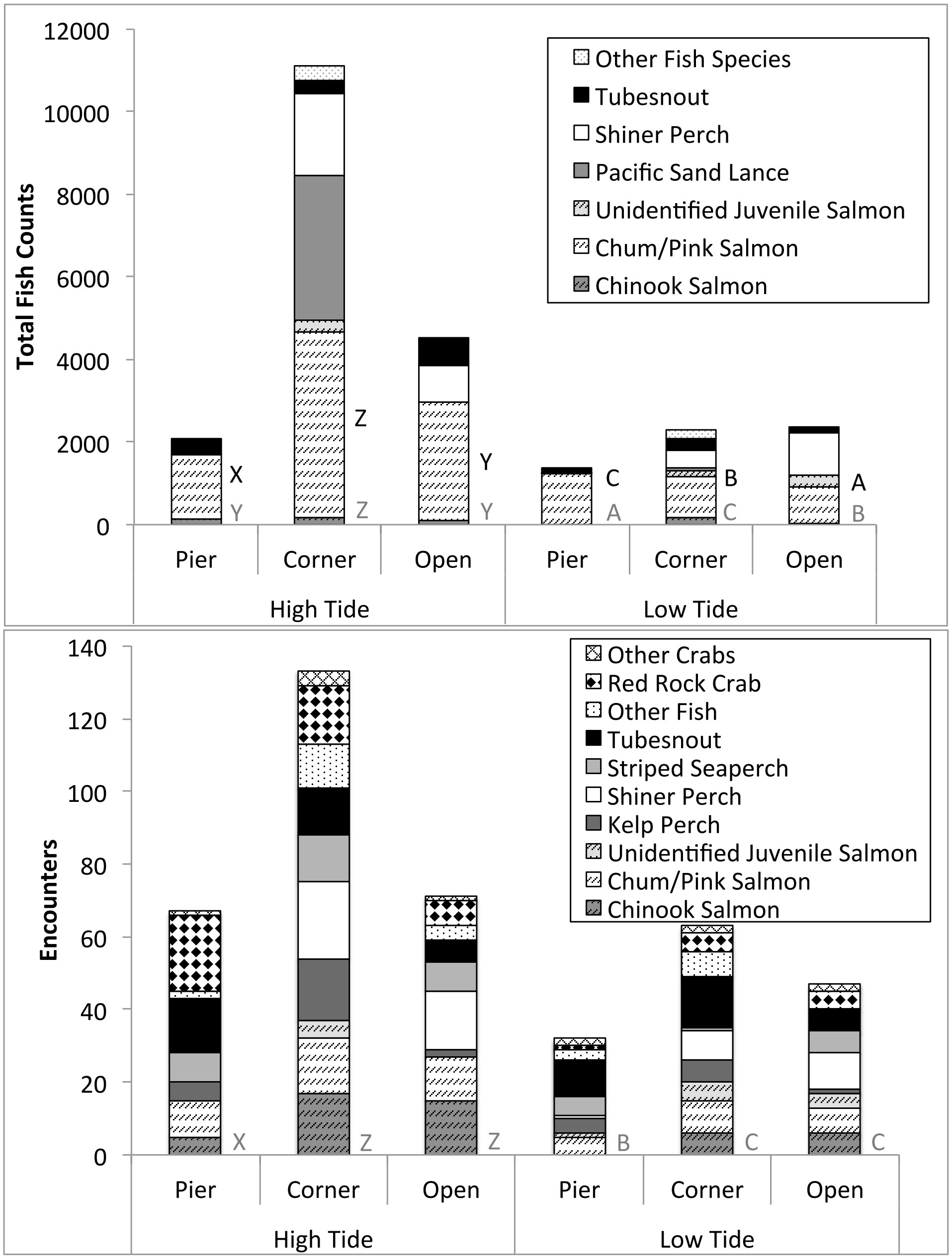

Figure 6. (Top) Total fish counts and (Bottom) encounter events in pier, corner, and open sections within seawall sites at high or low tide (sections were defined by their proximity to pier structures) in Elliott Bay. Chi-square tests were performed on data from Chinook Salmon and Chum/Pink Salmon for each tidal stage; significance is indicated by lettering (Z>Y>X; C>B>A).

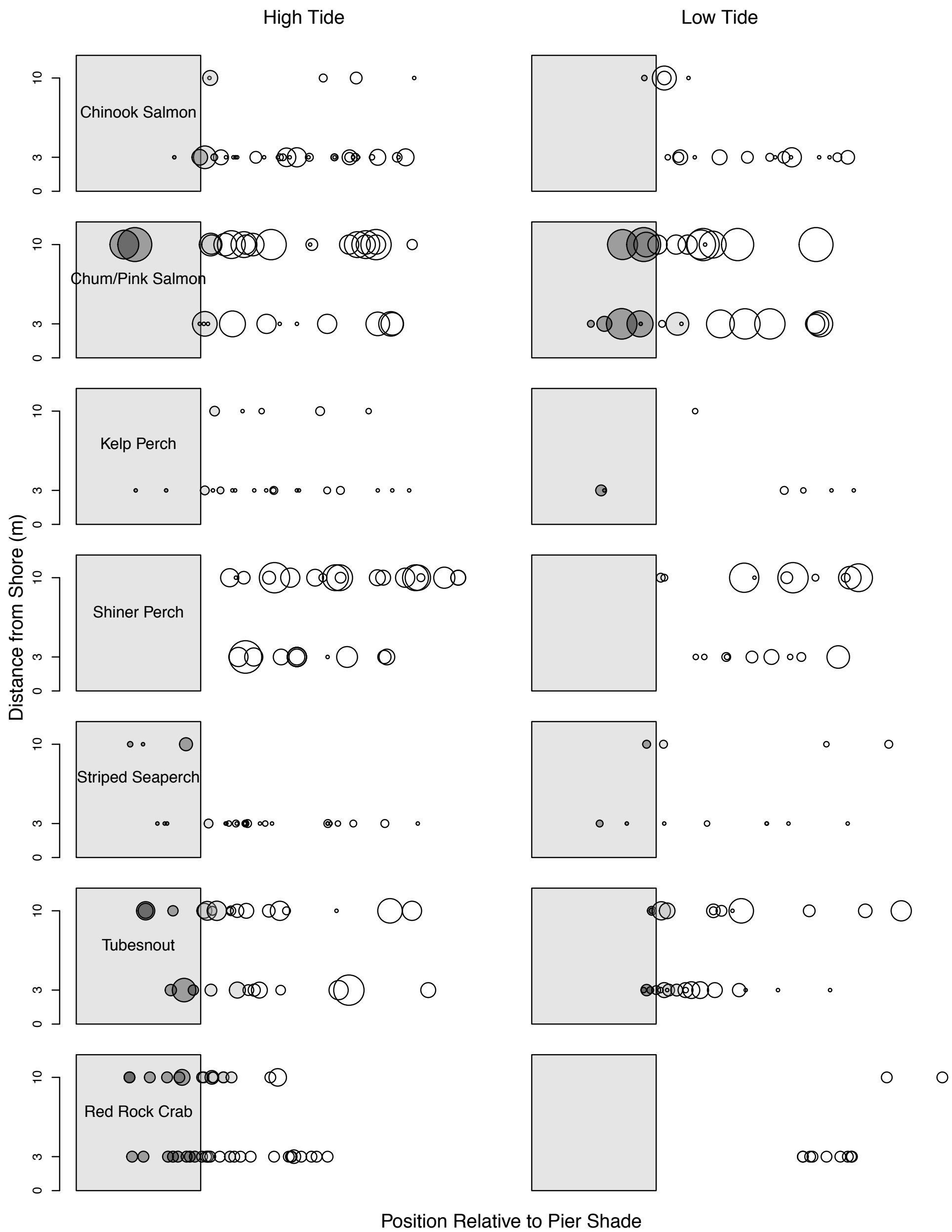

Figure 7. Locations of common fish and crab species relative to pier shade (gray rectangles) along linear transects positioned 3 and 10 m from shore in Elliott Bay during high or low tide. Data points are from all sampling days and sites (standardized by transect length) and are proportional in size to the logarithm of fish group size, which ranged from 1 to 1,000 individuals. Darkened points outside of pier shade boundaries indicate observations that occurred under pier structures but not in the shade.

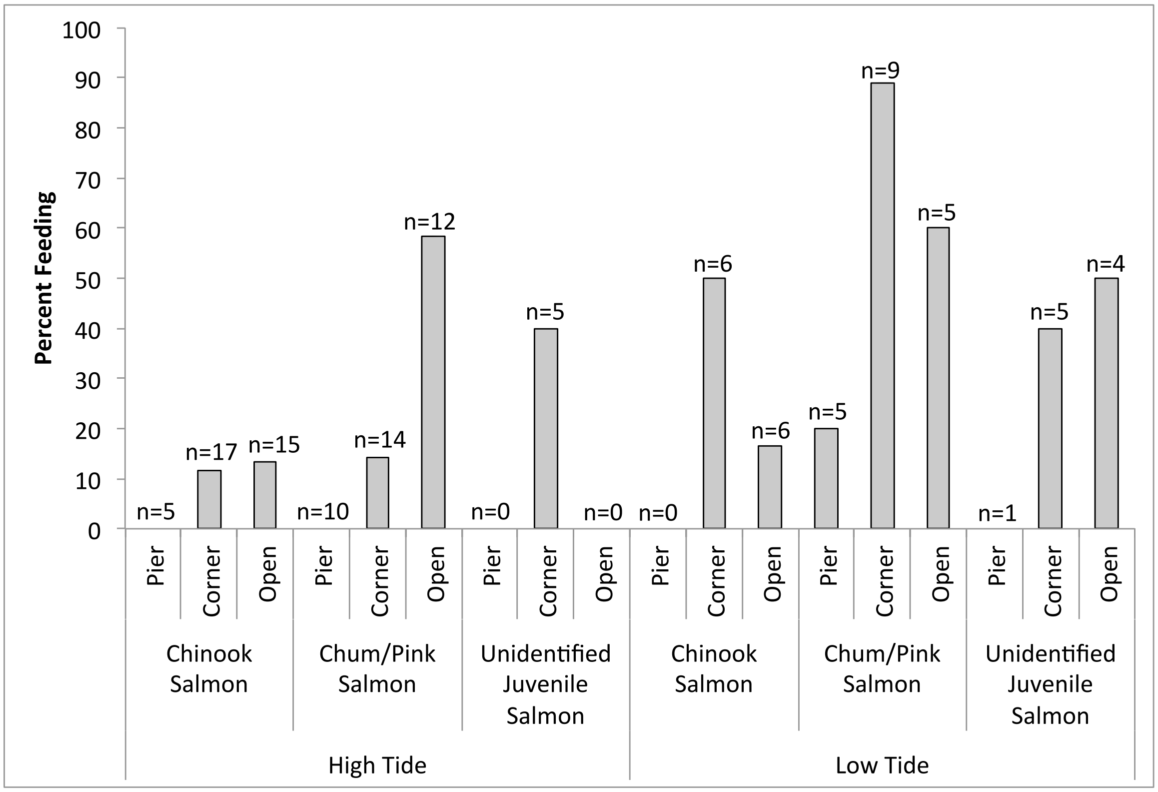

Figure 8. Percentages of juvenile salmon that were observed feeding in pier, corner, and open sections within seawall sites during high or low tide in Elliott Bay

Chapter Two: Effects of shoreline engineering on shallow subtidal fish and crab communities in an urban estuary: a comparison of armored shorelines and nourished beaches

SH Munsch, JR Cordell, JD Toft

Abstract

Shoreline armoring is common worldwide, yet its ecological effects have only recently been investigated. In this study, we surveyed shallow subtidal fish and crab communities at three sites with shorelines modified by seawall and riprap armoring and at three beaches with no armoring, all along the urbanized Elliott Bay shoreline of Seattle, WA (USA). Similar to many urban areas there is little natural shoreline remaining in Elliott Bay, and beach sites were nourished with sediment that was similar to the historical structure of ambient nearshore habitats. We visually surveyed fish and crabs along scuba dive transects at these sites for eighteen months to quantify the composition of their communities and the association of fish and crabs with substrate types. The community composition and substrate type associations were similar among seawall sites and distinct from those at nourished beaches. Some species were predominantly associated with one substrate type (e.g., sand, riprap) and their densities at each site corresponded to the availability of this substrate type. Our results suggest that hard structures in engineered subtidal habitats may benefit some species that select for these introduced structures despite these structures not occurring historically. It is also clear that the creation of nourished beaches within armored shorelines can maintain different fish and crab communities than those associated with armoring, even in highly urbanized systems. Our study contributes to a growing literature that suggests that

shoreline armoring and other types of habitat modifications affect the ecology of nearshore waters and the composition of nearshore communities.

Highlights

- Effects of shoreline engineering on fish and crabs are poorly understood
- We surveyed fish and crab communities at armored sites and nourished beaches
- Community composition differed between armored sites and nourished beaches
- Species that associated with one substrate type were most affected
- Fish and crabs respond to nourished beach engineering in an urban landscape

Introduction

Shoreline armoring is a common modification to nearshore ecosystems, especially in urban areas. Armoring such as seawalls and riprap (large, angular boulders) protects waterfronts from erosion and facilitates the aggregation of economically significant residential, commercial, and transportation activities in coastal areas. Shoreline armoring will be increasingly utilized along waterfronts worldwide as human populations continue to grow disproportionately in coastal regions (Grimm et al. 2008) and as sea level rise and climate change occur (Bulleri and Chapman 2010). Despite the global prevalence of shoreline armoring, its ecological impacts have only recently been studied.

The influence of shoreline structure on the composition of nearshore communities is well established under natural conditions (e.g., Valesini et al. 2004) and there is growing evidence that artificial change to the structure of shorelines causes ecological change in terrestrial-aquatic ecotones. Shoreline armoring can change the physical environment of nearshore ecosystems by truncating the intertidal zone, introducing hard structures to shallow areas, and reducing the transport of sediment that maintains beaches (Airoldi et al. 2005). In addition, shallow habitats modified by armoring often have harsher physical energy regimes than beaches because of increased wave reflection (Shipman et al. 2010). Shoreline armoring has been shown to influence the composition of fish communities in geographically and ecologically diverse systems including the Gulf Coast, MS (Peterson et al. 2000), the Hudson River, NJ (Strayer et al. 2012), the James River, VA (Bilkovic and Roggero 2008), Livorno, Italy (Clynick 2006), Puget Sound, WA (Munsch et al. 2014, Toft et al. 2007, 2013) and Sydney, Australia (Clynick et al. 2008). A possible mechanism for change in community composition is that shoreline armoring affects the availability of habitat attributes (e.g., substrate type) that fish and crabs select for or against, but this has yet to be investigated.

Soft shoreline engineering, which is the "develop[ment of] shorelines using ecological principles and practices that enhance habitat and improve aesthetics, while at the same time reducing erosion, providing stability, and ensuring shoreline safety," (Hartig et al. 2011) is an increasingly popular alternative to shoreline armoring (Davison et al. 1992, Speybroeck et al. 2006). Engineered beaches allow for the partial restoration of shoreline habitat in degraded systems that can provide improved habitat function for fish and crabs (e.g., Toft et al. 2013). Engineered beaches are often installed to benefit fish (e.g., as nursery areas), yet the ecological effectiveness of this approach is unclear in part because of a lack of quantitative monitoring (Hartig et al. 2011).

The impacts of shoreline engineering are of particular importance in Puget Sound, WA (USA). The beaches in Puget Sound are naturally composed of mixed sand and gravel sediments sustained by bluff erosion (Shipman 2010). However, 27% of the shoreline of Puget Sound is modified by armoring, especially that associated with major cities located at estuarine river mouths (Simenstad et al. 2011). Despite the extensive modification to its shorelines, fish and crabs utilize nearshore habitats in Puget Sound for critical functions including foraging, reproduction, predator refuge, and migratory corridors. These ecologically, commercially, and culturally valuable species include harvestable crabs (Cancridae), flatfish (Pleuronectiformes), salmon (*Oncorhynchus*), lingcod (*Ophiodon elongatus*), and rockfish (*Sebastes*), some of which are federally listed (e.g., Chinook salmon, *O. tshawytscha*). Surveys targeting surface-oriented fish in shallow water habitats of Puget Sound showed that shoreline armoring impacts their community composition (Munsch et al. 2014, Toft et al. 2007, 2013), but the effects of armoring on subtidal distributions of fish and crabs in this system, including demersal fish that interact directly with substrata, are relatively unknown.

The objectives of this study were to (1) evaluate whether there was a difference in shallow subtidal fish and crab communities between armored sites and nourished beaches, and (2) quantify fish and crab species associations with substrate types to understand how modifications to the substrate caused by shoreline armoring can affect fish and crab assemblages. For eighteen months, visual scuba surveys of fish and crab communities were conducted at three nearshore sites extensively modified by seawall and riprap armoring that replaced the natural intertidal zone, and at three beaches that had been nourished with sediments in the intertidal zone. We hypothesized that community composition and substrate associations differed between seawall sites and nourished beaches, and that species that were predominantly associated with one type of substrate would be most affected by the way that the shoreline was engineered.

Methods

Study sites

Puget Sound is located within the Salish Sea in the Pacific Northwest of the United States and is characterized by cold temperate waters and salinity above 25 psu when not near freshwater input. The study area, Elliott Bay, and the associated Duwamish River delta (Fig. 1) have experienced widespread wetland loss and the replacement of bluff-backed beaches with armored shorelines (Klingle 2007, Simenstad et al. 2011). Elliott Bay is a 21 km^2 estuarine embayment that is highly urbanized, occurring entirely within the City of Seattle and along the downtown waterfront. About 99% of the historic 15 km^2 mudflat estuary is now armored by seawalls and riprap (Simenstad et al. 2011).

We surveyed six shallow water sites consisting of three seawall sites and three nourished beaches within Elliott Bay (Fig. 1, Table 1). The shorelines of seawall sites were completely modified by seawalls that replaced the intertidal area. The substrate at these sites was primarily composed of riprap at the base of the seawalls with interspersed cobble, sand, shell hash, and scattered rocks. Two of the nourished beaches (B1 and B3) featured artificially nourished mixed cobble and sand intertidal zones with sandy shallow subtidal areas and scattered rocks. The nourished beach B2 featured an artificially nourished cobble and pebble intertidal zone that was supported by submerged subtidal riprap that began at ≈ -1 m MLLW and continued into deeper water outside the range of our surveys. The riprap that formed the buttress of this beach was salvaged as part of a habitat enhancement project at the Olympic Sculpture Park that converted the riprap shoreline to a pocket beach in 2007 (Toft et al. 2013). These three beaches were the only sites with intact intertidal zones in proximity to the seawall along Elliott Bay that were viable for surveys. During the last four months of the study (Dec 2012 – Mar 2013), construction activities at the pier next to site S2 necessitated that it be replaced by site S2a, which was composed of habitat similar to the other seawall sites and located 500 m northwest from S2 along the seawall.

Table 1. The predominant substrate types and their locations at the study sites.

Site	Predominant Substrates Types and their Locations
S1, S2, & S3	Riprap at base of seawalls; sand, rocks, and shell hash scattered away from seawalls.
B1 & B3	Cobble in intertidal areas; sand throughout.
B2	Cobble in the intertidal area and riprap buttress at -1 m MLLW.

Visual underwater surveys

We conducted systematic scuba surveys at each site twice per month from October 2011 through October 2012 and once per month from November 2012 through March 2013. All surveys occurred during daylight and at high tides of 2.9 ± 0.5 m (mean ± SD) relative to mean lower low water (MLLW) to allow for maximum inundation of nearshore tidal elevations. Each survey consisted of divers swimming 30 m linear transects 3 and 10 m parallel to shore at the bottom of the water column. At nourished beaches, the depths of transects 3 m and 10 m from shore were 3.3 ± 0.6 m and 6.5 ± 0.7 m, respectively. At seawall sites, the depths of transects 3 m and 10 m from shore were 3.3 ± 0.7 m and 4.8 ± 1.0 m, respectively. Horizontal visibility was measured at the beginning of each survey from the bottom of the water column 3 m from shore and surveys only occurred when visibility exceeded 2.5 m (Toft et al. 2007, 2013, Munsch et al. 2014). Horizontal visibility was also used to quantify the width of survey transects (width = 2 * horizontal visibility) and to estimate fish densities (# fish / m^2 = counts / [transect width * transect length]; Toft et al. 2007, 2013, Munsch et al. 2014). For each fish or crab observation, divers recorded the species or finest feasible taxonomic level, count, substrate type(s) nearest to the individual or group (cobble, riprap, rocks, sand, shell hash), and water column position of the individual or group (bottom, less than one meter above bottom, or mid-water). Riprap, rocks, and cobble were distinguished by their shape, size, and location within sites. Riprap was angular, typically 0.5 m or greater in size and located along the base of the seawall at seawall sites or in the buttress of site B2. Rocks were also angular, but typically less than 0.25 m in size, and scattered throughout sites. Cobble had smooth rather than angular edges, was typically less than 0.10 m in size, and was scattered throughout sites. We use the term “association” to describe a fish or crab occurring near a type of substrate. Sculpin (Cottidae spp.) and gunnel (Pholidae spp.) were often not identifiable to the species level and we therefore consolidated these data into the broader taxonomic categories of sculpin and gunnel for analyses. Surface oriented species were excluded because the surface was not consistently visible and these species were targeted by companion snorkel surveys (Munsch et al. 2014). Visual surveys were advantageous in this study because they allowed us to quantify the occurrence of species near substrate types, and are not confounded by substrate type as occurs in catch data from net surveys (Rozas and Minello 1997).

Analysis

Statistical analysis was conducted in R version 2.15.2 (R Development Core Team 2012) utilizing the packages *ggplot2* (Wickham 2009), *Pvclust* (Suzuki and Shimodaira 2013), and *Vegan* (Oksanen et al. 2013).

Time series of mean total fish and crab densities at each site were estimated by locally weighted regression (LOESS; Cleveland and Devlin 1988) utilizing the *stat_smooth* function in the R package *ggplot2* (Wickham 2009).

Multivariate analysis was performed excluding species that occurred in less than 5% of surveys. The influence of shoreline armoring on community composition and substrate associations was visualized by canonical correspondence analysis (CCA; ter Braak 1986) on $\log_e$-transformed total independent species encounters and total numbers of substrate type used at each site. Encounters were defined as an observation of independently schooling or singular fish, which was appropriate for use in the CCA because one datum on the substrate type nearest to the fish or crab was recorded for each independently schooling or singular fish or crab regardless of its group size. Similarities in species substrate associations were quantified using cluster analysis on Bray-Curtis similarity matrices (Bray and Curtis 1957). Statistically significant clusters were identified by utilizing bootstrapping to quantify cluster stability and a dendrogram was utilized to visualize similarities (Suzuki and Shimodaira 2013). The primary purpose of the cluster analysis was to incorporate direct measures of species-level substrate associations into the CCA that describes site-level differences in species composition and substrate associations. Permutational analysis of variance (PERMANOVA; Anderson 2001, McArdle and Anderson 2001) was used to test for significant differences in species assemblages among sites using the function *adonis* in the R package *Vegan* (Oksanen et al. 2013). Pairwise PERMANOVA tests compared species assemblages among sites based on Bray-Curtis similarity matrices calculated from square root-transformed species density data, excluding species that were observed on less than 5% of surveys. To account for temporal variation in species composition, time of year was treated as a blocking variable by constraining permutations by survey events in which all sites were surveyed in approximately one week (Oksanen et al. 2013). The PERMANOVA was only used on data from October 2011 – November 2012, which included 96% of fish and crabs observed, to restrict pairwise PERMANOVA tests to consistent site comparisons because one of the seawall sites was relocated in December 2012.

Univariate analysis was performed on species that associated with one substrate type on greater than 66% of encounters because we anticipated that these species would be most affected by the structure of the subtidal habitat. The density data of these species was often heteroscedastic among sites; therefore, the non-parametric Kruskal-Wallis test was utilized to compare densities followed by post-hoc Bonferroni-corrected pairwise non-parametric Wilcoxon tests.

Results

Summary of fish and crabs observed

Approximately 55,000 individuals including 42 species of fish and six species of crabs were observed from Oct 2011 – Mar 2013 (Table 2). Many species were observed in direct contact or within one meter of the substrate (Table 3). Crabs that were not in direct contact with the substrate were on structures such as the stipes of bull kelp (*Nereocystis luetkeana*) or debris. Fish densities varied seasonally and were generally greatest during the spring and summer months (Fig. 2). The sandy beaches B1 and B3 were often uninhabited by fish during the winter months and B2 maintained the greatest fish abundance of all sites during winter months. The numerically dominant fish species were tubesnout (43% of total fish observed), shiner perch (27% of total fish observed), and striped seaperch (5% of total fish observed). The most common large predator was lingcod (0.5% of total fish observed). The dominant crab species were kelp crabs (76% of total crabs observed) and red rock crabs (18% of total crabs observed). Eleven species were only observed at one site and four of these occurred at B2. These species included black rockfish, cabezon, high cockscomb, and quillback rockfish. Residential black rockfish and, less commonly, quillback rockfish were observed at B2 year-round. In May and June 2012, larval fish were abundant at B2, totaling 5,400 fish in six discrete schools. Larval fish did not occur during other months or at other sites.

Crab	Kelp Crab	*Pugettia producta*	70.1	118.4	8.4	11.9	11	7.7
(Brachyura)	Red Rock Crab	*Cancer productus*	8.7	13.3	9	3.6	0	8.8
	Unidentified Crab		0.7	5.9	0	0	0	0.5
	Helmet Crab	*Telmessus cheiragonus*	0.8	1.4	0	1.3	0.7	1.0
	Graceful Crab	*Cancer gracilis*	0.1	0.2	0.2	0.2	0	4.5
	Dungeness Crab	*Cancer magister*	0	0.1	0.1	0	0.1	0.7
	Pygmy Rock Crab	*Cancer oregonensis*	0.2	0.4	0	0	0.1	0
Flatfish	Speckled Sanddab	*Citharichthys stigmaeus*	0	0.8	0.2	2.1	0	19.7
(Pleuronectiformes)	Rock Sole	*Lepidopsetta bilineata*	0.3	0.3	0.6	0.5	0	6.5
	Unidentified Flatfish		0.1	0.3	0.2	0.1	0	0
	English Sole	*Parophrys vetulus*	0	0	0	0	0	0.6
	C-O Sole	*Pleuronichthys coenosus*	0	0	0.2	0	0	0.4
	Starry Flounder	*Platichthys stellatus*	0	0	0	0.1	0	0.3
	Sand Sole	*Psettichthys melanostictus*	0	0	0	0.1	0	0
Gunnel	Unidentified Gunnel	Pholidae spp.	0.2	0.2	0.4	0.3	0.3	0.45
(Pholidae)	Saddleback Gunnel	*Pholis ornata*	0	0.1	0.1	0.2	0.3	0.5
	Crescent Gunnel	*Pholis laeta*	0	0.1	0	0	0.1	0.2
	Penpoint Gunnel	*Apodichthys flavidus*	0	0.2	0	0	0	0.1
Rockfish	Black Rockfish	*Sebastes melanops*	0	0	0	0	27.1	0
(*Sebastes*)	Quillback Rockfish	*Sebastes maliger*	0	0	0	0	1.7	0
	Unidentified Rockfish	*Sebastes* spp.	0	0	0.2	0	0.1	0.4
	Brown Rockfish	*Sebastes auriculatus*	0	0.1	0	0	0.2	0
Sculpin	Unidentified Sculpin	Cottidae spp.	0.8	1.3	2.2	1.5	1.9	1.3
(Cottidae)	Tidepool Sculpin	*Oligocottus maculosus*	0.1	2.9	0.2	0.5	0	0.1
	Padded Sculpin	*Artedius fenestralis*	0.6	0.3	0.3	0.5	0.2	0.3
	Buffalo Sculpin	*Enophrys bison*	0	0.6	0	1.1	0	0.4
	Longfin Sculpin	*Jordania zonope*	0	0	0	0	1.2	0
	Scalyhead Sculpin	*Artedius harringtoni*	0.1	0	0.2	0.2	0.5	0.1
	Manacled Sculpin	*Synchirus gilli*	0.2	0	0	0.1	0	0
	Smoothhead Sculpin	*Artedius lateralis*	0	0	0	0.1	0.1	0
	Great Sculpin	*Myoxocephalus polyacanthocephalus*	0.2	0	0	0	0	0
	Staghorn Sculpin	*Leptocottus armatus*	0	0	01	0	0	0
Surf Perch	Shiner Perch	*Cymatogaster aggregata*	55.1	242.5	96.4	125.7	226.5	234.2
(Embiotocidae)	Striped Seaperch	*Embiotoca lateralis*	18.5	40.9	19.3	6.9	104.3	4.4
	Kelp Perch	*Brachyistius frenatus*	28.9	52.5	6	4.35	24.8	1.75
	Pile Perch	*Rhacochilus vacca*	2.3	1.4	2.1	0	30.0	0.3
	Unidentified Perch	*Embiotocidae*	0	0	0.2	0	0.12	0
Other	Tubesnout	*Aulorhynchus flavidus*	315.2	545.4	147.8	589.6	424.9	108.4
	Larval fish		0	0	0	0	652.4	0
	Surf Smelt	*Hypomesus pretiosus pretiosus*	0	0.4	0	24.9	0	167.1
	Sand Lance	*Ammodytes hexapterus*	0	132	0	0	0	0
	Lingcod	*Ophiodon elongatus*	1.8	5.9	2.0	0	11.4	0
	Ratfish	*Hydrolagus colliei*	1.6	0.6	1.4	5.0	0.3	0.4
	Unidentified Forage Fish		7.2	0	0	0	0	0
	Whitespotted Greenling	*Hexagrammos stelleri*	0	0	0.2	0	0	1.5

Red Irish Lord	*Hemilepidotus hemilepidotus*	0.2	0	0	0.2	0.1	0.1
Pacific Tomcod	*Microgadus proximus*	0	0	0.3	0	0	0
Kelp Greenling	*Hexagrammos decagrammus*	0	0	0	0	0	0.2
Bay Pipefish	*Syngnathus griseolineatus*	0.1	0	0.1	0	0	0
Wolf eel	*Anarrhichthys ocellatus*	0	0.2	0	0	0	0
Unidentified Pelagic Fish		0	0.2	0	0	0	0
Adult Coho Salmon	*Oncorhynchus kisutch*	0	0	0	0	0	0.1
Northern Clingfish	*Gobiesox maeandricus*	0	0	0.1	0	0	0
Unidentified Fish		0	0.1	0	0	0	0
Northern Spearnose Poacher	*Agonopsis vulsa*	0	0	0	0	0	0.1
Cod	Gadidae spp.	0	0	0.1	0	0	0
Cabezon	*Scorpaenichthys marmoratus*	0	0	0	0	0.1	0
High Cockscomb	*Anoplarchus purpurescens*	0	0	0	0	0.1	0

Table 2. Mean density of fish and crabs (#/1000 m^2) observed at seawall sites (S) and nourished beaches (B) over the eighteen-month study period. Individual taxa are listed in decreasing order of overall density within their broader taxonomic group.

Table 3. Vertical distribution of species observed on greater than 5% of transects. N refers to the number of independent encounters of each taxa.

Taxa	**Bottom**	**< 1 m from Bottom**	**Mid Water**	**N**
Tubesnout	1%	78%	21%	834
Pile Perch	2%	88%	10%	118
Striped Seaperch	3%	94%	3%	1133
Black Rockfish	3%	47%	50%	159
Kelp Perch	5%	92%	3%	742
Shiner Perch	6%	80%	13%	1203
Ratfish	10%	90%	0%	98
Lingcod	74%	25%	2%	269
Kelp Crab	81%	11%	9%	1137
Speckled Sanddab	85%	15%	1%	150
Rock Sole	92%	8%	0%	99
Sculpin	93%	5%	2%	215
Gunnel	95%	5%	0%	37
Red Rock Crab	97%	2%	1%	428

Graceful Crab	98%	2%	0%	55
Helmet Crab	100%	0%	0%	37

Community composition and occurrence near substrate types

Canonical correspondence analysis (CCA) indicated that seawalls and beaches were different in community composition and substrate associations of fish and crabs (Fig. 3). There were three primary groupings of sites: seawall sites, sandy beaches B1 and B3, and the riprap-buttressed beach B2. Seawall sites and nourished beaches separated vertically in ordination space and seawall sites were grouped more closely together than nourished beaches. Most species that were not near the center of CCA ordination space occurred at or near the bottom of the water column and there were many species that had similar abundances among sites, which included many pelagic species (e.g., shiner perch--Fig. 3). The types of substrate that fish and crabs associated with reflected the shoreline composition. Association of fish and crabs near cobble, rock, and shell hash substrates was positively correlated with seawall sites. Association of fish and crabs with sandy substrate was correlated with the nourished beaches B1 and B3 and negatively correlated with riprap habitat use. Association of fish and crabs with riprap was correlated with all seawall sites and the riprap-buttressed beach B2.

Cluster analysis on the substrate types that fish and crab species associated with indicated that there were four groupings of fish and two groupings of crabs that had similar substrate associations (Fig. 4). These groupings corresponded to the centroids of these species in ordination space of the CCA (Fig. 3). Five common species occurred near one substrate type on greater than 66% of observations: the flatfish speckled sanddab and rock sole, and graceful crabs were commonly associated with sandy substrate; lingcod and black rockfish were commonly associated with riprap substrate. These species were not near the center of CCA ordination space and their association with riprap and sandy substrates was consistent with the substrate vectors in the CCA (Fig. 3). Community composition was significantly different among all sites (Table 4). The greatest differences generally occurred between comparisons among seawall sites, sandy beaches (B1 & B3), and the riprap-buttressed beach (B2). There were also significant differences in species composition among seawall sites despite their close groupings in the CCA, but species composition differences among seawall sites were minor compared to the beaches and these species did not obviously associate with a substrate that was related to the shoreline engineering.

Table 4. Pseudo-$F_{1, 50}$ statistics (above diagonal) and p values (below diagonal) for pairwise PERMANOVA tests between seawall sites (S) and nourished beaches (B).

	S1	S2	S3	B1	B2	B3
S1		1.68	4.92	4.27	12.20	10.22
S2	0.002		3.37	5.58	9.18	10.41
S3	0.001	0.001		4.10	12.08	6.09
B1	0.001	0.001	0.001		11.36	4.37
B2	0.001	0.001	0.001	0.001		22.75
B3	0.001	0.001	0.001	0.001	0.001	

Comparing species densities among sites

The densities of species that associated with one substrate type on greater than 66% of encounters were compared among sites (Fig. 5). Speckled sanddab densities were greatest at the sandy beach B1 followed by the sandy beach B3 (Kruskal-Wallis; $X^2 = 48$, df = 5, p = 3e-09). Densities at B3 were significantly greater than densities at the riprap-buttressed beach B2 and the seawall site S1. Rock sole (Kruskal-Wallis; $X^2 = 68$, df = 5, p = 3e-13) and graceful crab (Kruskal-Wallis; $X^2 = 78$, df = 5, p = 2e-15) densities were greatest at the sandy beach B3. Lingcod densities were highest at the riprap-buttressed beach B2 followed by the seawall sites S1 and S3 and there were no observations of lingcod at the sandy beaches (Kruskal-Wallis; $X^2 = 115$, df = 5, p = 2e-16). Black rockfish were only observed at the riprap-buttressed beach B2 (Kruskal-Wallis; $X^2 = 169$, df = 5, p = 2e-16).

Discussion

Studies of engineered subtidal habitats can provide insight into how shoreline armoring affects fish and crab communities and how urban habitats can be designed to meet management objectives. In this study, we surveyed sites where seawalls and riprap dramatically changed the structure of natural subtidal habitats, and also surveyed nourished sand and cobble beaches that are a widely utilized alternative to armoring (Speybroeck et al. 2006). Similar to many urban systems, there is no pristine subtidal habitat in the Duwamish-Elliott Bay system (Simenstad et al. 2011), and it was thus not possible to compare fish and crab communities from preexisting natural conditions. Artificially nourished beaches are often described as a preferable alternative to armored sites for fish despite their effects rarely being quantified (Hartig et al. 2011), and our study addresses this data gap. To our knowledge, this is the first rigorous study to quantitatively describe shallow subtidal fish and crab assemblages in Puget Sound where armoring is widespread and presents major habitat management issues (e.g., Simenstad et al. 2011).

Shoreline engineering affected the composition of fish and crab communities and the types of substrate they associated with. Most species that varied in density among sites associated predominantly with one substrate type, which was either riprap or sand. These species included a range of trophic levels, taxa, and morphologies within the subtidal fish and crab community. Our findings suggest several hypotheses describing how shoreline engineering affects the composition of fish and crab communities: (1) shoreline engineering is an important determinant of habitat attributes (e.g., substrate type), (2) species vary in their selection of these attributes, and (3) the abundance of a species is a function of its selectivity for and the availability of habitat attributes. For example, flatfish utilize sandy substrate for camouflage (Ellis et al. 1997, Ryer et al. 2008) and were present in greatest densities at the sandy beaches. Future studies that employ quantitative behavioral observations could improve our understanding of why species associate with or avoid certain types of engineered habitats, and could provide urban shoreline managers information on how to design habitats that benefit targeted taxa.

Landscape must be considered when assessing and managing effects of anthropogenic disturbance on habitat quality (Boström et al. 2011, Kleijn and Langevelde 2006, Simenstad and Cordell 2000). Our study compared fish communities at the relatively small scale of one highly urbanized bay, but fish assemblages, including those at rehabilitated habitats, may also be affected by larger scale processes such as recruitment of fish from other sources (e.g., Lowry et al. 2014). In highly modified landscapes, management decisions that create potentially novel communities or that target specific ecosystem functions may be more practical than traditional restoration goals (Hobbs et al. 2006, 2014). Furthermore, managers must decide if it is beneficial to artificially increase diversity (Angermeier 1994) of fish communities within a managed landscape by creating habitats that are utilized by different species. Disproportionate effects of shoreline engineering may also be observed in modified landscapes, for example if fish spawning is limited by the availability of beach habitat in heavily armored systems (e.g., Penttila 2007).

Shorelines can be designed to address both ecological and social objectives of urban waterfronts. Armored shorelines inevitably fall into disrepair as wave energy or other events occur and their reconstruction offers opportunities to incorporate habitat enhancements. For example, the 2001 Nisqually earthquake damaged the seawall along Elliott Bay and its shoreline is currently undergoing reconstruction with a new design that targets habitat improvements, particularly for juvenile Pacific salmon. Removing shoreline armoring is often ecologically desirable because armoring severs linkages among naturally interconnected aquatic, terrestrial, and pelagic habitats (e.g., Sobocinski et al. 2010, Morley et al. 2012, Heerhartz et al. 2014). Our study suggests that the types of substrate utilized in urban waterfront design can also affect fish communities, including species of management interest. Nourished beach designs can benefit society directly because they are more resilient to flooding than conventional armoring approaches (Temmerman et al. 2013) and protect shorelines from wave erosion (Speybroeck et al. 2006). Furthermore, beaches provide people with recreational opportunities and interactions with natural or semi-natural environments in urban settings (Standish et al. 2012).

Conclusions

Shoreline modifications are prevalent worldwide and this study contributes to a broader literature that suggests shoreline modifications affect the composition of fish and crab communities in shallow systems. The structural diversity of subtidal habitats provided by seawall and riprap armored sites, nourished sandy beaches, and a riprap-buttressed beach may increase the species richness of fish and crab communities at the embayment scale, compared to an entirely armored system. Our study showed that community composition and substrate associations were different between seawall sites and nourished beaches. Species that predominantly associated with one type of substrate were affected most by the engineering of the shoreline. All species did not respond uniformly to variation in shoreline structure and the type of shoreline engineering did not have a measurable effect on the abundance of many species within the urbanized landscape that we studied. In general, pelagic species that rarely interacted with the substrate were least affected, while those strongly associated with substrata such as sand (flatfishes) and riprap (lingcod) were most affected. Our findings of different communities at artificially nourished beaches within the urban landscape suggest that partially restoring the physical structure of degraded habitats may rehabilitate some of their lost ecological functions, although further work is required to quantify effects of shoreline engineering on fitness.

Future studies should place these findings in a larger spatial context to understand how the presence of armoring or the introduction of engineered beaches affects communities along a continuum of landscape development. It is also important to explore whether it is beneficial to engineer habitats for species that were not historically present at particular locations, especially when these locations are already degraded beyond restoration or when the new habitat facilitates the recovery of a protected species. Understanding why specific fish and crabs benefit from natural or modified habitats will allow for managers to better target species of interest for habitat enhancement or restoration efforts, and enable informed shoreline management decisions as shorelines are increasingly modified worldwide.

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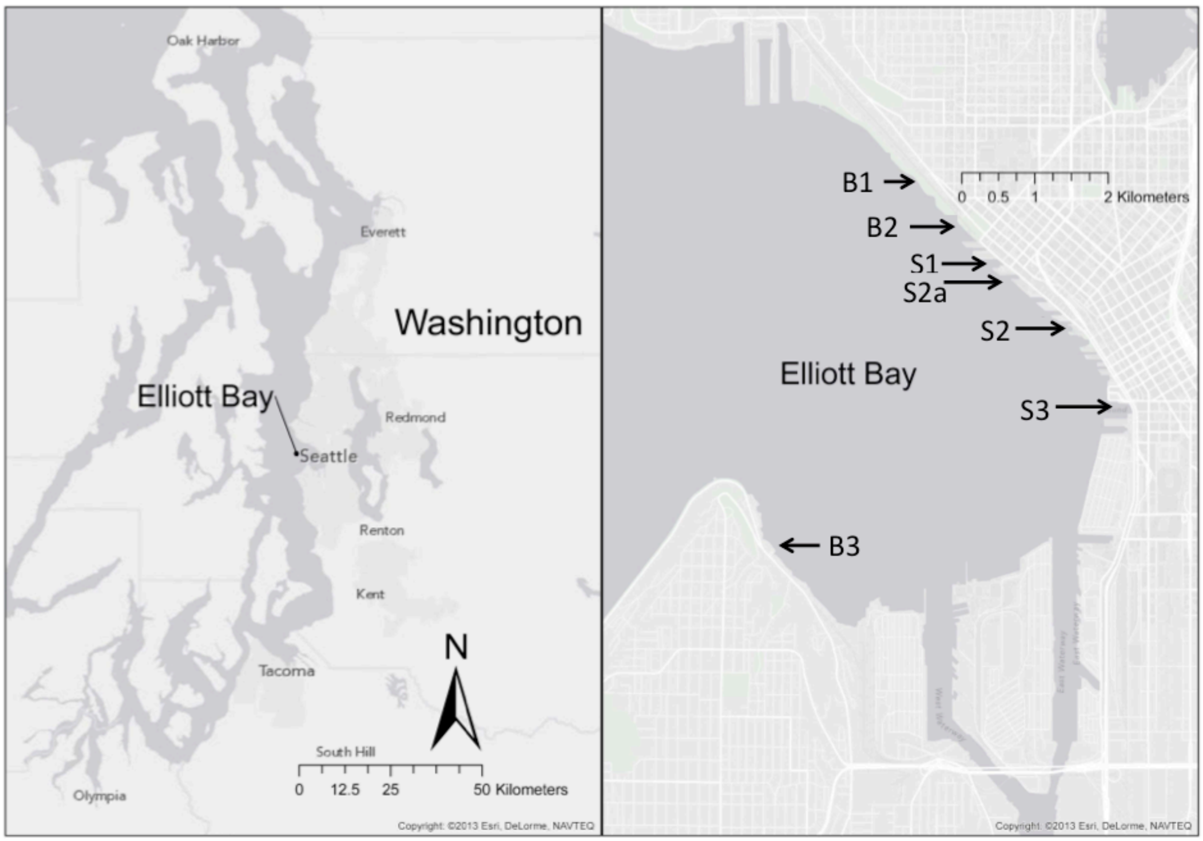

Figure 1. Locations of seawall sites (S) and nourished beaches (B) in Elliott Bay, WA.

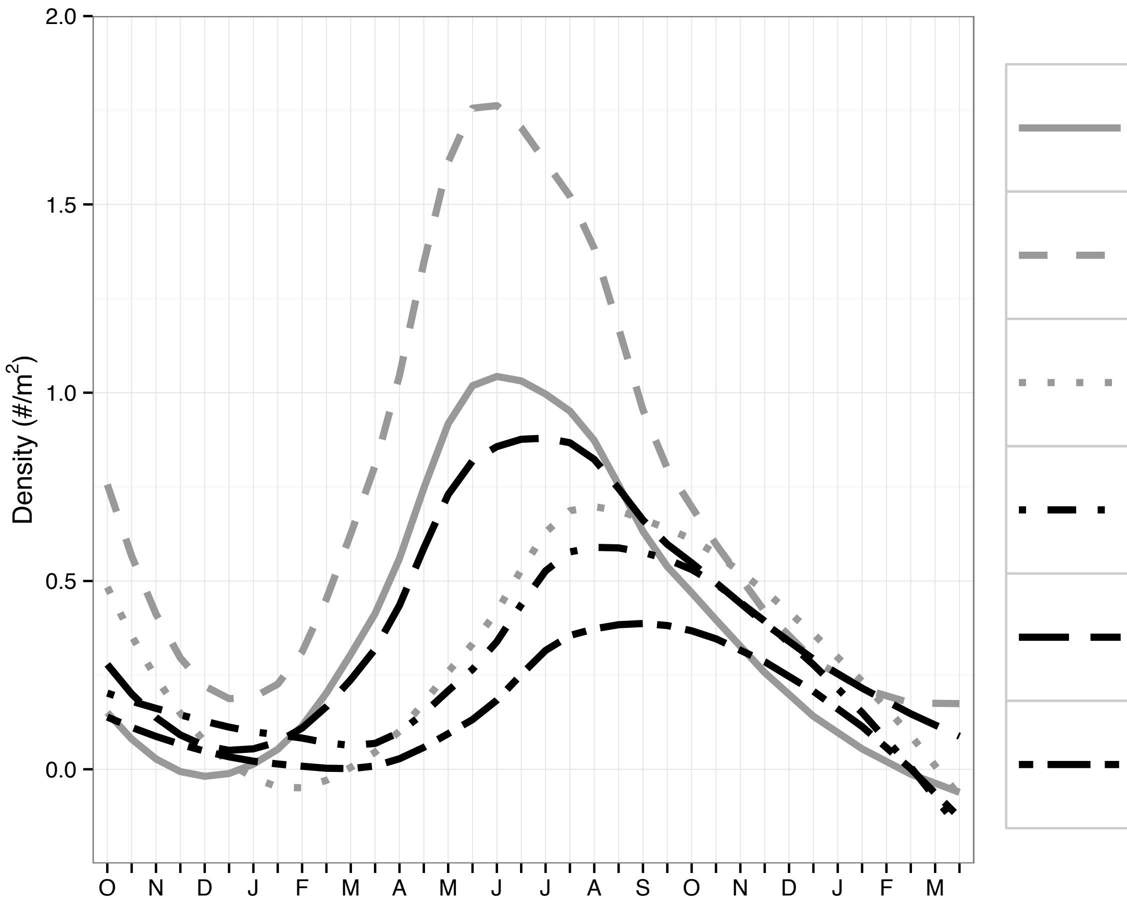

Figure 2. Time series of total fish and crab densities (#/m^2) for each site for the duration of the study period 2011-2013.

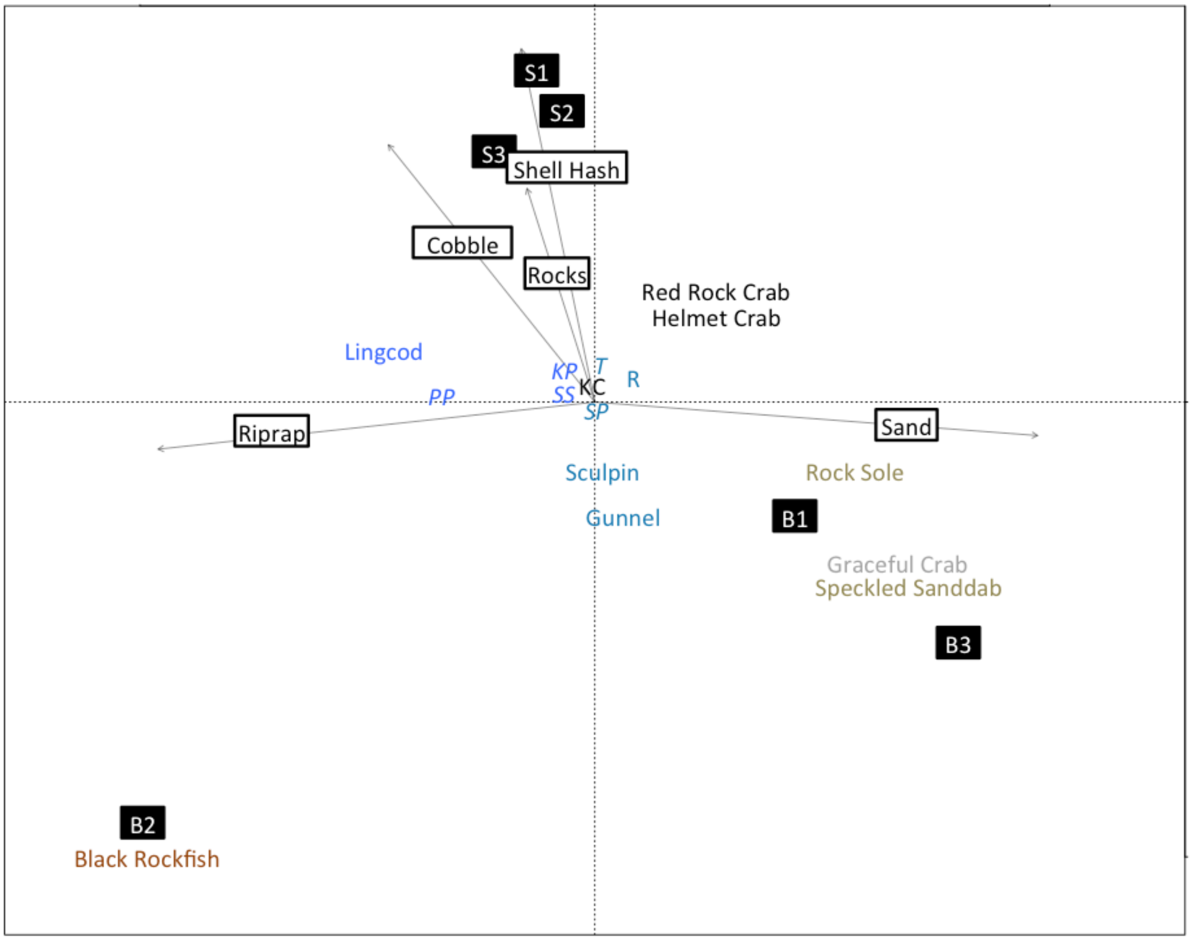

Figure 3. Canonical correspondence analysis (CCA) triplot showing species composition of sites, vectors of substrate type use, and centroids of species in ordination space. Font colors correspond to groups of species that occurred near similar substrate types as quantified by cluster analysis (Fig. 4). Pelagic fish are italicized. Abbreviations: kelp crab (KC), kelp perch (KP), pile perch (PP), ratfish (R), shiner perch (SP), striped seaperch (SP), and tubesnout (T).

Alternative black and white version

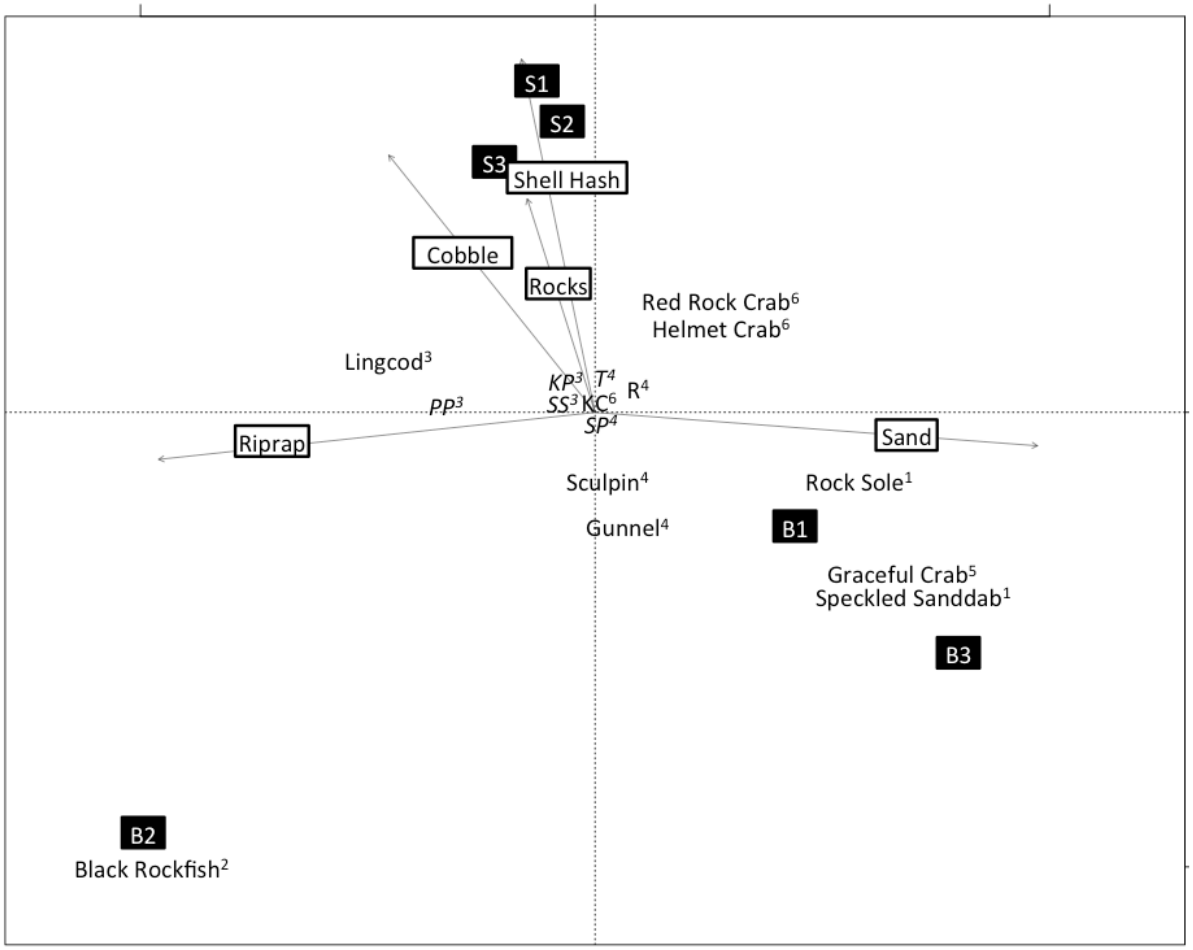

Figure 3. Canonical correspondence analysis (CCA) triplot showing species composition of field sites, vectors of substrate type use, and centroids of species in ordination space. Superscripts correspond to groups of species that occurred near similar substrate types as quantified by cluster analysis (Fig. 4). Pelagic fish are italicized. Abbreviations: kelp crab (KC), kelp perch (KP), pile perch (PP), ratfish (R), shiner perch (SP), striped seaperch (SP), and tubesnout (T).

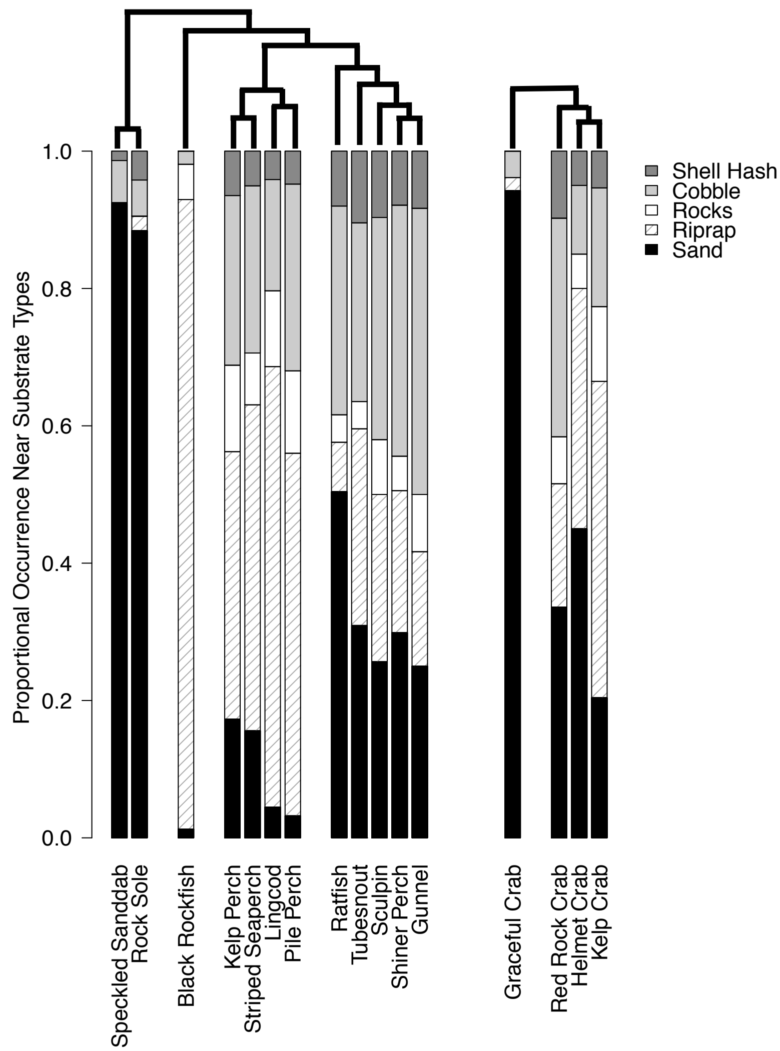

Figure 4. Proportional occurrence of species near substrate types for species occurring on greater than 5% of surveys. Species are grouped by statistically significant clusters and similarities are visualized by the dendrogram. The number of independent encounters for each species is shown in Table 3.

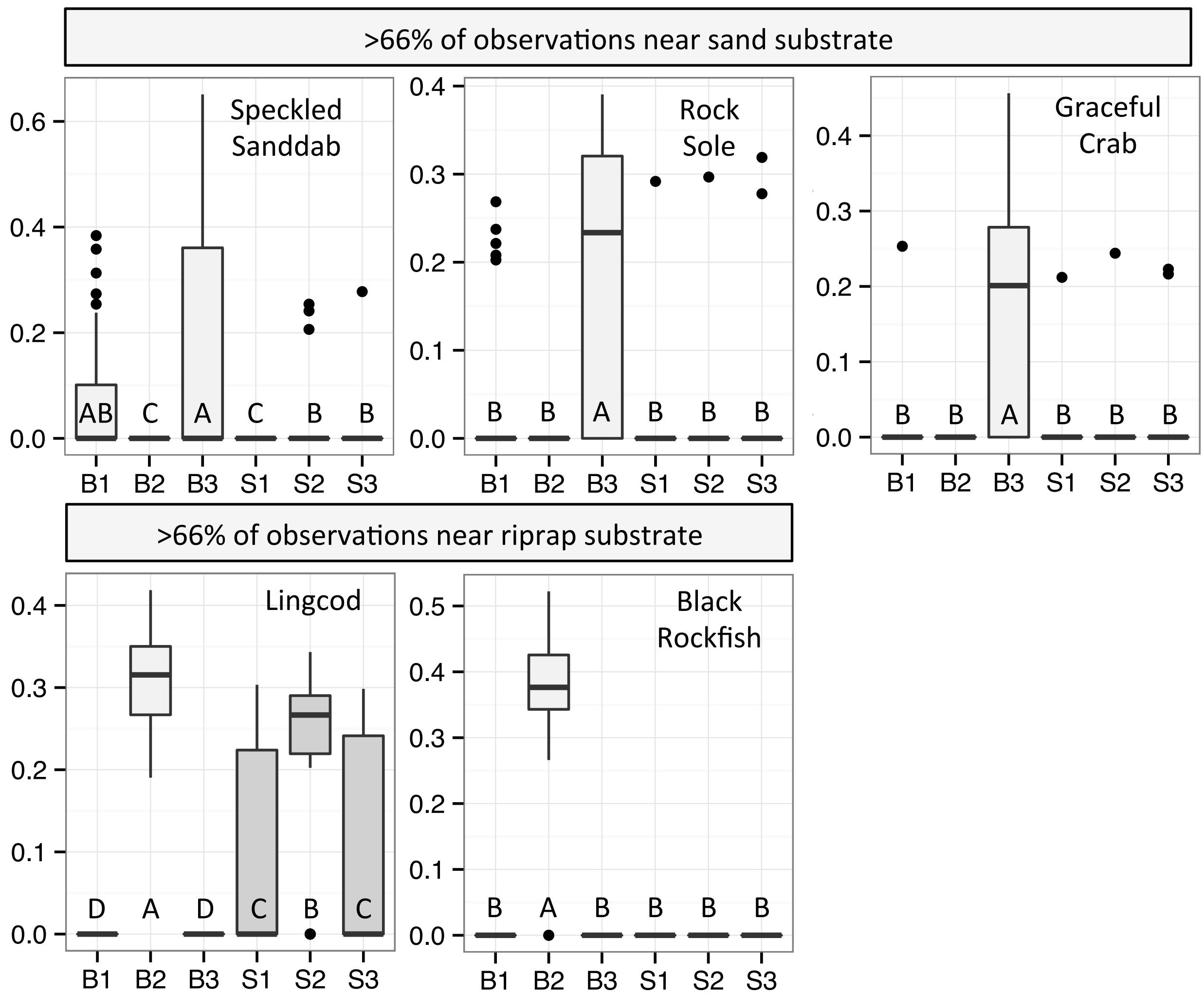

Figure 5. Densities of species that occurred over one substrate type on greater than 66% of encounters compared among sites. Boxplot hinges indicate first and third quartiles; whiskers indicate highest and lowest values within 1.5 times the interquartile range from top and bottom hinges, respectively. Letters above boxplots indicate statistically significant differences (A>B>C>D).

Chapter Three: 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 to juvenile fish. While shoreline armoring compromises epibenthic and terrestrial prey resources, 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 three species of juvenile Pacific salmon (*Oncorhynchus* spp.) in shallow habitats of an extensively armored urban estuary. We compared sites armored by intertidal seawalls to 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. These fish selected for epibenthic copepods at both shoreline types, but selected for planktonic copepods only at seawall sites. 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 if there are energetic costs to the predator.

Introduction

Estuarine shorelines interface a connected ecosystem comprised of terrestrial, pelagic, and benthic habitats (Polis et al. 1997, Sobcinski 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 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.

Salmon use habitats modified by armoring during a life stage important to their overall survival. During their early estuarine and marine residence, juvenile salmon experience high growth rates and mortality rates that are inversely related to fish size (Parker 1962, LeBrasseur & 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, WA (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 salmon (*O. gorbuscha*) in shallow habitats along shorelines armored by seawalls in the intertidal area to those at unarmored beaches, and examined relationships between prey availability and fish diets.

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 2,144 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 twentieth 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 six sites within Elliott Bay (Fig. 1) during high tides to allow for maximum inundation of shoreline habitat. The shorelines of three 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 MLLW. The shorelines of three 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 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 three 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 three sampling events that took place at each site June – August 2012. For each sampling event, two 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 x 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 invertebrates 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 same 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 study period. SDDN refers to snorkel diver deployed net.

Month	Mar-12	Apr-12	May-12	Jun-12	Jul-12	Aug-12	Mar-13	Apr-13
Day Netting Events	2	2	2	2	2	2	2	2
Night 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 x 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 x 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 x 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 that were greater than 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 less than 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. Diets were sampled from euthanized chum and pink salmon that were less than 60 mm in length because lavage was ineffective for these small fish. These fish were euthanized by an overdose of the anesthetic MS-222 and then fixed in 10% buffered formaldehyde solution, and 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 the incorporation of two random effects, non-normal response variable distributions, and zero inflation.

The juvenile salmon diet data was organized into five 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 these fish 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 less than 50 mm length were analyzed separately from those that were greater than or equal to 50 mm because chum salmon transition from epibenthic prey to planktonic prey at this length (Simenstad 1997, 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 five 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 was arcsine square root transformed (e.g., McPeek et al. 2014). 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 = 9,999) and the corresponding vectors were plotted (Oksanen 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 (McArdle and Anderson 2001, 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 decreasing 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 if 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) and 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 by observing a homogenous variance around a mean of zero when residuals were plotted against fitted values and fixed effects.

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

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

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).

Table 2. Prey taxa in the environment and diets of juvenile salmon. Sources are epibenthic (E), planktonic (P), and terrestrial (T). Asterisks indicate that the source refers to a juvenile life stage of the prey taxa.

Taxa	Common Name	Source
Aphididae	aphids	T
Arachnida	arachnids	T
Brachyura	crabs	P
Calanoida	calanoid copepods	P
Cirripedia	barnacles	E/P*
Coleoptera	beetles	T
Copepoda	copepods	E/P
Crustacea	crustaceans	P/T
Cyclopoida	cyclopoid copepods	P
Diptera	true flies	T/E*
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*
Larvacea	larvaceans	P
Ostracoda	seed shrimp	E
Polychaeta	annelid worms	E/P*
Psocoptera	booklice	T

The NMDS ordination of environmental prey composition indicated differences between shoreline types (Fig. 4). There were significant gradients of barnacle larvae increasing in the direction of samples from seawall sites and of harpacticoid copepods increasing in the direction of samples from reference beaches. There was also a significant gradient of calanoid copepods in ordination space, but this occurred in the direction of samples taken from both shoreline types. PERMANOVA indicated significant differences in environmental prey composition between shoreline types (Table 3).

Table 3. Summary statistics of PERMANOVA tests on differences in environmental prey composition according to the factors shoreline type (Sh), net (Ne), site (Si), and netting event (Ev).

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

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.

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).

Response Variable	Fixed Effect	Parameter Estimate	SE	p	Random Effect	Variance	SD
Cirripedia Abundance	Intercept	4.319	0.475	2E-16	Site	1.284E-08	1.133E-04
	Shoreline Type	1.375	0.691	0.046	Netting Event	1.776	1.333
Harpacticoida Abundance	Intercept	3.207	0.384	2E-16	Site	1.99E-08	1.411E-04
	Shoreline Type	-1.353	0.558	0.015	Netting Event	0.8457	0.9196
Calanoida Richness	Intercept	0.9505	0.1844	2.50E-07	Site	9.43E-08	3.07E-04
	Shoreline Type	-0.1555	0.225	0.49	Netting Event	3.56E-09	5.97E-05
	Net Type	-0.0247	0.2229	0.91			
Cyclopoida Richness	Intercept	0.5077	0.2222	0.022	Site	7.16E-08	2.68E-04
	Shoreline Type	0.0553	0.2507	0.825	Netting Event	1.16E-07	3.41E-04
	Net Type	0.1881	0.2517	0.455			
Gammaridea Richness	Intercept	0.6016	0.4380	0.170	Site	7.16E-08	2.68E-04
	Shoreline Type	-0.0511	0.4235	0.904	Netting Event	1.16E-07	3.41E-04
	Net Type	-1.2203	0.4840	0.012			
Harpacticoida Richness	Intercept	1.777	0.151	2E-16	Site	2.815E-08	1.678E-04
	Shoreline Type	-0.474	0.229	0.038	Netting Event	0.03581	0.1892
Insecta Richness	Intercept	-0.95	0.566	0.093	Site	1.582E-07	3.977E-04
	Shoreline Type	1.561	0.622	0.012	Netting Event	0.2896	0.5382

Juvenile Salmon 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. The diets of these fish 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 change whether a prey taxa was positively or negatively selected for (Fig. 6). All groups of juvenile salmon positively selected insects and crab larvae and negatively selected barnacle larvae.

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

Species	Fork Lengths	Day/Night	n
Chinook Salmon	All	Day	173
Chinook Salmon	All	Night	81
Chum Salmon	<50	Day	73
Chum Salmon	≥50	Day	68
Pink Salmon	All	Day	64

Table 6. Summary statistics for linear mixed effects models comparing stomach fullness of salmon groups between shoreline types (baseline: reference beach).

Salmon Group	Fixed Effect	Parameter Estimate	SE	p	Random Effect	Variance	SD
Chinook Salmon (Day)	Intercept	0.249	0.0113	2.00E-16	Site	2.06E-09	4.54E-05
	Shoreline Type	0.0293	0.0194	0.13	Netting Event	0.001317	0.03629
Chinook Salmon (Night)	Intercept	0.276	0.0162	2.00E-16	Site	2.06E-09	4.54E-05
	Shoreline Type	0.0103	0.0219	0.64	Netting Event	5.55E-04	0.02347
Chum Salmon (Small)	Intercept	0.2985	0.0125	2.00E-16	Site	2.06E-09	4.54E-05
	Shoreline Type	-0.0075	0.0159	0.62	Netting Event	2.06E-09	4.54E-05
Chum Salmon (Large)	Intercept	0.2442	0.019	2.00E-16	Site	2.06E-09	4.50E-05
	Shoreline Type	0.0246	0.0298	0.41	Netting Event	0.001827	0.04275
Pink Salmon	Intercept	0.2525	0.02955	2.00E-16	Site	0.002122	0.04607
	Shoreline Type	0.00726	0.04335	0.87	Netting Event	7.84E-04	0.028

The diets of Chinook salmon were comprised of 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 (including the groups 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).

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

Salmon Group	Factor	DF	SS	MS	Pseudo-F	p
Chinook Salmon (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	1.99E+05	6433.7	0.0001
	Res	131	2.90E+05	2212.2	2.9083	
	Total	167	5.23E+05			
Chinook Salmon (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
	Res	64	2328	2328		
	Total	79	2.47E+05			
Chum Salmon (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
	Res	56	77269	1379.8		

	Total	70	2.02E+05			
Chum Salmon (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
	Res	53	98467	1857.9		
	Total	66	1.87E+05			
Pink Salmon	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
	Res	51	54761	1073.8		
	Total	63	1.29E+05			

Chum salmon under 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 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. 7). They also positively selected for larvaceans only at seawall sites. Diets of chum salmon more than 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 two 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 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 copepod 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 two 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 (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 prior in Table 4).

Table 8. Summary statistics of linear mixed effects models quantifying copepods in the diets of small chum salmon (Diet) and in the environment (Env). Baseline values for shoreline type and net depth are reference beach and neuston net, respectively.

Data	Response Variable	Fixed Effect	Parameter Estimate	SE	p	Random Effect	Variance	SD
Diet	Epibenthic Copepods	Intercept	1.96	0.413	2.10E-06	Site	1.83E-08	1.25E-04
		Shoreline Type	-1.504	0.52	0.0038	Netting Event	0.770	0.878
	Planktonic Copepods	Intercept	1.098	0.382	0.004	Site	6.25E-09	7.91E-05
		Shoreline Type	1.37	0.492	0.0053	Netting Event	0.716	0.846
	Total Copepods	Intercept	2.368	0.4444	9.90E-08	Site	2.08E-09	4.56E-05
		Shoreline Type	0.165	0.574	0.77	Event	1.04	1.022
Env	Planktonic Copepods	Intercept	5.17	0.367	2.00E-16	Site	1.56E-09	1.25E-04
		Net Type	0.763	2.39	0.017	Netting Event	1.47	1.21

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 estuary 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 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 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 energetic costs of consuming alternative prey along armored shorelines could impair habitat value there. Moving forward, the effects of armoring on habitat value will be better understood if studies take into account energetic consequences of detecting, capturing, and consuming alternative prey (e.g., Giacomini et al. 2013, Van Deurs et al. 2015).

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 because 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 larger.

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 have 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 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 results 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 built nearshore environments so that more ecologically beneficial shorelines can be designed

(Wilson et al. 2015). In circumstances when 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 quantitative 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 and 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. Moving forward, 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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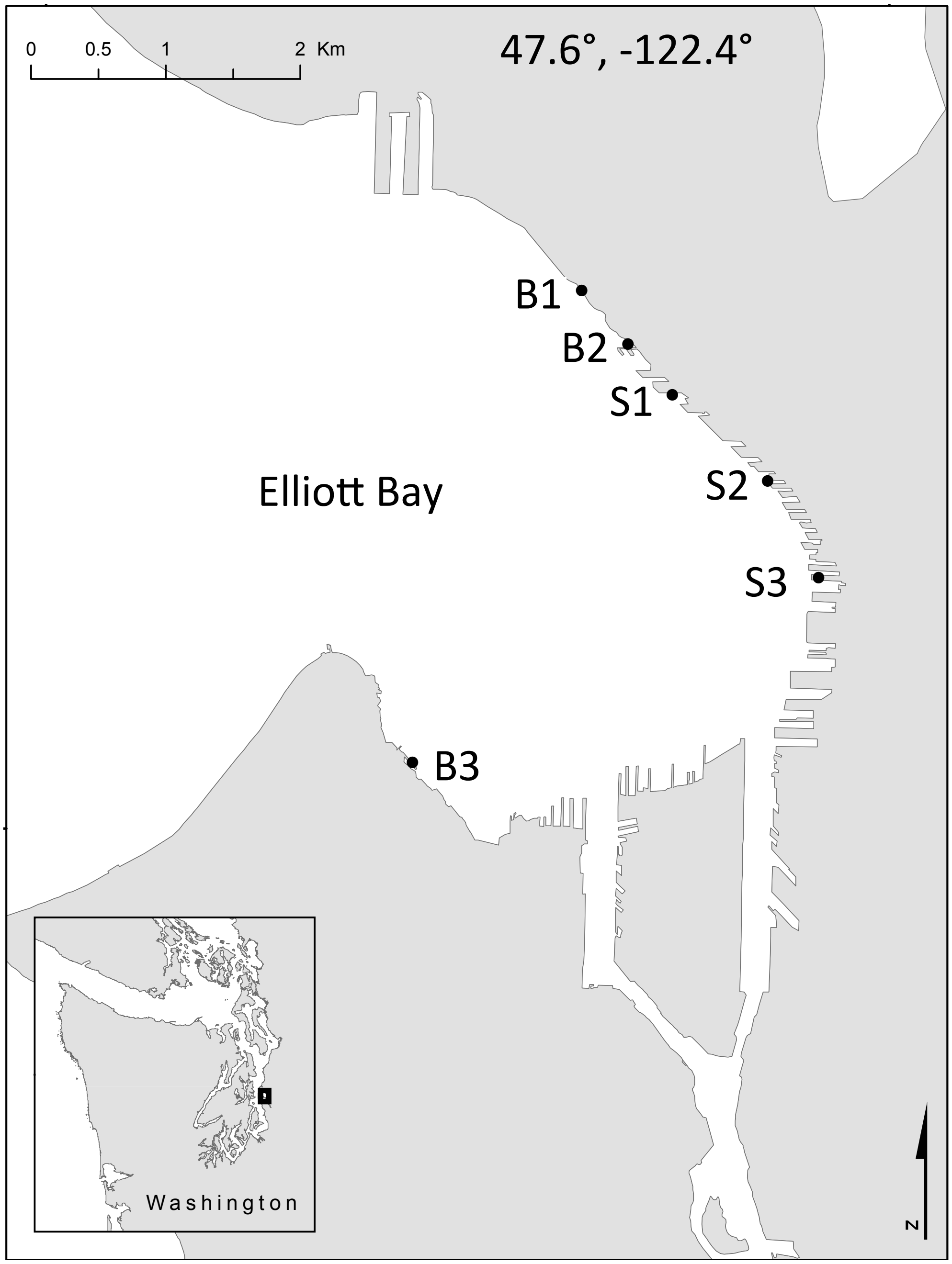

Figure 1. Location of reference beaches (B) and seawall sites (S) within Elliott Bay, Washington (USA).

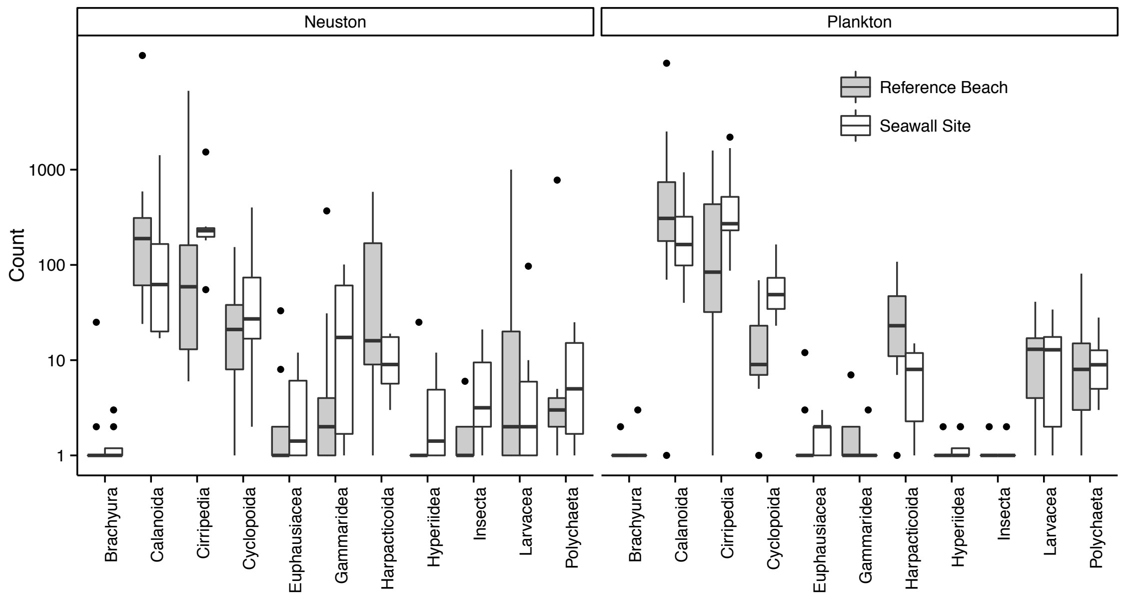

Figure 2. Counts of prey in the environment as sampled by neuston and plankton nets. Counts are shown under log(x+1) transformation.

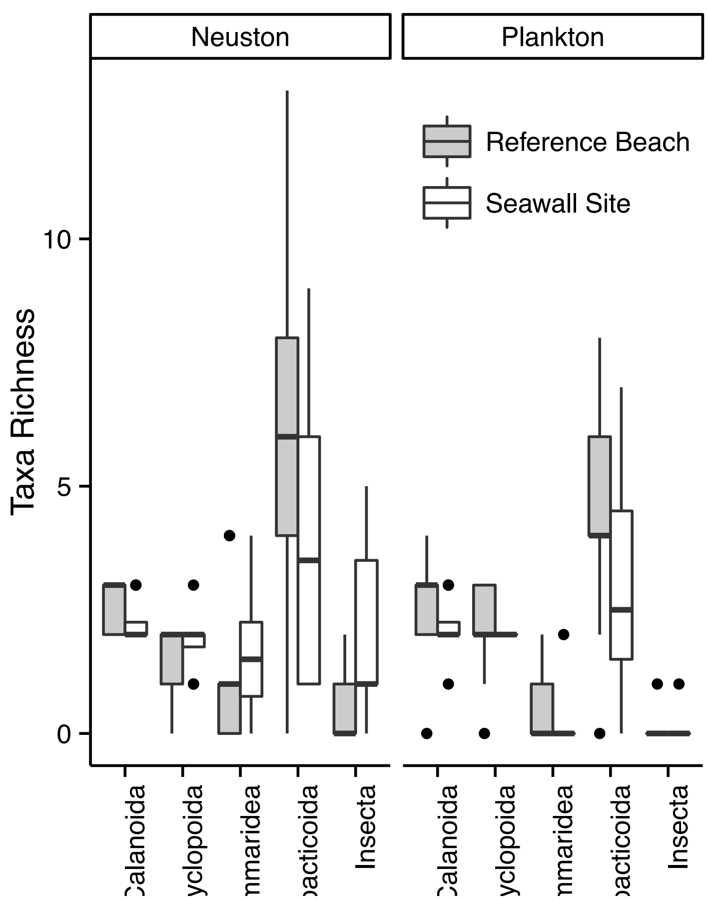

Figure 3. Taxa richness of prey in the environment as sampled by neuston and plankton nets.

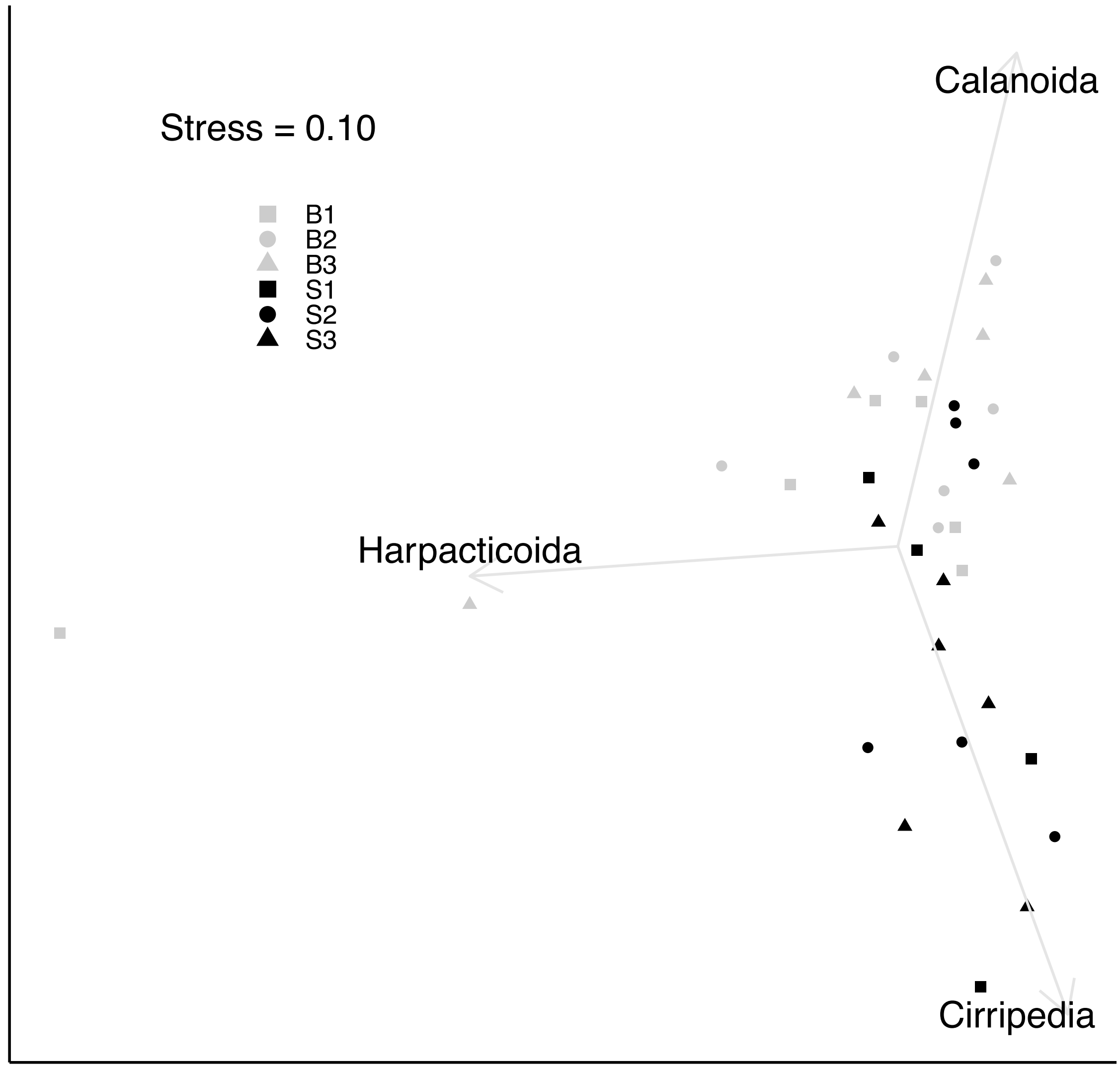

Figure 4. NMDS of prey composition in the environment of reference beaches (B) and seawall sites (S). Vectors indicate prey taxa with significant loadings on the axes.

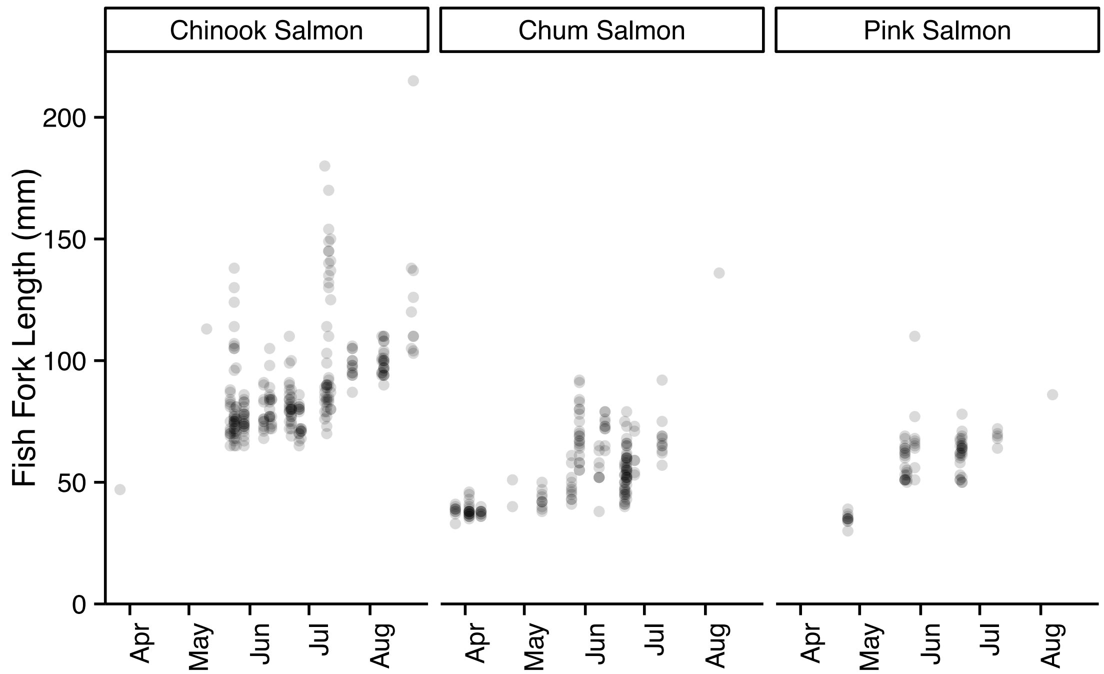

Figure 5. Size and timing of Chinook, chum, and pink salmon. Points are overlaid such that multiple points in the same area appear darker. Diets of chum salmon before May were sampled in 2013; all other diets were sampled in 2012.

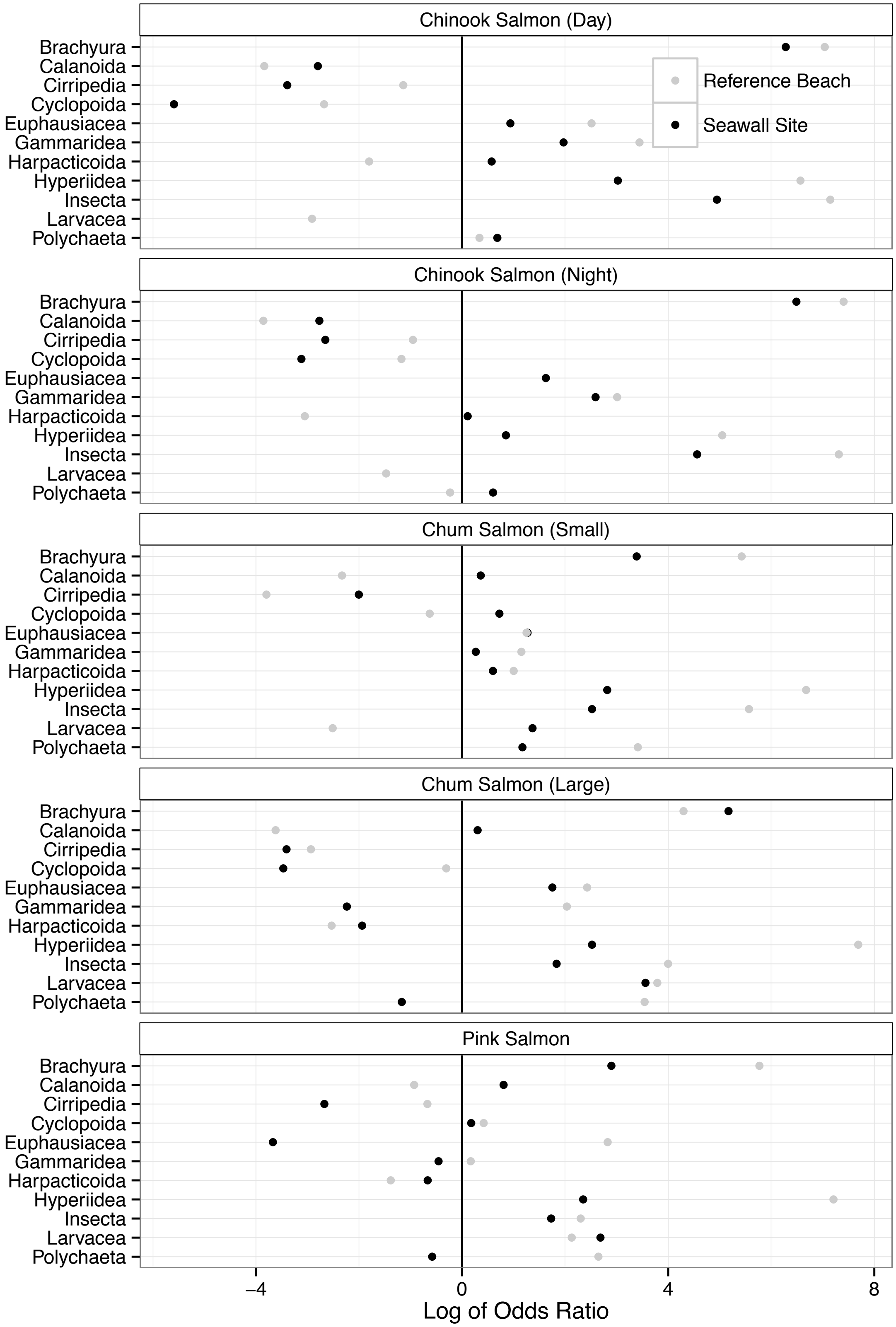
Chinook Salmon (Day)
Chinook Salmon (Night)
Chum Salmon (Small)
Chum Salmon (Large)
Pink Salmon
Brachyura
Calanoida
Cirripedia
Cyclopoida
Euphausiacea
Gammaridea
Harpacticoida
Hyperiidea
Insecta
Larvacea
Polychaeta
Reference Beach
Seawall Site
−4
0
4
8
Log of Odds Ratio

Figure 6. Selection of prey taxa by salmon groups separated by shoreline type quantified by log of odds ratio. Positive and negative values indicate positive and negative prey selection, respectively.

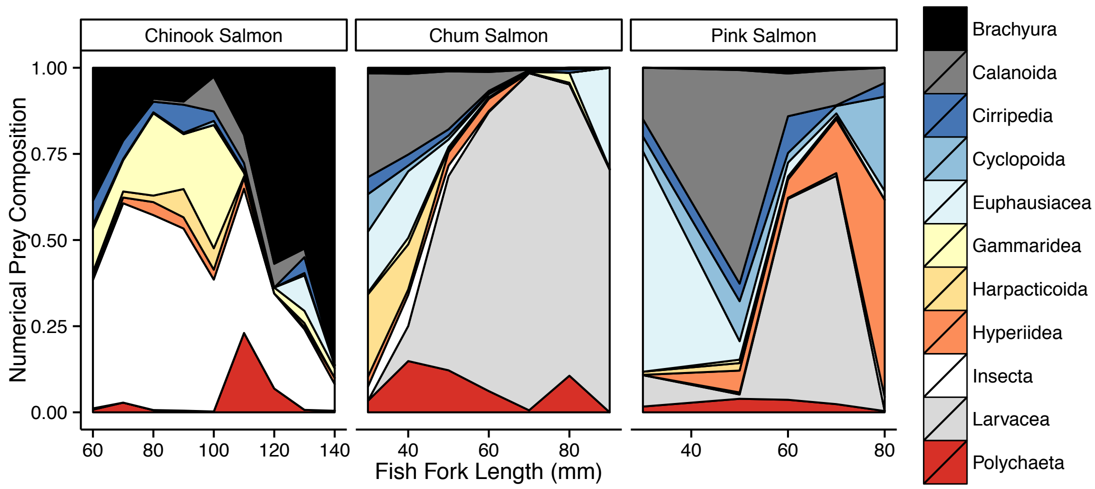

Figure 7. Numerical composition of prey for Chinook, chum, and pink salmon, binned by 10 mm length increments.

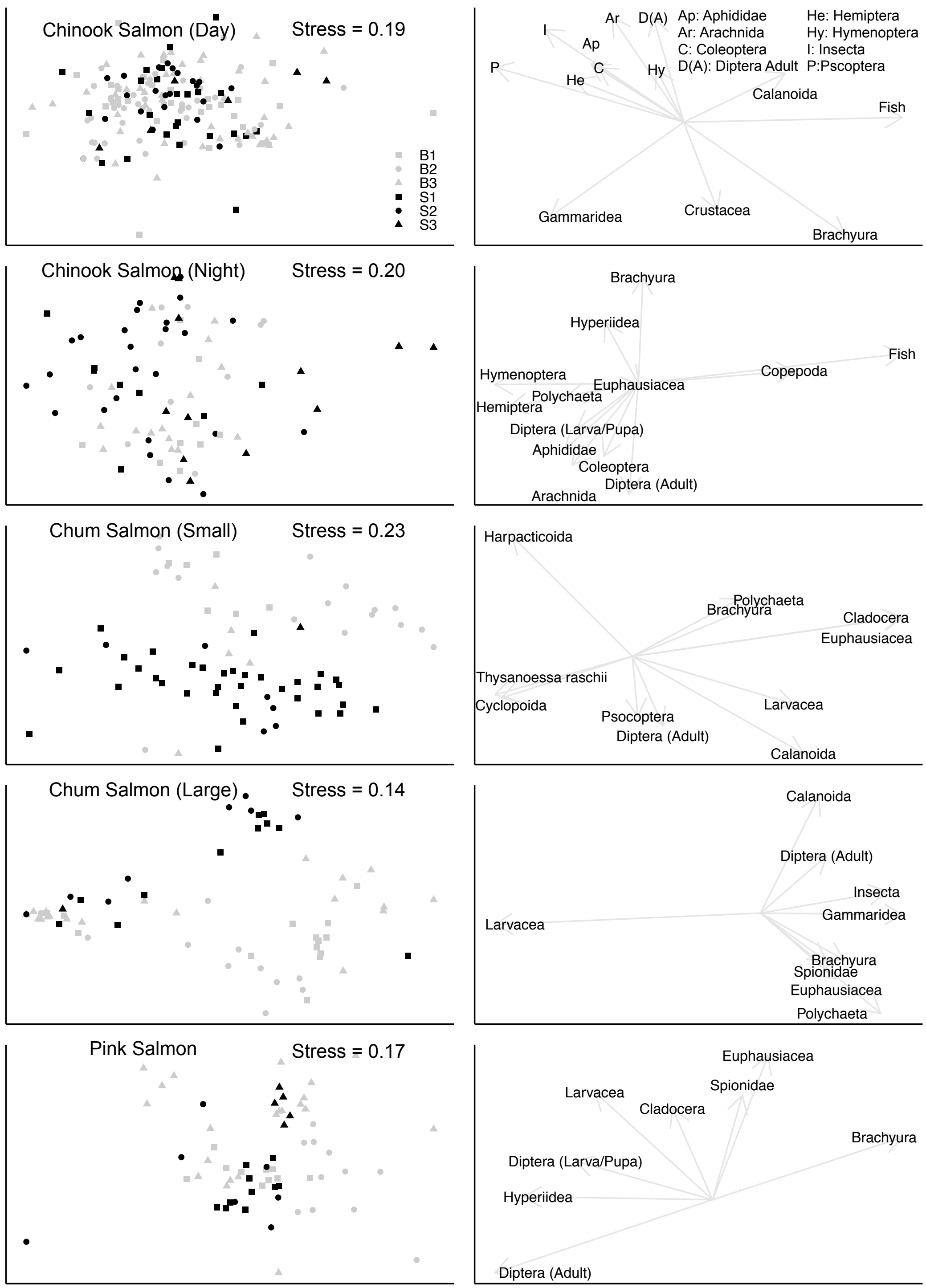

Figure 8. NMDS of prey composition for each salmon group at reference beaches (B) and seawall sites (S). Vectors indicate prey taxa with significant loadings on the axes.

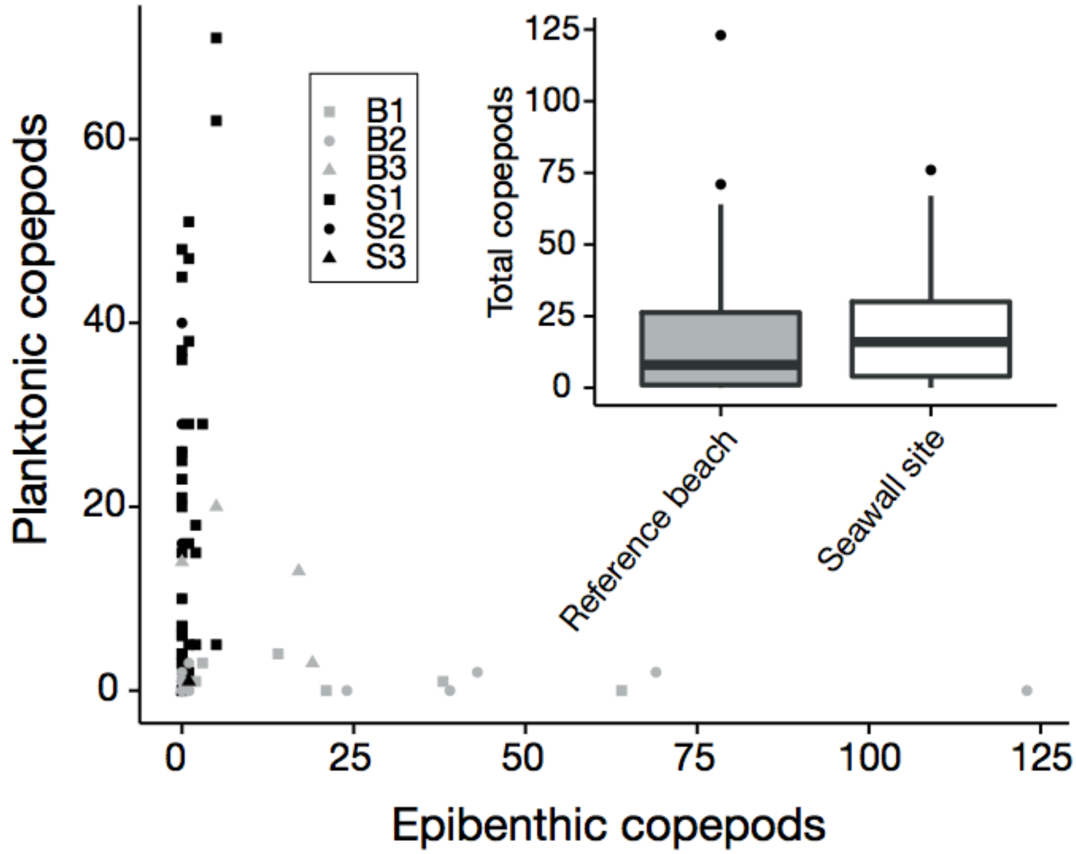

Figure 9. Number of planktonic and epibenthic copepods in the diets of small chum salmon (main figure). Total number of copepods in the diets of small chum salmon (inset).

Chapter Four: Fine-scale habitat use and behavior of a nearshore fish community: nursery functions, predationavoidance, and spatiotemporal habitat partitioning

SH Munsch, JR Cordell, JD Toft

Abstract

We have a limited understanding of habitat use and behavior in nearshore fish communities because they are rarely observed in situ. Consequently, ecologists recommend a process-based conceptualization of nursery habitats, but lack knowledge of nursery processes on fine scales along shore, and studies in controlled settings suggest that context-dependent behaviors allow fish to balance predation avoidance with other objectives, but there is little observational corroboration of these behaviors in situ. We used a long-term dataset of underwater observations to quantify the fine-scale habitat use and behavior of a shallow estuarine fish community. We asked, "Within species, how does behavior vary with habitat context and developmental stage?" and "Do species partition habitats in space and time?" We found that smaller fish occupied shallower depths where predators were less abundant; smaller fish schooled in larger groups; pelagic fish schooled in larger groups in deeper water; demersal fish schooled in larger groups when occupying the water column; and species partitioned habitats by depth and season. Additionally, smaller fish were proportionally less abundant along deep shorelines created by intertidal armoring. Overall, habitat use was suggestive of nursery functions, including ontogenetic habitat shifts, provision of predator refuge, and appropriate food/predation risk tradeoffs. Additionally, fish behaved in a manner consistent with adaptive decision-making to avoid predation, and time and space may be important axes on which transient juveniles partition habitats. Some nursery functions

appeared to be mediated by a shallow depth gradient, which may be compromised by shoreline infrastructure and rising sea levels along built shorelines.

Introduction

Ecology and conservation are founded on natural history. To guide management and research, we must understand "how and where [organisms] live, and the biotic and abiotic interactions that link them to communities and ecosystems" (Tewksbury et al. 2014). In fish, this understanding is often incomplete because their behavior is difficult to observe in situ (Able 2016). Two consequences of this knowledge gap are (1) we recognize that nearshore waters provide nursery functions for fish (Beck et al. 2001), but have an incomplete understanding of fine-scale processes and habitat features that promote juvenile fitness (Sheaves et al. 2015), and (2) studies in controlled settings suggest that context-dependent behaviors are essential for fish to balance predation avoidance with other life history objectives (e.g., Hoare et al. 2004), but there are few in situ observations to corroborate these behaviors occurring in nature. Behavioral linkages between fish and their shallow habitats are important to understand because shallow areas have been modified globally by anthropogenic activities (Doody 2004, Bulleri & Chapman 2010, Temmerman et al. 2013) and their ecological functions cascade to connected systems (Sheaves et al. 2015). Thus, we can inform the conservation of aquatic ecosystems and basic fish ecology by understanding the natural history of nearshore communities.

Nearshore ecosystems provide nursery functions to fish. Ecologists have long recognized that shallow waters are often densely inhabited by juvenile fish, highly productive, and low in predator densities (Beck et al. 2001). Building on these observations, nursery habitats were conceptualized as areas that contributed substantial numbers of juveniles to adult populations and were evaluated by their output of juvenile biomass (Beck et al. 2001, Dahlgren et al. 2006). However, this model was criticized because it did not account for dynamics of habitat use and the functions that support them (Sheaves et al. 2006). A recent, more sophisticated nursery concept has shifted to a process-based perspective and included habitat functions such as predictable ontogenetic habitat shifts, appropriate food/predation tradeoffs, and connectivity (Nagelkerken et al. 2015, Sheaves et al. 2015). That is, nurseries facilitate the survival of juveniles by providing access to resources or environments at appropriate stages. Following this framework, we can better understand how fish benefit from nearshore ecosystems by studying their fine-scale habitat use and behavior.

Nearshore fish communities are typically studied using physical capture (e.g., netting) rather than observing behavior directly. As a consequence, it is difficult to connect their fine-scale habitat use and behavior to basic ecological theory. First, the behavior of fish in nearshore waters may be driven by tradeoffs between predation risk and other life history objectives (Lima and Dill 1990). Microhabitat selection and schooling can reduce predation risk, but at potential cost. Shallower habitats are thought to offer relatively safe environments because larger aquatic predators are uncommon or ineffective in confined spaces (Paterson & Whitfield 2000), but these areas also limit the search space of foragers, and their prey fields (e.g., small invertebrates) may become less preferable as juveniles grow (e.g., Duffy et al. 2010). Likewise, structured areas offer camouflage and cover, but fish restricted to these areas may experience limited foraging (Werner et al. 1983). In a similar tradeoff, schooling reduces predation risk by diluting the probability of capture, increasing vigilance, and confusing predators (Pitcher & Parrish 1993), but increases competition for resources with conspecifics (Alexander 1974, Grand & Dill 1999, Hoare et al. 2004). Size is an additional determinate of predation risk that may mediate habitat selection and schooling because larger fish have fewer gape-limited predators and greater escape capabilities (Sogard 1997). Collectively, these factors may influence context-dependent behavior in nearshore communities because fish employ behaviors that minimize predation, while scaling these behaviors to balance safety with the benefits of other objectives (Lima & Dill 1990, Dill 1983, Hoare et al. 2004).

Next, nearshore fish communities may partition habitats in time and space. Compared to space, time is a less studied yet important axis on which consumers partition habitats (Kronfeld-Schor & Dayan 2003). In nearshore waters, juveniles are often transient (Nagelkerken et al. 2015) and species occupy variable depth distributions (e.g., Munsch et al. 2015b). Fish may thus reduce competition by minimizing overlap in time and space, but to understand this requires fine-scale knowledge of when and where they occur.

Here we used a long-term dataset of in situ observations to quantify the fine-scale habitat use and behavior of a shallow estuarine fish community. Our first, broader question was, “Within species, how does fish behavior vary with habitat context and the developmental stage of fish?” We addressed this question through a series of comparisons. First, we compared the size of fish to the depth at which they occurred. We hypothesized that smaller fish would occupy shallower depths because smaller fish are more vulnerable to predation (Sogard 1997) and shallow areas provide protection from predators (McIvor & Odum 1988, Paterson & Whitfield 2000). Given the anticipated relationship between fish depth and length, we also compared the size distribution of fish along shorelines with shallow habitat to shorelines where intertidal armoring (e.g., seawalls, riprap) eliminated shallow waters directly adjacent to shore. We hypothesized that small fish would be proportionally more abundant along shores with low-gradient, shallow habitat. Second, we compared the size of fish groups to the length of fish in these groups. We hypothesized that smaller, more vulnerable fish would occur in larger groups because (1) schooling reduces risk of predation (Pitcher & Parrish 1993) and (2) for some species, smaller individuals are most abundant and fish school with conspecifics of similar size (Hoare et al. 2000). Third, we compared the group size of water column-using fish to water depth. We hypothesized that these fish would occur in larger groups when they were in deeper waters because (1) deeper waters did not provide spatial refuge from larger predators and deeper waters provided predators vantage points to detect backlit fish in the water column; and (2) school size is spatially limited in shallow areas. Finally, we compared the school size of demersal fish to the portion of the water column they occupied. We hypothesized that these fish would occur in larger groups when they were away from camouflaging substrate and algae on the bottom and presumably more conspicuous to predators. Our second, more specific question was, “How do species partition habitats in space and time?” We described spatiotemporal habitat partitioning by examining how the composition of the fish assemblage varied by depth and month.

Methods

Study system

Fish were observed in nearshore waters of Puget Sound, WA (USA), a 31,440 km^2 fjordal estuary with cold temperate waters. The bottom structure of shallow areas is comprised of mixed sediments, including sand, gravel, and large rocks. In addition, seawalls and riprap (angular boulders) are commonly used as shoreline armoring in Puget Sound, especially around urban centers. Brown, green, and red macroalgae are common on bottom substrates. The middle and top of the water column lacks structure, with the exception of beds of bull kelp (*Nereocystis luetkeana*) buoyed by pneumatocysts. Pilings that support piers are also common along shore and add structure to the water column; however we excluded observations of fish under piers in this analysis because pier shading can influence fish behavior (e.g., Able et al. 2013, Munsch et al. 2014).

Abundant fish in the nearshore waters of Puget Sound include surfperches (family Embiotocidae), juvenile Pacific salmon (*Oncorhynchus* spp.), and forage fish (e.g., Pacific herring [*Clupea pallasii*], surf smelt [*Hypomesus pretiosus*]), which we refer to in functional groupings (Table 2) based on similarities in morphology, life history, and habitat use. These fish primarily consume small invertebrates and are potential prey for larger fish, marine mammals, and birds (Buchanan 2006, Duffy & Beauchamp 2008, Lance et al. 2012, Munsch et al. 2015a). They are mobile and in some cases migratory; thus, it is unlikely to observe the same individuals in replicate surveys. The salmon were almost entirely age-0 transients migrating through the estuary to marine habitats. Puget Sound is also inhabited by demersal predatory fish such as lingcod (*Ophiodon elongates*) and larger sculpins (family Cottidae) that utilize relatively deep nearshore waters (Toft et al. 2007, 2013, Munsch et al. 2014, 2015b). In addition, larger life-stages of salmonids (e.g., cutthroat trout [*Oncorhynchus clarkia*], Chinook salmon [*O. tshawytscha*]) are the primary predatory fish in the water column.

Surveys

We assembled a long-term dataset of underwater fish surveys to quantify fine-scale habitat use and behavior of the nearshore fish community (original studies: Southard et al. 2006, Toft et al. 2005, 2007, 2009, 2013, Munsch et al. 2014, 2015b). Snorkel surveys occurred between 2003 and 2013 at 20 sites, and scuba surveys occurred in 2012 at six sites (Fig. 1). Snorkel and scuba surveys were conducted by observers at the surface and bottom of the water column, respectively. A total of 817 snorkel and 103 scuba surveys took place April – August to coincide with peak fish presence. Surveys occurred throughout daylight hours, ranging from sunrise to late afternoon (earliest: 5:15 AM, latest: 7:40 PM).

Surveys followed the same general protocol with minor variations tailored to the original studies. First, observers would swim to a starting position in the water and measure underwater visibility. Surveys only occurred when visibility exceeded 2.5 m to maximize the accuracy of observations and minimize effects of observers on fish behavior (Toft et al. 2007). Next, observers recorded the depth of the water directly below them using a weighted measuring tape. Then, observers surveyed fish while swimming a transect parallel to shore. Snorkel transects ranged from 26 – 75 m in length and were swum in water 2.25 ± 1.04 m (mean ± sd) deep. Scuba transects were 30 m in length and were swum in water 3.22 ± 0.75 m (mean ± sd) deep. Surveys were often conducted at predetermined distances from shore (typically 3 and 10 m), and water depths thus varied by tidal height and bottom slope.

Observers quantified the fine-scale behavior and habitat use of fish. The instant fish were encountered, observers recorded the species or finest identifiable taxon of the fish, the visually estimated length of the fish to the nearest 2.5 cm, the number of individuals in the group, and the water column position of the fish. That is, group size and water column position are described as instantaneous metrics of behavior. Group size was estimated in especially large schools by extrapolating counts from a portion of the school and rounding (e.g., to nearest 100). Observers would then continue swimming until the next fish encounter. This set of data was referred to as an observation and was the unit of replication (n) for our study. When fish were not identifiable to the species level, names of lower taxonomic resolution were used to describe their identity (e.g., "unidentified salmon", "chum/pink salmon"). If there was a range of fish lengths in a school, mean length was recorded. For snorkel surveys, water column positions were described in thirds: top, middle, and bottom. Scuba surveys targeted fish near the bottom of the water column and scuba divers described the water column position of fish as greater than 1 m from the bottom, less than 1 m from the bottom, or touching the bottom. Fish depths were estimated for snorkel surveys by multiplying the depth of the water by 1/6, 1/2, and 5/6 for observations at the top, middle, and bottom of the water column, respectively (i.e., it was assumed that fish were centered in the portion of the water column described). Fish depths for scuba surveys were estimated by calculating the water depth / 2, water depth – 0.5 m, and taking the entire water depth, for observations greater than 1 m, less than 1 m, and at the bottom, respectively.

Analysis

Our analysis focused on a subset of the nearshore fish community. The focal community was defined as mid-trophic level species that occupied the water column and were observed by snorkelers a minimum of 35 times. This included the vast majority of all fish observed, and the most abundant taxa excluded were flatfish (order Pleuronectiformes), gunnels (family Pholidae), and sculpin. These taxa rarely occupied the water column and often associated with substrata or algae and may have been under-counted by visual surveys. For some analyses, we included only species that used habitats similarly based on the portion of the water column that they occupied. We termed fish observed at the top of the water column in less than 5% of snorkel observations as "demersal" and refer to the remainder as "water column-using." Analysis occurred in R version 3.2.2 using the lme4, Matching, merTools, and Vegan packages (Bates et al. 2015, Oksanen et al. 2015, R Core Team 2015, Sekhon 2015, Knowles & Frederick 2016).

We examined habitat partitioning in time and space by visualizing the fish community via nonmetric multidimensional scaling (NMDS). The NMDS was constructed using a Bray-Curtis dissimilarity matrix describing total density estimates (fish counts / [transect length x horizontal visibility]) for each combination of species, month, and 1 m estimated depth bin. We used snorkel data only for this NMDS because snorkel surveys were replicated most, and because the snorkelers' field of view was more conducive to surveying the entire water column.

Behavioral comparisons were made using linear mixed effects models and generalized linear mixed models (Zuur et al. 2009). The variables in these models are defined in Table 1. Species were treated as random effects so that models indicated within-species trends. Site was also treated as a random effect in models because the slope of the bottom varied among sites, which may have influenced the depth distribution of fish. Models examining the response variable of group size always included the fixed effect of fish length because we anticipated a relationship between fish length and group size. When making comparisons of school size among water column positions (but not for fish depth comparisons), scuba observations of fish at the bottom and <1 m from the bottom were binned into one category because the focal community was rarely observed in contact with the bottom. A linear mixed effects model with a normal distribution and identity link was used for models describing the response variable of fish depth. A generalized linear mixed model with a negative binomial distribution and log-link function was used for models describing the response variable of group size. We attempted to build random slope and intercept models for each comparison. If random slope and intercept models did not converge, we constructed random intercept models. As visual aids, we plotted models fit individually for each species using the same parameters as the community models except omitting the species terms. In rare cases, these models would not converge and we plotted models fit omitting the random parameters. We analyzed snorkel and scuba data separately because depth estimations of fish may not be quantitatively comparable between these methods.

We examined the influence of armoring on the size distribution of fish in the shallowest available habitats. We compared fish at armored sites where intertidal seawalls and riprap created deep habitat adjacent to shore to fish at sites with low-gradient, shallow waters. One of the low-gradient, shallow sites was an artificial “habitat bench” that created sloping habitat adjacent to an urban shoreline (further details: Toft et al. 2013). Of observations along armored shorelines, we only included surveys that took place 3 m from shore. Of observations along unarmored shorelines, we only included observations that took place in water equal to or shallower than the mean depth of surveys 3 m from shore at armored sites (2.39 m). We only included observations at high tide because shoreline waters of armored sites were deepest at high tides. Juvenile salmon, which were only observed by snorkelers, were selected for this comparison because they were known to occupy waters directly adjacent to shore, including areas modified by shoreline infrastructure (Toft et al. 2007).

As a supplement, we qualitatively compared the depth distribution of piscivores to that of the focal community to examine whether predators generally occupied greater depths. Piscivores were uncommon and therefore coarsely defined as individuals ≥15 cm in length and of species that consume fish. We chose this length because cutthroat trout in Puget Sound begin feeding on the focal community at 15 cm (Duffy & Beauchamp 2008). To our knowledge, this is the best information available on the size at which a predator feeds on species of the focal community. We regard this examination as supplemental because piscivores constituted a heterogeneous grouping of fish species, preventing a rigorous quantitative analysis of their depth distribution. While acknowledging this limitation, the data were included to provide evidence that shallow waters were inhabited by fewer predators.

Results

Description of the fish community

The focal fish community consisted of thirteen species that included 99.7% and 98.9% of all fish observed by snorkel and scuba divers, respectively (Table 2, Fig. 2). Fish occasionally swam in schools that were quite large, but the majority of groups were relatively small (quartiles: 1, 2, and 9 individuals [snorkel], 1, 2, and 12 individuals [scuba]). On rare occasions, fish occurred in groups exceeding 1000 individuals (0.57% of observations), and these schools are plotted as 1000s in figures so that trends among the majority of the data are more interpretable. Forage fish and salmon occurred mostly in the upper part of the water column and were categorized as water column-using. They swam constantly, often in relatively large schools. Surfperch often occurred near the bottom next to substrate or macroalgae and were categorized as demersal. They swam in punctuated movements and, except for shiner perch, occurred in small schools. Tubesnout were categorized as demersal, occasionally occurred in relatively large groups, and swam in punctuated movements. Stickleback were categorized as water column-using, occurred in relatively small schools, and swam in punctuated movements. In addition to these fish, 16 species of piscivores were present. The piscivorous status for most of these fish could be corroborated by literature on their diets or the diets of closely related species (greenling: Reisewitz, Estes, & Simenstad 2006); lingcod: Beaudreau and Essington 2007; ratfish and sculpin: Reum and Essington 2008; rockfish: Brodeur, Lorz, & Pearcy 1987; salmonids: Duffy and Beauchamp 2010). Piscivores were distributed in deep waters relative to the focal community (Supplemental Figure 1, Supplemental Table 1).

Context-Dependent Behavior and Habitat Partitioning

Snorkel observations indicated that larger fish occupied significantly greater depths (Table 3, Fig. 3). A positive or neutral trend of fish size relative to depth was detected in all species except stickleback and tubesnout, and the most positive trends occurred in salmon and surfperch. Scuba divers also observed larger fish with increasing depths, but this was not statistically significant (Table 3, Fig. 3). As observed by scuba divers, larger surfperch tended to occupy greater depths, but larger tubesnout did not.

The size distribution of juvenile salmon was significantly different along armored shorelines compared to shorelines with low-gradient, shallow waters (Fig. 4; bootstrap Kolmogorov-Smirnov test, $p < 2.22$ E-16). At sites with low-gradient shallow waters, the size distribution was skewed toward smaller fish whereas larger fish were proportionally more abundant along armored shorelines.

Snorkel and scuba observations indicated that larger individuals occurred in significantly smaller group sizes (Table 3, Fig. 5). This trend was consistent for most species, except coho salmon and pink salmon observed by snorkelers, and kelp perch and pile perch observed by scuba divers. A decline in school size with increasing fish size was most apparent in species that occurred in a range of sizes and had large maximum school sizes.

Snorkel observations of water column-using species indicated that significantly larger schools of fish occurred in deeper waters (Table 3, Fig. 6). We observed this trend for most species, excluding surf smelt and stickleback. Salmon in particular were often observed in shallow waters and exhibited a strong positive relationship between school size and water depth.

Snorkel and scuba observations of demersal species indicated that these fish occurred in significantly larger schools when they were away from the bottom of the water column (Table 3, Fig. 7). This trend was consistent among all species except pile perch, and was most apparent in shiner perch and tubesnout.

Fish partitioned nearshore waters in space and time. There was separation of habitats among species by depth and month (Fig. 2). Surface waters were occupied predominantly by chum and pink salmon in April and May, and by Chinook salmon, coho salmon, forage fish, and stickleback in June and July. There was little temporal variation in abundances of surfperch and tubesnout, which occupied greater depths. Thus, there was seasonal variation in fish assemblage composition near the surface, but the assemblage remained stratified by depth.

Discussion

We used a long-term dataset of in situ observations to quantify in unprecedented detail the fine-scale habitat use and context-dependent behavior of a nearshore fish community. Our major findings were documentation of (1) fine-scale patterns of habitat use suggestive of process-based nursery functions directly adjacent to shore, (2) context-dependent behaviors consistent with decisions to balance safety from predation with other life-history objectives, and (3) seasonality and fine-scale depth as simultaneous axes of habitat partitioning. These findings have management implications for protecting process-based nursery functions in shallow areas that have only recently been appreciated (Sheaves et al. 2015). They also fill empirical gaps in our understanding of in situ fish ecology. Most fundamentally, our study underscores the limited knowledge about complexity in aquatic ecosystems, including systems facing considerable anthropogenic threats. Thus, it supports current arguments for a renewed focus on natural history in these systems that will ultimately benefit ecology and conservation (Tewksbury et al. 2014, Able 2016).

Our observation that larger fish utilized deeper habitats suggested that shallow sloping areas supported a continuum of habitat functions that benefited different fish sizes. Animals often utilize safe habitats to the extent that avoiding predation is in balance with other life history objectives (Lima and Dill 1990). Many studies have found predation risk in nearshore habitats increases with increasing depth (e.g., McIvor and Odum 1988, Linehan et al. 2001, Ruiz et al. 1993, but see Baker & Sheaves 2007) and, increasing fish length with depth (Macpherson & Duarte 1991, Ruiz et al. 1993). This is thought to drive Heincke's Law (developed from Heincke 1913) whereby smaller fish occupy shallower waters because they are more vulnerable to predation (Sogard 1997, Linehan et al. 2001), and was consistent with our observations of few potential piscivores in relatively shallow water. In addition to lowering mortality, shallow areas may also benefit fish through sublethal effects of protected areas. For example, tethering experiments found no relationship between depth and predation despite their focal fish aggregating in shallow areas (Baker & Sheaves 2007). The authors discussed that fish may utilize shallower areas so that they can allocate less time and energy into antipredator behaviors (e.g., evasion, vigilance) rather than necessarily to decrease probability of mortality. We observed ontogenetic habitat shifts to greater depths that may have allowed juveniles to balance the benefits of feeding with the costs of predation risk (Sheaves et al. 2015): small juveniles may benefit most from the lack of predators at shallow depths whereas larger, less vulnerable juveniles may trade this benefit for larger foraging areas and different prey fields in deeper waters. This is consistent with the development of Chinook salmon that move from nearshore to offshore habitats and shift prey from insects and amphipods to crab larvae and fish (Duffy et al. 2010). We also observed that stickleback, which were relatively small as adults, utilized shallower areas at all sizes, suggesting that shallow areas may benefit smaller species throughout their life histories. Thus, shallow sloping waters were a potentially critical component of nearshore habitats, an important consideration given losses of this habitat type in developed landscapes.

Ontogenetic habitat shifts occurred close to shore and shoreline armoring may compromise this nursery function. A relationship between fish length and depth was only detected by snorkelers, who were able to observe fish closer to shore than scuba divers. Thus, a major portion of ontogenetic habitat shifts may occur in the shallowest waters directly adjacent to shore. In addition, shoreline armoring appeared to alter the fish distribution in the shallowest available habitats. Smaller salmon were proportionally more abundant along shorelines with shallow habitat compared to the deeper waters along armored shorelines, suggesting that smaller juveniles select for shallower habitats when they are available. Armoring may compromise nursery functions by forcing smaller juveniles to occupy deeper habitats that are dangerous or offer inappropriate prey sources, i.e., by disrupting ontogenetic habitat shifts and providing suboptimal food/predation tradeoffs (Sheaves et al. 2015). Managers may therefore conserve nursery functions of shallow ecosystems by protecting shallow sloping areas adjacent to shore.

Schooling may further mediate tradeoffs between predation risk and other objectives. We observed darker-colored demersal fish schooling in larger groups when they occurred away from camouflage at the bottom of the water column. Visual piscivores typically rely on contrast to detect prey (Breck 1993), and schooling may have allowed demersal fish to offset predation risk when they were away from camouflaging backdrops. We also observed that smaller fish occurred in larger schools, and schooling may primarily benefit smaller, more vulnerable fish through diluting risk of capture, increasing predator vigilance, or confusing predators (Sogard 1997; Pitcher and Parrish

1993). We must also consider that this trend may have been influenced by the size distribution of species because fish tend to school with fish of the same size (Hoare et al. 2000). Such an influence would manifest most in chum and pink salmon: small individuals were probably most abundant because these species immigrate over a short period of time, grow rapidly, and suffer high mortality (Quinn 2005). However, smaller tubesnout and surfperch in particular were comparatively rare and schooled in large groups, consistent with these fish schooling to offset vulnerability to predators. Overall, our observations were consistent with schooling as a context-dependent behavior that mediates predation risk.

Schooling may allow fish to maximize habitat benefits. Water column-using fish formed larger schools in deeper water, potentially allowing them to occupy patches where safety was lower but foraging potential was greater. For example, schooling may facilitate forays by planktivorous forage fish (Pentilla 2007) or juvenile salmon (Munsch et al. 2015a) into deeper waters where plankton are more abundant and foraging spaces are larger. Others have demonstrated an analogous scenario in aquaria whereby fish in larger schools forgo predator refuge to occupy exposed foraging patches (Magurran & Pitcher 1983). We must also consider that relationships between depth and school size may be influenced by spatial constraints of shallower water, in which case fish may directly trade off the safety of shallow waters for that of larger groups. Demersal fish may have also benefited from schooling if it allows them to mitigate risk when locating epibenthic prey patches from more effective vantage points in the water column, and because group sensing allows fish to locate resources more quickly (Berdahl et al. 2013). These fish may school when they risk predator detection by searching for prey from the water column, and then disperse to minimize competition when feeding on epibenthos, similar to the behavior of fish exposed to variable predator cues and food in aquaria (Hoare et al. 2004). Overall, schooling appeared to be a context-dependent antipredator behavior, a concept that has received considerable research attention yet has rarely been examined in situ.

Schooling is typically investigated in pelagic environments, but this behavior may be similarly beneficial in shallow waters. Theoretically, an optimum school size exists for fish in a given scenario that balances the costs and benefits of grouping (Rieucau et al. 2015b). However, in massive pelagic schools, optimum school sizes are probably rarely realized due to complex dynamics of splitting and joining groups, and because substantial sensory capabilities of fish would be required to determine the exact size of larger groups (Fernö et al. 1996, Rieucau et al. 2015b). In addition, an individual or undersized school of fish may behave optimally by joining another group regardless of its size; thus, groups may increase to suboptimal sizes as others join to their own benefit (sensu Sibly 1983). This choice is presumably most constrained in environments where conspecific encounters are rare and unpredictable, creating a greater expected cost for an individual to forgo joining a group of any size. We hypothesize that, in contrast to pelagic waters, relatively linear nearshore waters benefit fish through predictable conspecific encounters that allow fish greater choice over their group sizes, ultimately resulting in maximal habitat use. Results from our focal fish community support this hypothesis: forage fish were the most pelagic of the functional groups and formed the largest schools. Thus, connectivity may be important in shallow habitats to facilitate predictable conspecific encounters that enable fish to school in more optimal school sizes.

We observed a spatiotemporal structure to the fish community that was suggestive of broader ecological concepts. The first concept was time and space as simultaneous axes of habitat partitioning. Time is an important axis of resource partitioning that may allow species that use the same habitats to coexist by minimizing competition (Kronfeld-Schor and Dayan 2003). For example, chum and pink salmon may minimize competition with other species that forage in the water column by inhabiting nearshore systems earlier in the year. Temporal habitat partitioning in nearshore waters may be widespread given that juveniles often use habitats temporarily as they develop (Nagelkerken et al. 2015). One management application of spatiotemporal habitat partitioning is that artificial propagation programs may aim to release juvenile fish at times that minimize overlap with competing species. Furthermore, temporal habitat partitioning may enhance the stability of water column-using fish as a prey source. The water column-using fish group was present longer and had more stable abundances than the individual, transient species that comprised it (sensu Schindler et al. 2015). Thus, temporal habitat partitioning may benefit predators through lower variation in overall prey availability, and managers may conserve these benefits by protecting species that partition similar habitats in time as a unit. An additional ecological concept was that these fish may be adapted to minimize different parts of the predation process (sensu Heithaus & Dill 2006). Demersal species were slow, deep-bodied, and colored similar to substrate and algae backdrops. Species that occupied the water column were faster, spindle-shaped, and silvery. Thus, demersal species may primarily be adapted to minimize predator detection while species that used the water column may be more adapted to evade capture. Overall, there was evidence that the fine-scale depth distribution and seasonality of the nearshore community were potentially important natural history adaptations.

Limitations of our study should be considered in the interpretation of our findings. First, we conducted an analysis that combined observational studies and did not measure predation risk directly. We infer factors that influence predation risk from other studies (e.g., Sogard 1997, McIvor and Odum 1988), and our work would benefit from further manipulative approaches that directly quantify how behaviors mediate cost/benefit tradeoffs. We also inferred piscivory from fish length using a study of diets in one predatory species (Duffy & Beauchamp 2008), yet length-piscivory relationships are likely to vary among species. Further, smaller fish including species not considered major piscivores may exert great predation pressure on juvenile fish if these predators are abundant (Baker & Sheaves 2009). Thus, the focal community and their predators may overlap to a greater extent than we present here, and our study would have benefited from a greater understanding of the diets of all species present. Next, our study was conducted in an urbanized setting. Many sites had been modified by shoreline development and their shallow areas were truncated by shoreline armoring. Consequently, our study may underestimate the magnitude of ontogenetic habitat shifts from shallow to deep waters because fish sometimes lacked accesses to shallow areas. In addition, the animal assemblage probably differed from historical conditions. Predator encounters influence the decision-making of consumers (Lima and Dill 1990) and potential changes to the predator assemblage could have affected the behaviors we observed.. In addition, we surveyed fish only during daylight hours, and diel cycles are well known to influence the behavior of fish, including sizes of schools in shallow waters (Rieucau et al. 2015a).

Finally, we estimated some measurements (e.g., fish length, school size), thus trends in this study are more appropriately interpreted in relative rather than absolute terms. These factors are potential avenues for further research, but beyond the scope of our opportunistic study.

In conclusion, fish behaved in ways that would maximize habitat use and avoid predation, and they partitioned shallow habitats in time and space. Juvenile behaviors were indicative of their use of shallow waters as nursery habitat, potentially reflecting the habitat's provision of predator refuge, ontogenetic habitat shifts, and appropriate food/predation risk tradeoffs (Beck et al. 2001, Sheaves et al. 2015). These functions may be diminished by changes to shallow ecosystems. It is of particular concern that shallow waters and their associated nursery functions (e.g., ontogenetic habitat shifts) are disappearing globally due to shoreline armoring (Bulleri and Chapman 2010) and coastal squeeze whereby rising sea levels encroach on built shorelines (Doody 2004). It is also concerning that the connectivity of shallow habitats and their associated benefits (e.g., access to appropriate habitats, frequent conspecific encounters) are threatened by habitat elimination and behavioral barriers such as shading from large piers (Able et al. 2013, Munsch et al. 2014, Ono and Simenstad 2014). However, some of the functions of degraded ecosystems can be repaired and the benefits of habitat improvements need not be limited to fish. For instance, conventional shoreline designs of impervious surfaces place society at risk because they are incompatible with a future of sea level rise. It is therefore advantageous for city planners to protect flood-prone areas by creating or restoring shallow ecosystems rather than armoring shorelines (Temmerman et al. 2013). Also, urban waterfronts can be designed that provide corridors of sloping shallow areas and reduce the shading impacts of piers without sacrificing waterfront utility to people (Toft et al. 2013, Cordell et al. In Press). Ultimately, by understanding the natural history of shallow water fish communities, we may identify and account for critical habitat functions in order to manage shoreline features that benefit fish and people.

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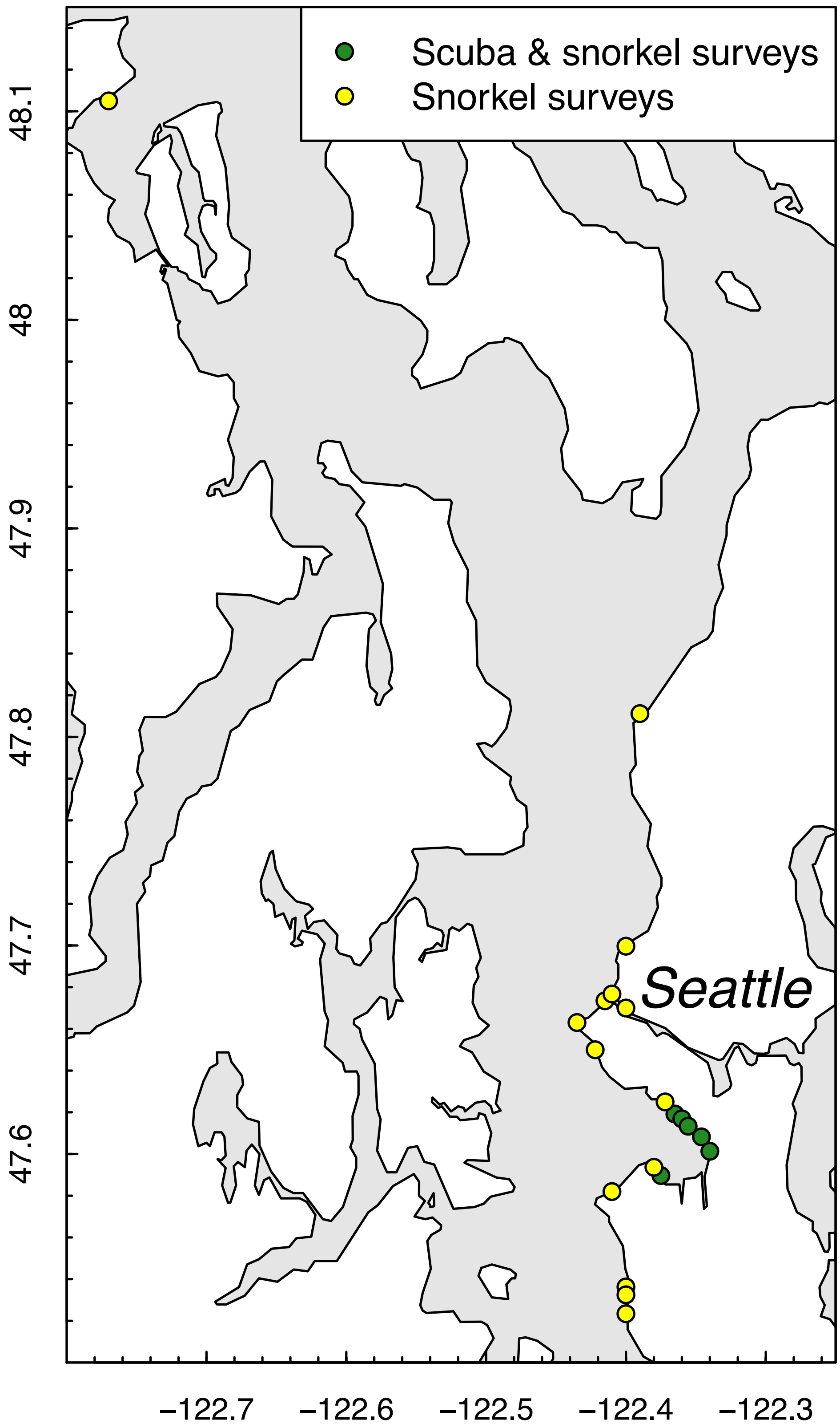


Figure 1. Map of study sites in Puget Sound, WA (USA). Green indicates sites surveyed by snorkelers and scuba divers. Yellow indicates sites surveyed by snorkelers only.

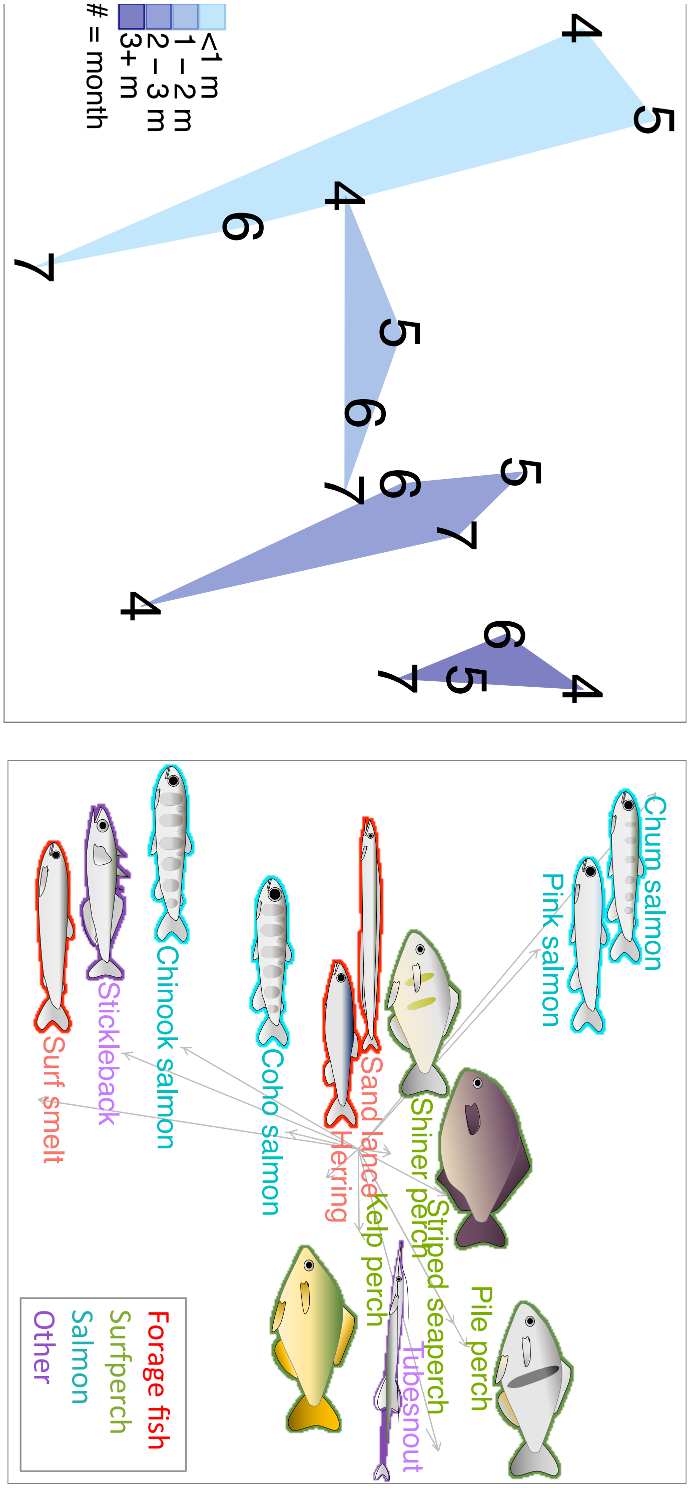


Figure 2. NMDS plots of the fish assemblage. Each point indicates a unique combination of depth bin and month of the year. Polygons are shaded to connect observations at the same depth observed over time. Vectors indicate increasing gradients of species densities in ordination space. The outline color of fish illustrations corresponds to the functional grouping of the fish (Table 2).

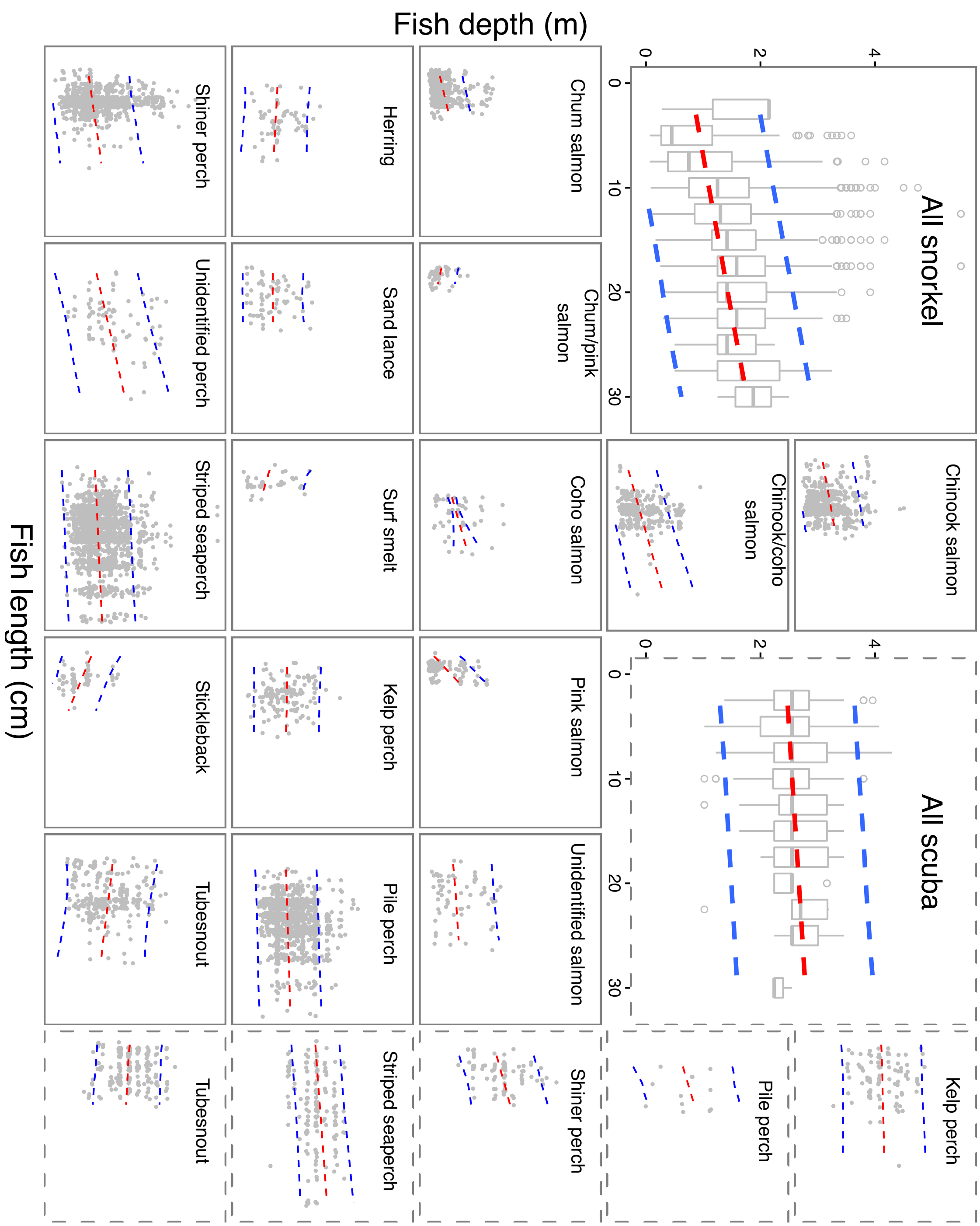


Figure 3. Fish depth vs. fish size as observed by snorkelers (solid panels) and scuba divers (dashed panels). Within observation method, panel axes are shown on the same scale. Upper and lower hinges: first and third quartiles; mid-line: median; whiskers: points within 1.5 × interquartile range; dots represent data outside of 1.5 × interquartile range. Red and blue lines indicate values predicted by models and 95% confidence intervals, respectively.

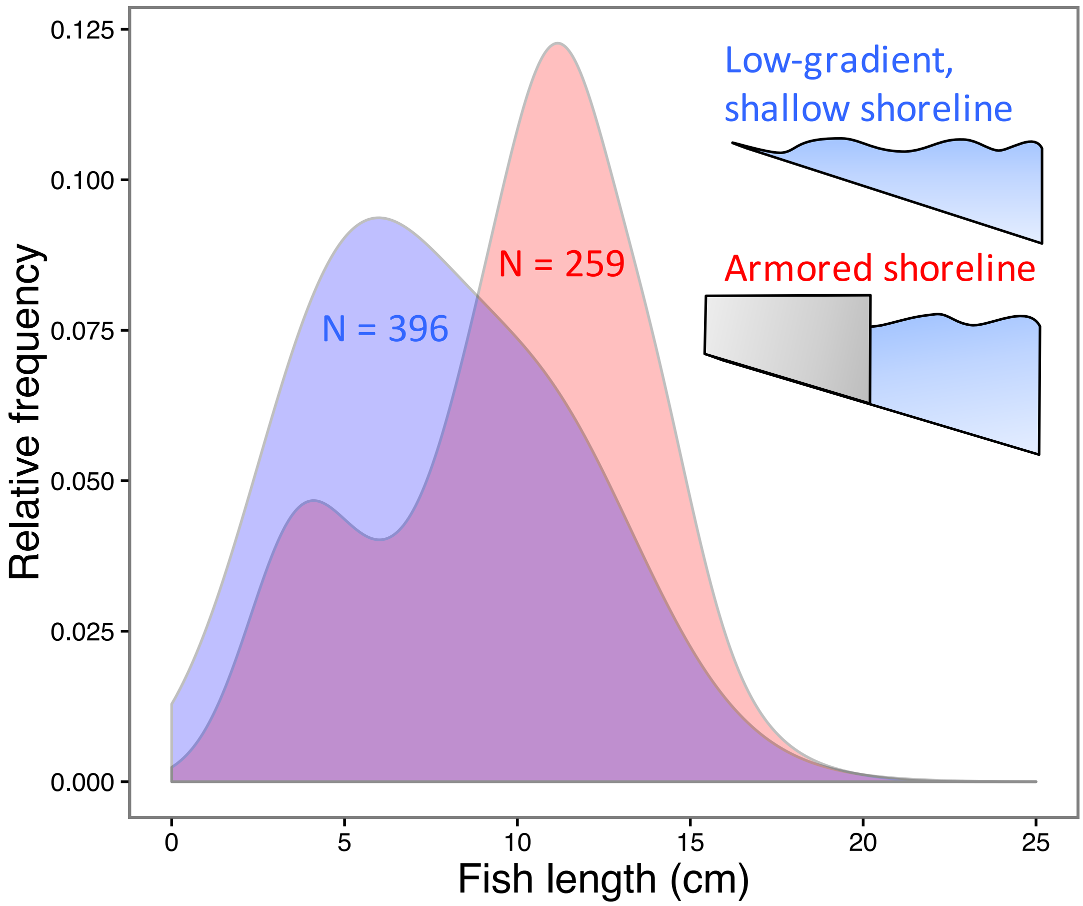


Figure 4. The size distribution of juvenile salmon compared between the shallowest available habitats in low-gradient, shallow shorelines and armored shorelines.

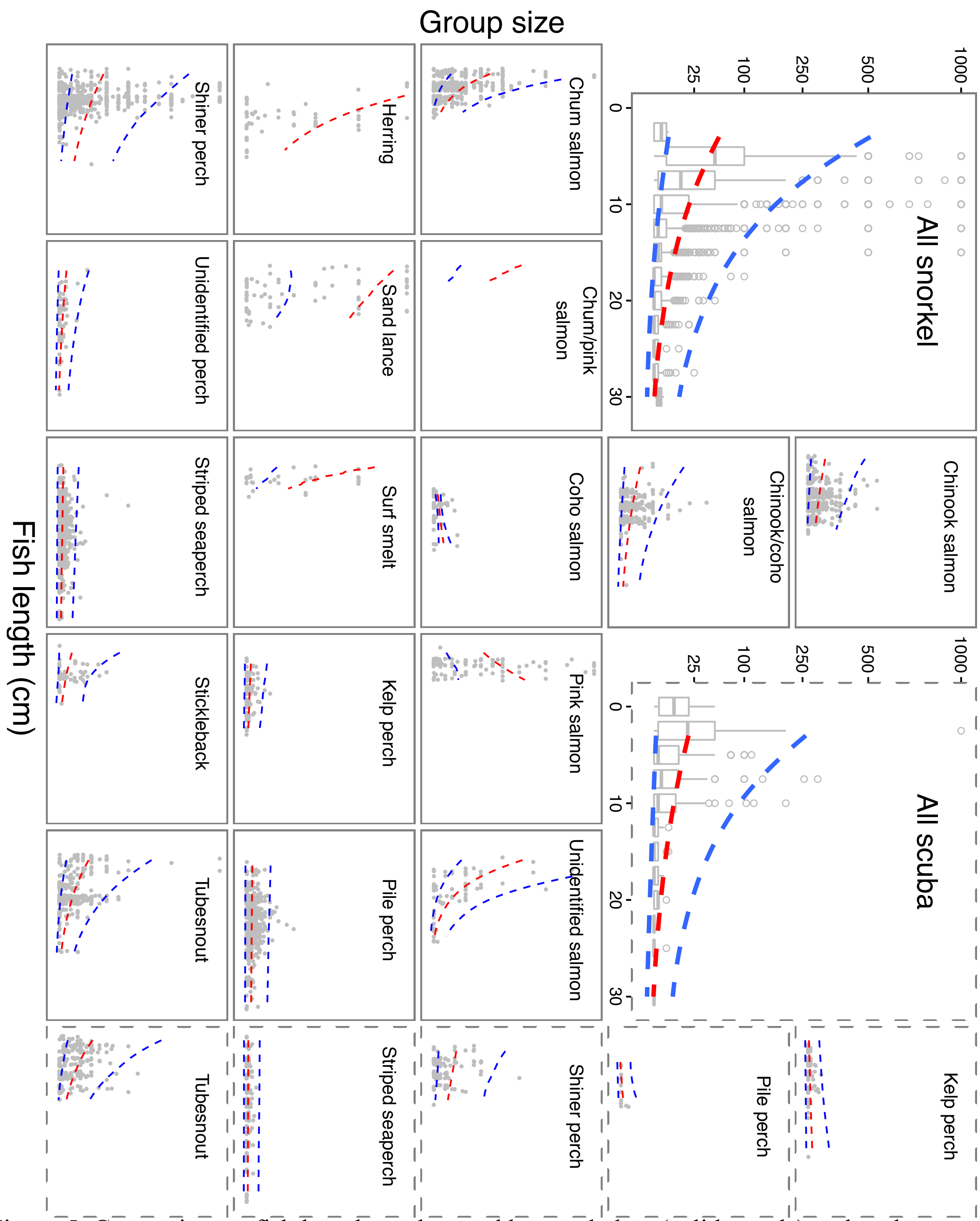


Figure 5. Group size vs. fish length as observed by snorkelers (solid panels) and scuba divers (dashed panels). Within observation method, panel axes are shown on the same scale. See Figure 3 for box plot and confidence interval definitions.

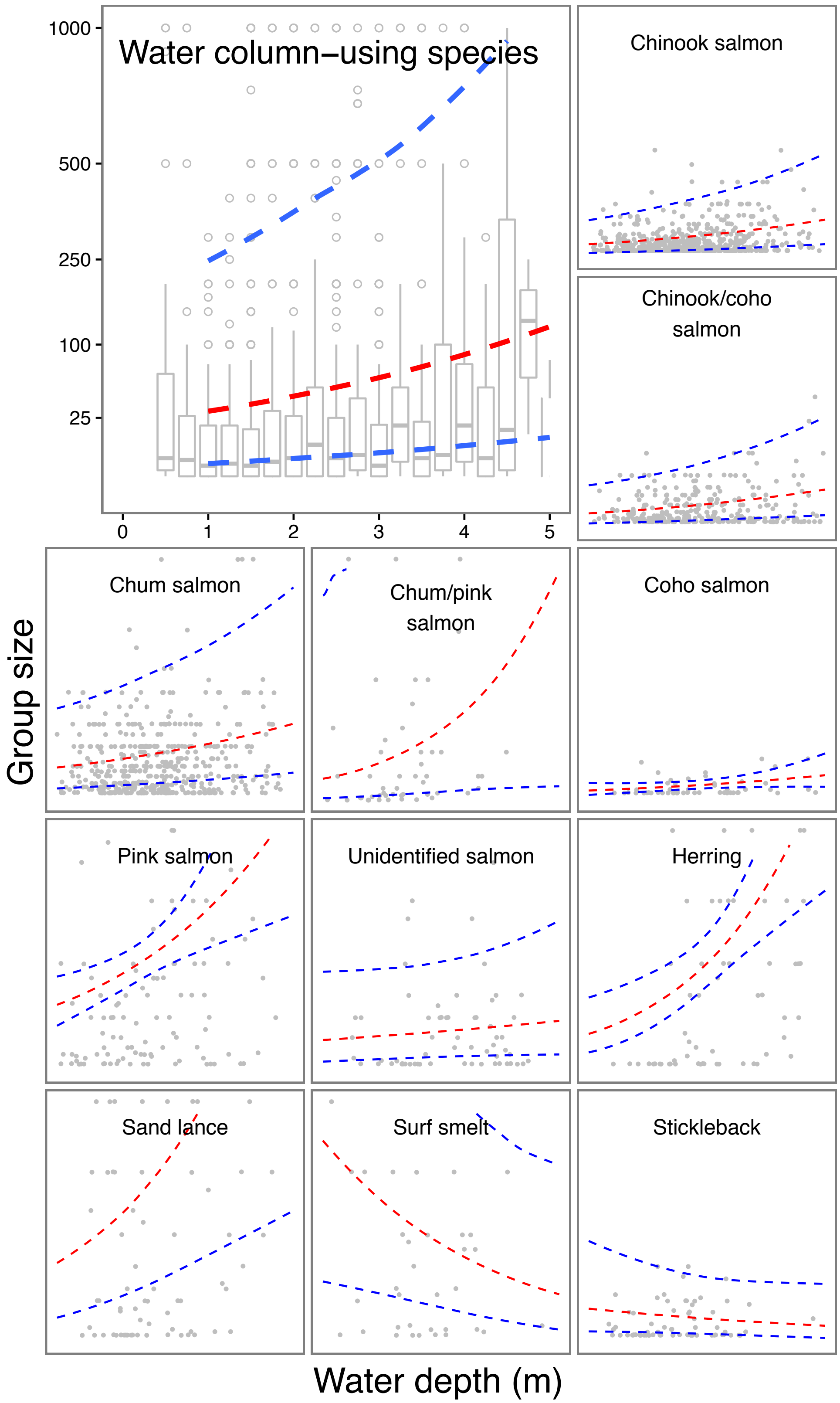


Figure 6. Group size vs. water depth of water column-using species as observed by snorkelers. Panel axes are shown on the same scale. See Figure 3 for box plot and confidence interval definitions.

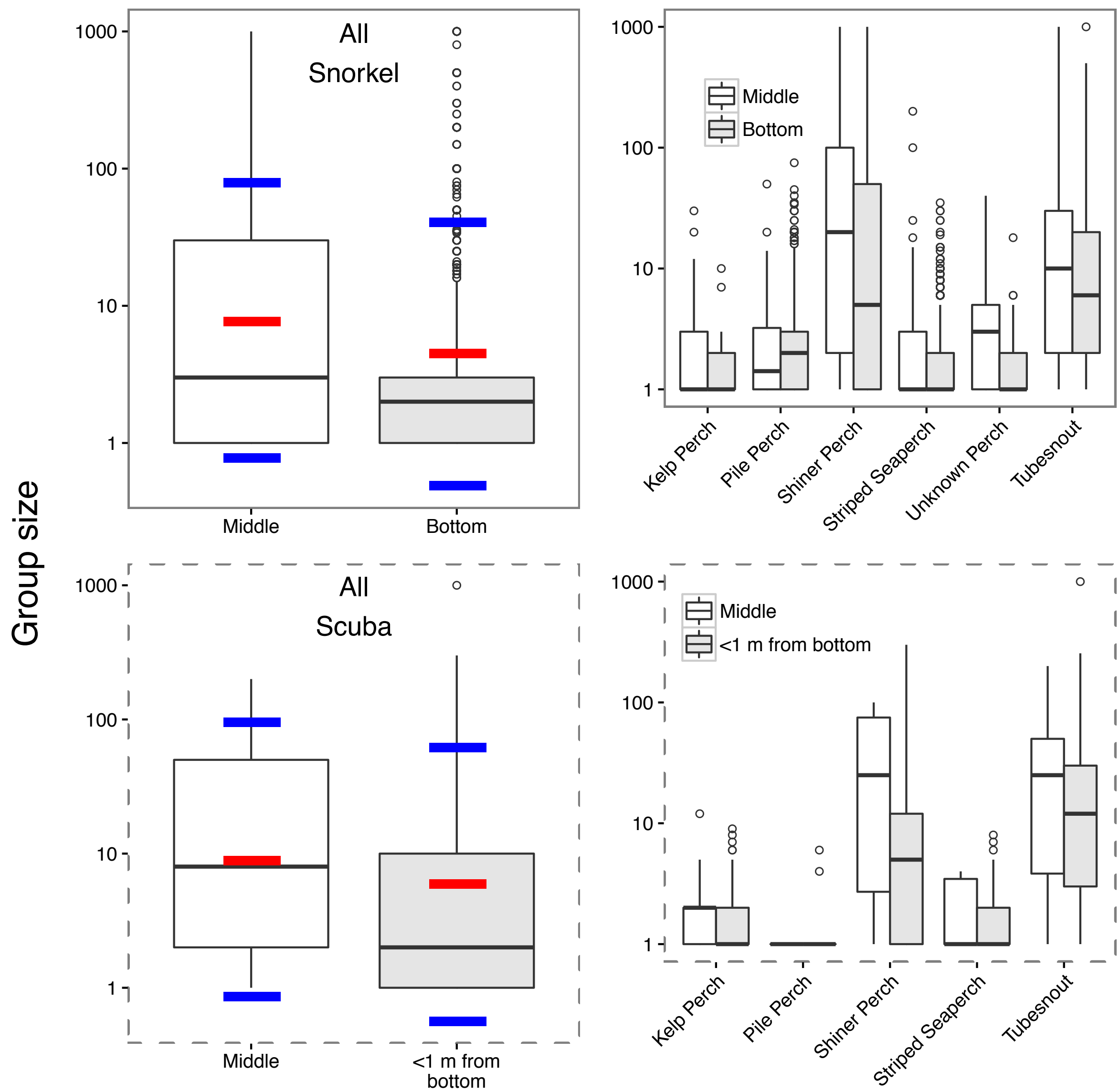
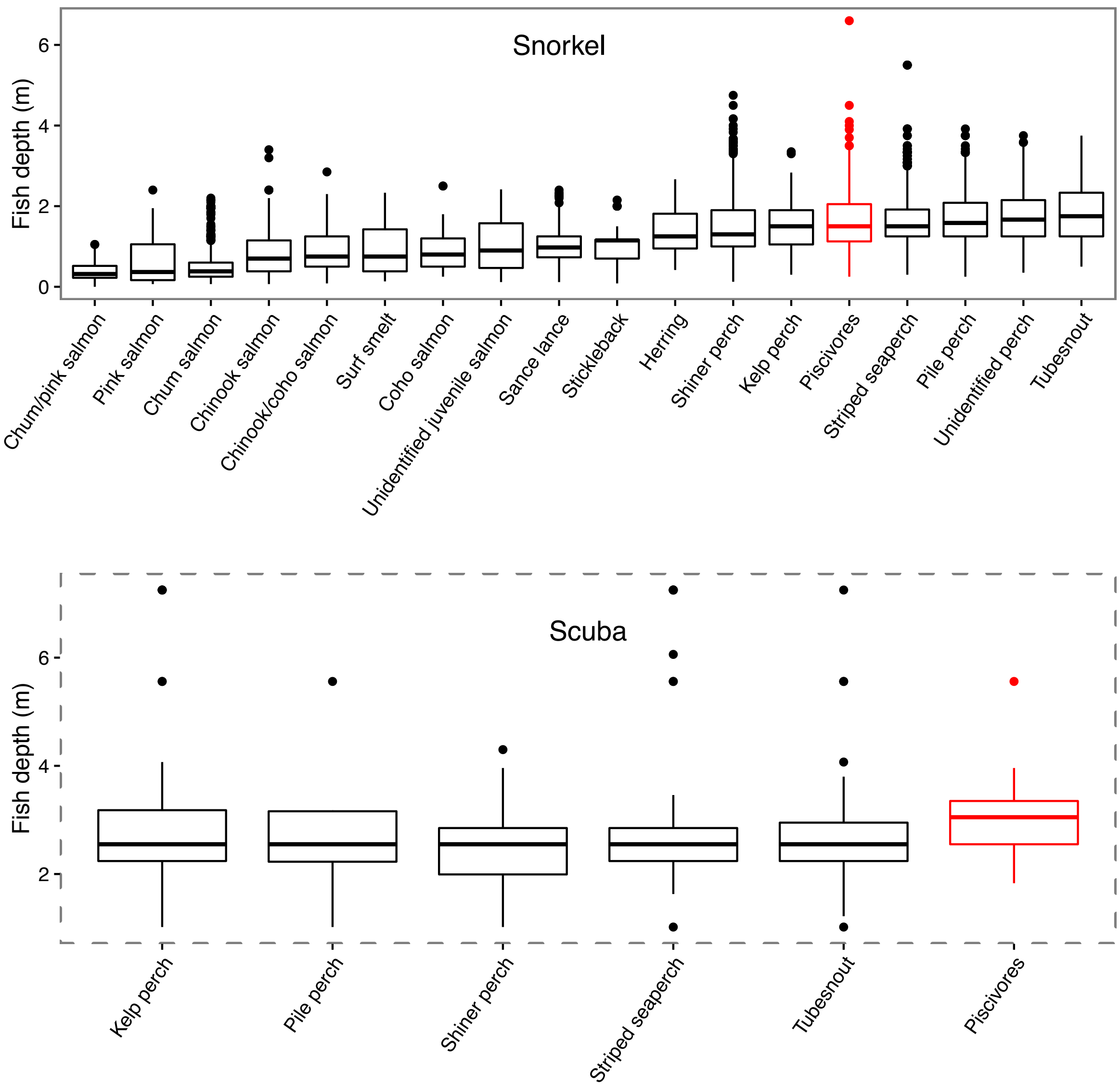


Figure 7. Group size vs. water column position for demersal species as observed by snorkelers (solid panels) and scuba divers (dashed panels). See Figure 3 for box plot and confidence interval definitions.



Supplemental Figure 1. Depth distributions of the focal community and piscivores. See Figure 3 for box plot definitions. Species and the piscivore grouping are ordered by median depth.

Table 1. Definitions of parameters used in linear models.

Variable	Definition	Type
Fish depth	Vertical distance between fish and surface	Numeric
Fish length	Distance between mouth and tail fork (salmonids) or caudal peduncle (non-salmonids)	Numeric
Group size	Number of fish swimming together	Numeric
Species	Finest identifiable taxon of fish	Categorical
Water column position	Vertical portion of habitat occupied	Categorical
Water depth	Vertical distance between surface and bottom	Numeric

Table 2. Observations (n) and total counts of fish species observed by snorkel and scuba divers, separated by functional group. Total counts are approximate because the sizes of large schools were estimated.

Method	Functional Group	Species	Scientific Name	Observations	Total Count
Snorkel	Salmon	Chinook salmon	*Oncorhynchus tshawytscha*	564	5106
		Chinook/coho salmon		309	4012
		Chum salmon	*Oncorhynchus keta*	479	25399
		Chum/pink salmon		52	12512
		Coho salmon	*Oncorhynchus kisutch*	52	230
		Pink salmon	*Oncorhynchus gorbuscha*	106	24611
		Unidentified juvenile salmon		62	3788
	Forage fish	Pacific herring	*Clupea pallasii*	61	27362
		Surf smelt	*Hypomesus pretiosus*	35	9768
		Sand lance	*Ammodytes hexapterus*	70	42757
	Surfperch	Kelp perch	*Brachyistius frenatus*	141	347
		Pile perch	*Rhacochilus vacca*	1169	4020
		Shiner perch	*Cymatogaster aggregata*	1121	142312
		Striped seaperch	*Embiotoca lateralis*	1925	4242
		Unknown perch		79	261
	Other	Three-spined stickleback	*Gasterosteus aculeatus*	73	893
		Tubesnout	*Aulorhynchus flavidus*	296	9349
Scuba	Surfperch	Kelp perch	*Brachyistius frenatus*	101	196
		Pile perch	*Rhacochilus vacca*	13	21
		Shiner perch	*Cymatogaster aggregata*	88	1941
		Striped seaperch	*Embiotoca lateralis*	171	281
	Other	Tubesnout	*Aulorhynchus flavidus*	227	7529

Table 3. Parameter estimates and summary statistics of linear models. Vertical bars indicate random slope parameters separating random terms (right) from their interacting fixed terms (left), otherwise random effects were treated as an intercepts only.

Response Variable	Method	Fish Group	Parameter	Estimate	SE	p	Random Effect
Fish depth	Snorkel	All	Intercept	0.772955	0.161139	3.99E-05	Length|species
			Fish length	0.032932	0.008184	0.000704	Length|site
Fish depth	Scuba	All	Intercept	2.39506	0.14086	4.28E-05	Length|species
			Fish length	0.01797	0.01513	0.306	Length|site
Group size	Snorkel	All	Intercept	4.48705	0.61696	3.52E-13	Length|species
			Fish length	-0.14803	0.03512	2.50E-05	Site
Group size	Scuba	All	Intercept	3.32411	1.0276	1.22E-03	Length|species
			Fish length	-0.11428	0.04484	0.0108	Site
Group size	Snorkel	Water column-using	Intercept	4.74119	0.49120	2E-16	Water depth|species
			Water depth	0.35854	0.08854	5.13E-05	Site
			Fish length	-0.19559	0.01739	2.00E-16	
Group size	Snorkel	Demersal	Intercept	2.455709	0.623607	8.22E-05	WCP|species
			WCP (baseline: bottom)	0.518641	0.172526	2.65E-03	Site
			Fish length	-0.032743	0.005381	1.16E-09	
Group size	Scuba	Demersal	Intercept	2.15032	0.07217	2.89E-03	WCP|species
			WCP (baseline: bottom)	0.38036	0.15526	0.0143	Site
			Fish length	-0.03614	0.02267	0.11096	

Supplemental Table 1. Observation counts of piscivores, defined as individuals that were >15 cm in length and of species likely to consume fish.

Species	Scientific Name	Snorkel Observations	Scuba Observations
Black rockfish	*Sebastes melanops*		5
Buffalo sculpin	*Enophrys bison*		5
Bull trout	*Salvelinus confluentus*	1	
Chinook salmon	*Oncorhynchus tshawytscha*	4	
Chinook/coho salmon		11	
Coho salmon	*Oncorhynchus kisutch*	8	
Cutthroat trout	*Oncorhynchus clarkii*	4	
Kelp greenling	*Hexagrammos decagrammus*	2	1
Lingcod	*Ophiodon elongatus*	34	140
Quillback rockfish	*Sebastes maliger*		1
Ratfish	*Hydrolagus colliei*	10	19
Red Irish lord	*Hemilepidotus hemilepidotus*		3
Sockeye salmon (adult)	*Oncorhynchus nerka*	1	
Staghorn sculpin	*Leptocottus armatus*	8	
Steelhead trout	*Oncorhynchus mykiss*	3	
Unidentified juvenile salmon		10	
Unidentified rockfish		1	2
Unidentified salmon		8	
Unidentified salmon (adult)		1	
Unidentified sculpin		45	1
Unidentified trout		8	
Whitespotted greenling	*Hexagrammos stelleri*	4	8
Wolf eel	*Anarrhichthys ocellatus*	1	

Chapter Five: A quantitative chronology of diurnal feeding in juvenile Pacific salmon

SH Munsch, JR Cordell, JD Toft

Abstract

Daily cycles in feeding intensity are common among fish and suggestive of ecological tradeoffs and constraints. However, feeding chronologies are typically estimated from diets rather than in situ observations. As a consequence, our understanding of daily feeding patterns is often imprecise, which limits our ability to infer connections between these patterns and their drivers. Here we quantify in unprecedented temporal resolution the real-time diurnal feeding behavior of a fish assemblage. Snorkelers observed juvenile Pacific salmon *Oncorhynchus* spp. in estuarine waters between dawn and early evening. Fish fed throughout the day and feeding declined after dawn, with individuals allocating ≈20% of their time to feeding at sunrise declining to ≈5% in the early evening. Many factors potentially influenced this behavior, including predation avoidance, physiological constraints, prey availability, and mandates for growth and migration. Prey mass in the stomachs of these fish increased shortly after dawn to relatively stable levels through the afternoon. Thus, diet metrics detected the presence of feeding, but not temporal changes in feeding intensity. Diets appear to provide limited information on the timing and intensity of feeding, and we may therefore only vaguely understand daily feeding patterns of fish when examining diets alone.

Introduction

Ecologists have long recognized that diel cycles mediate feeding in aquatic consumers. Despite this, we have only a basic understanding of daily feeding patterns in most fish species because we lack quantitative knowledge of when and how often they feed. Diel feeding in fish has conventionally been studied using time series of diets. Interpreting real-time trends from diet chronologies is problematic because of many factors, including: uncertainty in the timing of prey consumption, digestion or regurgitation after consumers are captured, nonlinear gastric evacuation rates that do not indicate feeding discontinuity or that slow during starvation, and variable digestion rates among prey taxa and temperatures (Talbot 1984, Bowman 1986, Gerking 1994, Cortés et al. 1997). In addition, diets only reflect feeding efforts that result in prey capture and thus account for an unknown proportion of feeding attempts. Further, diets may not directly indicate diel patterns in feeding attempts if consumers experience temporal patterns in capture efficiencies. In contrast to diets, real-time observations of behavior measure the exact timing of feeding attempts and quantify temporal trends in absolute terms (e.g., Green et al. 2011, Fox and Bellwood 2011). Thus, in situ observations can provide us with a more complete and accurate understanding of temporal feeding patterns.

There are many influences and constraints that potentially drive daily feeding patterns. First, consumers often risk detection by their own predators when they feed and behave to optimize tradeoffs between feeding benefits and predation risk (Lima and Dill 1990). Light affects prey detection differently in visually-feeding planktivores and piscivores, creating “antipredator windows” of intermediate lighting when the ratio of risk to reward is favorable (Clark and Levy 1988, Hansen and Beauchamp 2015). For example, diel vertical migrations of juvenile Sockeye Salmon *Oncorhynchus nerka* suggest that they forgo feeding in bright surface waters where plankton are easiest to detect (Clark and Levy 1988, Scheuerell and Schindler 2003). Instead, they track intermediate light levels where they detect prey adequately without becoming overly conspicuous to their own predators. Similarly, stream-rearing juvenile Atlantic Salmon *Salmo salar* fed most efficiently in bright conditions, but occupied predator refuge during the day unless prey was scarce (Fraser and Metcalfe 1997, Orpwood et al. 2006). Given the relationship between light and detection by visual predators, lighting may also affect feeding frequency because fish minimize conspicuous feeding actions (e.g., darting motions) in environments of high predation risk (Dill 1983). Daily feeding patterns may therefore reflect behaviors that balance predation risk and feeding benefits (e.g., growth, metabolism).

Daily feeding patterns may also be driven by physiological constraints of the consumer or prey availability. Predators can be limited by light (e.g., Lazzaro 1987) and digestive capacity (e.g., Jeschke et al. 2002), and their feeding intensity increased by hunger (e.g., Dill 1983, Angradi and Griffith 1990). Some fish may therefore not feed at night, feed intensely at dawn, and then feed intermittently to maintain satiation. Prey availability can also create feeding patterns; for example, aquatic insects can emerge at dawn and drive the timing of feeding in birds (Sjöberg and Danell 1981). Many zooplankton migrate between surface waters at night and deeper waters during the day to avoid detection by predators (Lambert 1989, Hays 2003). If zooplankters are advected into shallow areas or mistime their downward migrations, their daytime availability to nearshore consumers may peak at dawn. Thus, diel feeding trends could reflect factors that limit when fish are able to feed.

Here we quantified the diurnal feeding chronology of juvenile Pacific salmon *Oncorhynchus* spp. during their estuarine migration phase. We assembled a dataset of real-time underwater observations that occurred between dawn and early evening. The domain of our findings is therefore restricted to this temporal period that we refer to as "diurnal" to indicate that observations occurred only during daylight. We addressed three descriptive questions that are difficult to assess from conventional diet analyses: (1) how often do salmon attempt to feed? (2) how much does this behavior vary with time of day? (3) are there discontinuities in their feeding and, if so, when do discontinuities occur? In addition, we assembled a diet dataset from juvenile salmon captured concurrently with underwater observations to compare stomach fullness to behavior.

Methods

We combined data from previous studies (snorkel surveys: Toft et al. 2007, 2009, 2013, Munsch et al. 2014; diet sampling: Toft et al. 2007, Munsch et al. 2015b) to produce a diurnal chronology of juvenile salmon feeding behavior and stomach contents. These studies examined juvenile salmon habitat use in nearshore estuarine waters of Central Puget Sound, WA (Fig. 1). Nearshore waters were inhabited by schools of age-0 Chinook *O. tshawytscha*, Chum *O. keta*, Coho *O. kisutch*, and Pink Salmon *O. gorbuscha*. Chinook Salmon were the focal species of the original studies because the evolutionarily significant unit in Puget Sound is listed as threatened under the United States Endangered Species Act. Pink Salmon were only abundant in even numbered years because they have a unique two-year life cycle. Juvenile salmon were advantageous for studying behavior because they (1) occupied surface waters where they were easily observed by snorkelers, (2) fed in conspicuous darting motions, and (3) were highly mobile (Quinn 2005), minimizing the risk of observing the same individuals in replicated surveys.

Snorkel surveys and diet sampling occurred between April and August to correspond with the estuarine migration phase of juvenile salmon. Fish were observed between sunrise (earliest survey = 0530 hours) and late afternoon (latest survey = 1948 hours) primarily during the slack of high and low tidal levels. Juvenile salmon fed on small invertebrates produced in epibenthic, terrestrial, and water column habitats (Toft et al. 2007, Munsch et al. 2015b). Shoreline armoring (e.g., seawalls, riprap) affected the epibenthic prey field at some of our sites (Toft et al. 2013, Munsch et al. 2015b), but there was no evidence that armoring influenced salmon feeding rates (Heerhartz and Toft 2015) or number of total prey consumed (Munsch et al. 2015b).

Feeding behavior of juvenile salmon in shallow waters was observed via 818 snorkel surveys by swimming 26 – 75 m linear transects at the surface of the water. Transects were located parallel to shore in water 0.4 – 6.8 m (2.11 ± 0.94 m, mean ± sd) deep. Fish were only surveyed when visibility exceeded 2.5 m to maximize the accuracy of observations and minimize observer effects on fish behavior (Toft et al. 2007). Each time fish were encountered, the following data were recorded: identification to finest possible taxonomic resolution, school size, and instantaneous presence or absence of feeding activity by any of the fish. This instantaneous metric of behavior was the unit of replication (n) for our study. Feeding activity was defined as a sudden change in orientation and acceleration to a presumed prey item, often independent of the fish's school (Fig. 2). Feeding activity was defined as absent if fish swam steadily through the water, often in uniform as a school. We were unable to discern whether feeding attempts resulted in prey capture and therefore use the term "feeding activity" to describe successful and unsuccessful feeding actions. On rare occasions (n = 33 of 1,610), fish swam rapidly away from observers and these observations were excluded from analysis.

Diets of juvenile salmon were sampled concurrently with snorkel surveys. Fish were captured close to shore using beach seines and lampara nets, and their stomach contents retrieved either by gastric lavage or by euthanasia followed by stomach dissection. Fork length was measured for all fish, and mass was measured for most fish. When mass was not measured directly, it was estimated from a quadratic formula relating data from fish that were measured for mass and length. Stomach contents were patted dry and weighed in the laboratory. Stomach content mass was described by instantaneous ration, a metric calculated by dividing the mass of all prey in the stomach by the mass of the fish.

We used generalized linear mixed-effects model (GLMMs) to test the hypothesis that feeding activity declined with time after dawn. Models were built and analyzed in R version 3.1.2 using the lme4 and merTools packages (Bates et al. 2015, R Core Team 2015, Knowles and Frederick 2016). In these models, the response variable was the presence or absence of feeding activity and the fixed effect was daylight elapsed. Daylight elapsed was calculated by dividing the time after sunrise by the total time from sunrise to sunset for that day to account for seasonal variation in day length. In addition, we included random intercepts for salmon taxa, site, and dataset (i.e. the original study that the data was obtained from) to account for potential heterogeneity in feeding activity among these variables. Models were constructed using a binomial variance structure and a logit link function. In the primary model, we treated the log-transformed school size of fish as an offset because the probability of observing feeding should increase as more fish are observed simultaneously. Thus, the probability p of observing feeding activity in an encountered salmon school i was modeled as:

$$(1) \qquad \log\left(\frac{p_i}{1-p_i}\right) = \beta_0 + A_{0a} + B_{0b} + C_{0c} + \beta_1 X + \log(Q) + \varepsilon_i$$

$$A_{0a} \sim N(0, \sigma_a^2);\ B_{0b} \sim N(0, \sigma_b^2);\ C_{0c} \sim N(0, \sigma_c^2);\ \varepsilon_i \sim N(0, \sigma_i^2)$$

where A represented salmon taxa, B represented site, C represented dataset, X represented percent daylight elapsed, and Q represented salmon school size.

In addition to the primary model, we built an ancillary model with the same parameters except omitting the offset term using only observations where a singular salmon was observed (n = 431). We built this model because a metric of feeding probability for a singular salmon was more interpretable than a metric requiring an additional parameter of school size. Rather than making predictions from the primary model given a school size of one, we anticipated that the ancillary model would more accurately quantify feeding trends for singular salmon because (1) it did not assume a relationship between feeding activity and school size and (2) the average school size was substantially larger than one salmon.

As visual aids, we plotted relationships of feeding activity vs. the single explanatory variables of (1) daylight elapsed separated by salmon taxa and (2) school size for all taxa combined using binomial generalized linear models (GLMs). We also overlaid a loess line fit to raw data examining feeding activity vs. daylight elapsed for all observations.

To assess differences in instantaneous ration with daylight elapsed, we built a linear mixed effects model using similar parameters as the models describing feeding activity. In this model, the response variable was the fourth-root transformed instantaneous ration, the fixed effect was a categorical variable of percent daylight elapsed created by binning observations by each ten percent daylight elapsed, and the random effects were salmon species, site, and dataset. This approach was appropriate because instantaneous ration varied non-linearly with percent daylight elapsed.

Results

Snorkelers observed 1,577 schools or single juvenile salmon at times corresponding to 1-90% of daylight elapsed. Species composition of these fish was 47% Chinook, 40% Chum, 4% Coho, and 9% Pink salmon. Feeding activity occurred in 28% of observations and the average school size was 42 ± 127 (sd) fish. Feeding activity was greatest at dawn and declined significantly through late afternoon (Fig. 3, top left; Table 1, $P = 1.10 \times 10^{-4}$). Salmon fed during the entire observation window, but feeding activity declined steeply after ≈70% of daylight had elapsed. There was a 51% probability of feeding activity occurring at dawn compared to 20% at the end of our observation window, given the average school size of 42 salmon (primary GLMM). Confidence intervals around these estimates were relatively large due in part to heterogeneity in feeding activity among the random effects of salmon taxa, site, and dataset. All salmon taxa showed a qualitatively similar decline in feeding with daylight elapsed (Fig 3, bottom). Feeding activity was more likely to occur in larger schools of salmon (Fig. 3, top right). In observations of single salmon, feeding activity declined significantly from a probability of 20% at dawn to 5% at the end of the observation window (ancillary GLMM, Table 1, $P = 0.034$).

Diets were sampled from 547 juvenile salmon at times corresponding to 5-46% of daylight elapsed. Species composition of these fish was 50% Chinook, 34% Chum, 4% Coho, and 13% Pink Salmon. Instantaneous rations were lowest just after dawn, and increased to relatively stable levels thereafter (Fig. 4). Differences in instantaneous ration between fish captured at dawn (0-9 percent daylight elapsed) and other periods of the day were statistically significant (20-29 and 30-39 percent daylight elapsed) or marginally insignificant (10-19 and 40-49 percent daylight elapsed) (Table 1).

Discussion

We quantified a diurnal feeding pattern in juvenile salmon through real-time, in situ observations. Salmon fed often overall, with individuals allocating roughly 20% of their time to feeding at dawn declining to 5% in the early evening. There was some evidence that salmon stopped feeding near the end of our observation window, but fish generally fed throughout the day. This enhances our relatively vague understanding of daily feeding patterns based on time series of diets (e.g., Godin 1981, Schabetsberger et al. 2003) by providing novel, empirical evidence that (1) diurnal feeding in juvenile salmon is characterized by a slow decline in feeding from dawn to early afternoon and (2) salmon feed relatively often throughout the day. Daily feeding trends are conventionally studied through diets, an approach that can be useful because it allows us to detect qualitative temporal patterns, quantify prey composition, and examine energetic intake. However, real-time observations provide us with a more exact understanding of behavior. For example, while our time series of stomach fullness indicated that feeding occurred immediately after dawn, it provided no quantitative information on overall feeding intensity or evidence that feeding intensity declined immediately after dawn. This shows that diet metrics can indicate the presence of feeding, but not changes in feeding intensity over time, and thus studies that examine diets alone may not have the precision to detect changes in feeding intensity.

Many factors potentially contributed to decreased salmon feeding intensity after dawn. Diurnal feeding patterns may reflect a balance between feeding gain and predation risk mediated by light regime (Hansen and Beauchamp 2015) during a salmon life stage characterized by size-selective predation and high growth rates (Parker 1971, Simenstad et al. 1982, Duffy and Beauchamp 2008). Salmon moved rapidly and often reflected light when attacking prey, suggesting a predation risk cost of feeding because they were more conspicuous. Juvenile salmon in estuaries of the Pacific Northwest are prey for visual predators such as trout (Duffy and Beauchamp 2008), sea and shoreline-oriented birds (Roby et al. 2003, Lance and Thompson 2005), and marine mammals (Olesiuk et al. 1995). Salmon may limit detection by these predators by minimizing conspicuous feeding actions during the brightest parts of the day. Daily feeding patterns may also arise from physiological constraints. Ours and other diet sampling (e.g., Godin 1981, Schabetsberger et al. 2003) are consistent with estuarine juvenile salmon feeding primarily during the day, potentially because their feeding is limited by light. Salmon that do not feed at night may feed most often at dawn in response to hunger (sensu Dill 1983) and then gradually feed less often as their stomachs reach capacity. Rapidly filling stomachs at dawn and a slow decline in feeding intensity thereafter were consistent with such physiological constraints having great influence on the overall timing of feeding. Diurnal variation in prey availability may also have contributed to daily patterns in feeding, as the composition of salmon diets can vary on a daily scale (Schabetsberger et al. 2003).

Our study indicates that juvenile salmon in estuaries feed often and throughout the day, which may reflect energetic requirements to support growth and migration. Over the long-term, juvenile fish must grow enough to overcome gape-limited predation (Duffy and Beauchamp 2008), become more evasive (Sogard 1997), and avoid starving during the winter (Schultz and Conover 1997). Stream-rearing Chinook Salmon also fed often during the day (mean = 5.9 feeding events / min [Macneale et al. 2010]), suggesting that they maintain a high feeding rate for a substantial portion of their juvenile phase. Salmon are among the fastest growing fish species within their geographic range (Quinn 2005), and feeding often during the day may be necessary to maintain this growth. In addition, juvenile salmon must fuel their constant swimming behavior and seaward migrations (Wissmar and Simenstad 1988). A high baseline of feeding may be common in juvenile fish overall because many species must fuel ontogenetic migrations (e.g., Nagelkerken et al. 2015) and energy reserves in underfed fish may deplete faster in smaller fish (Kieffer and Tufts 1998). Thus, long-term energetic investments such as growth and migration may require that salmon feed often, even if feeding exclusively during certain times (e.g., crepuscular hours) has short-term adaptive advantages.

Real-time, quantitative feeding chronologies are uncommon, but they make clear that diurnal feeding patterns vary among fish in different ecological contexts. We are aware of two feeding chronologies of fish in addition to ours that were quantified through real-time observations. First, Lionfish (*Pterois volitans*) that were piscivorous, stalked prey, and lacked local predators fed exclusively during crepuscular periods. Second, at one site Rabbitfish (*Siganus lineatus*) that were detritivorous–herbivorous and presumably prey for other fish fed throughout the day, with feeding intensity peaking in the morning, declining until afternoon, and increasing before sunset (Fox and Bellwood 2011). At another site, they fed completely nocturnally. Given the different ecological settings of these fish (e.g., predation risk, prey type, life stage) it is apparent that no single factor drives their daily feeding patterns. Furthermore, these studies in addition to ours suggest that fish exhibit a diversity of daily feeding patterns that may not be detectable by examining diets alone (e.g., feeding often vs. feeding exclusively at certain times), and represent markedly different behaviors that are associated with ecological contexts.

The limitations and context of our study should be considered when interpreting our findings. First, our observations were limited to a period between dawn and early evening, which omitted pre-dawn and dusk periods. Some studies of diel consumption patterns suggest that salmon feeding peaks at dusk similarly to dawn (Godin 1981, Brodeur and Pearcy 1987, Schabetsberger et al. 2003). Had we surveyed juvenile salmon during all daylight hours, we may have observed a parabolic relationship between feeding activity and daylight elapsed, which would have provided more evidence that these fish exploit intermediate light levels to avoid predation (Clark and Levy 1988). Likewise, our diet sampling was limited to hours between dawn and the afternoon. Had we sampled in the evening, we may have detected a lagging decline in stomach fullness that would provide indirect evidence for a decline or cease in feeding earlier in the day. In addition, our study would have been improved by quantifying potential drivers of diel feeding behavior, such as comparing feeding activity to the predation risk environment (e.g., light levels, predator presence) or to prey availability. Finally, we must consider that the urbanized landscape of our study may affect the feeding activity of fish. For instance, prey and predator assemblages at our sites probably differ from natural areas (Munsch et al. 2015a, 2015b) and light pollution may alter the daily light regime (Nightingale et al. 2006). These concepts were beyond the scope of this opportunistic study and they represent potential extensions for further work.

A more exact understanding of the timing and intensity of feeding can inform management and model parameterization. First, salmon appeared to maximize energy intake during the day: they fed often and throughout the observation window, and their stomachs filled shortly after dawn. Bioenergetic modeling indicates that high prey densities are required to support rapid growth and migration of juvenile salmon (Wissmar and Simenstad 1988), and our observations of frequent feeding further suggest that juvenile salmon benefit from abundant prey fields. This is of interest to resource managers because nearshore ecosystems in Puget Sound are focal areas for conservation and restoration (e.g., Cereghino et al. 2012), and shoreline modifications such as seawall armoring and piers can affect the availability and consumption of preferred prey by juvenile salmon (Munsch et al. 2015b, Cordell et al. In Press). Second, ecologists have recently advocated for a greater understanding of dynamic habitat use in shallow waters (Sheaves et al. 2015). Our observations suggest that salmon interactions with their prey are relatively intense at dawn and steadily decrease thereafter. Given that salmon prey abundances can vary on a daily scale (Schabetsberger 2003), ecologists may consider assessing prey availability during morning hours that overlap with periods of high feeding intensity. Third, we provide a parameter estimate for individual-based models that account for time allocated to feeding. For instance, movement models that quantitatively account for diurnal variation in feeding and increased path sinuosity while feeding (Heerhartz and Toft 2015) may suggest that large-scale movements including migrations occur primarily in the late afternoon after salmon are satiated. Overall, understanding when and how often fish feed may provide insights into their natural history that remain inaccessible by examining diets alone.

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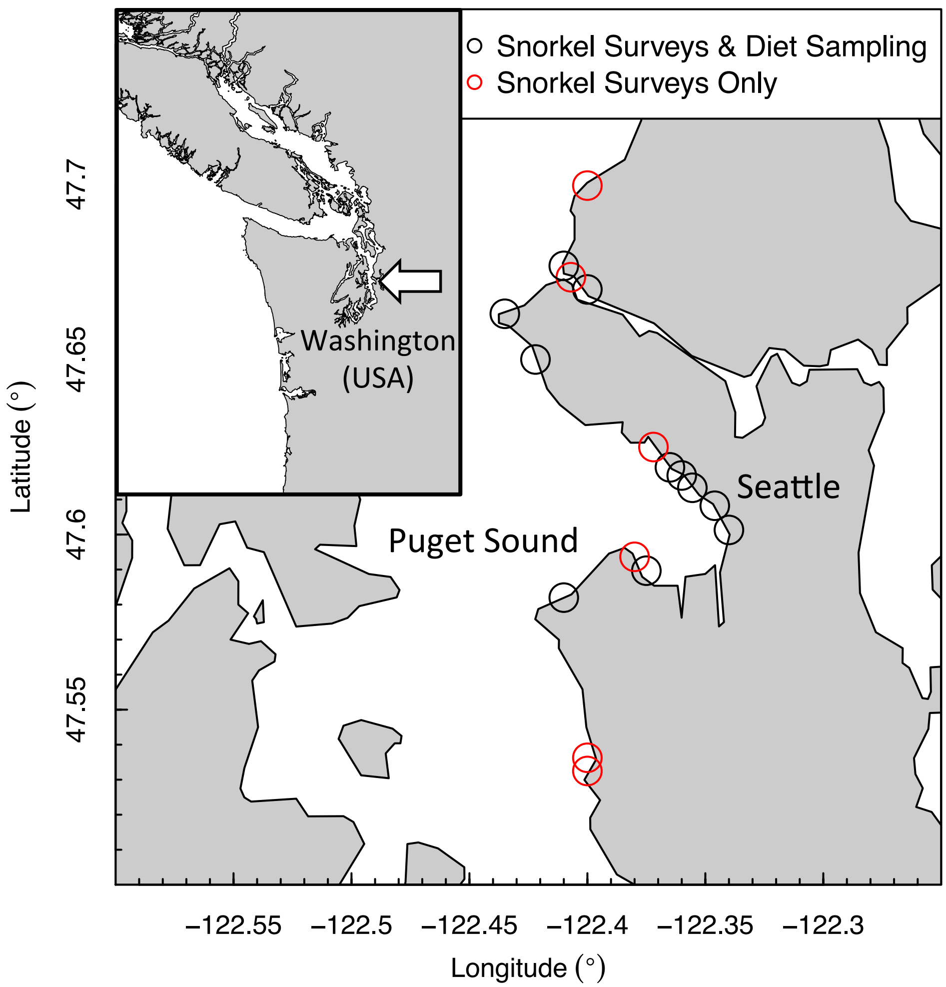

Figure 1. Location of study sites in Puget Sound, Washington (USA).

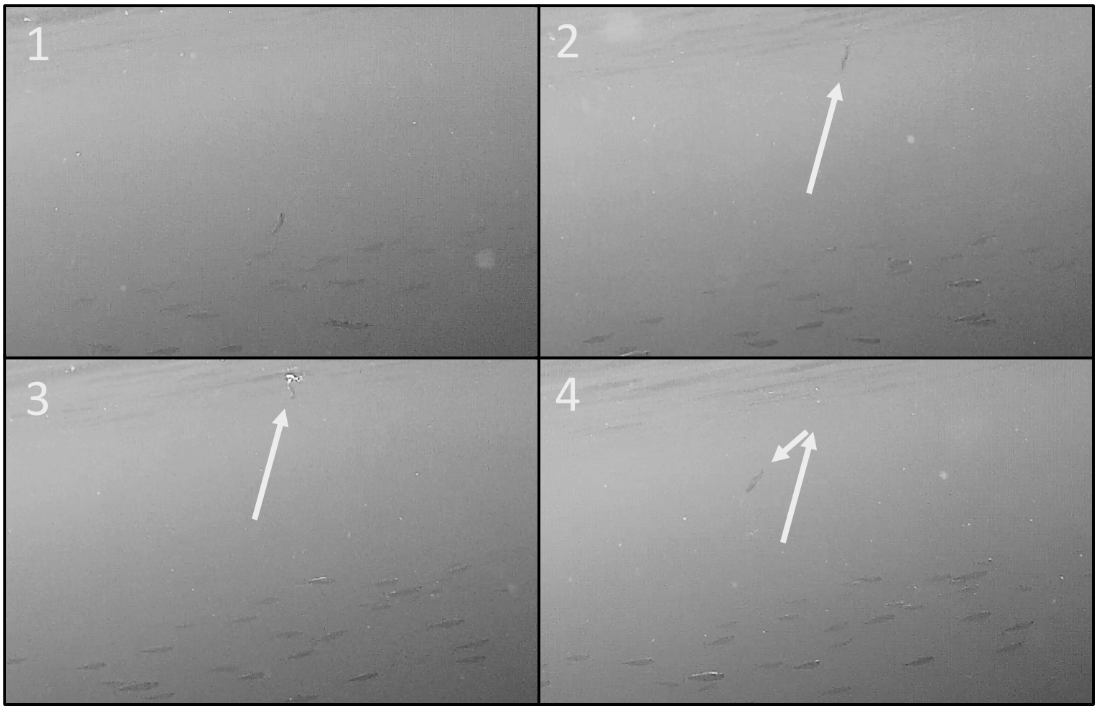

Figure 2. A juvenile Chinook Salmon swims away from its school, feeds at the surface, and returns. Note conspicuous reflection while feeding (panel 3).

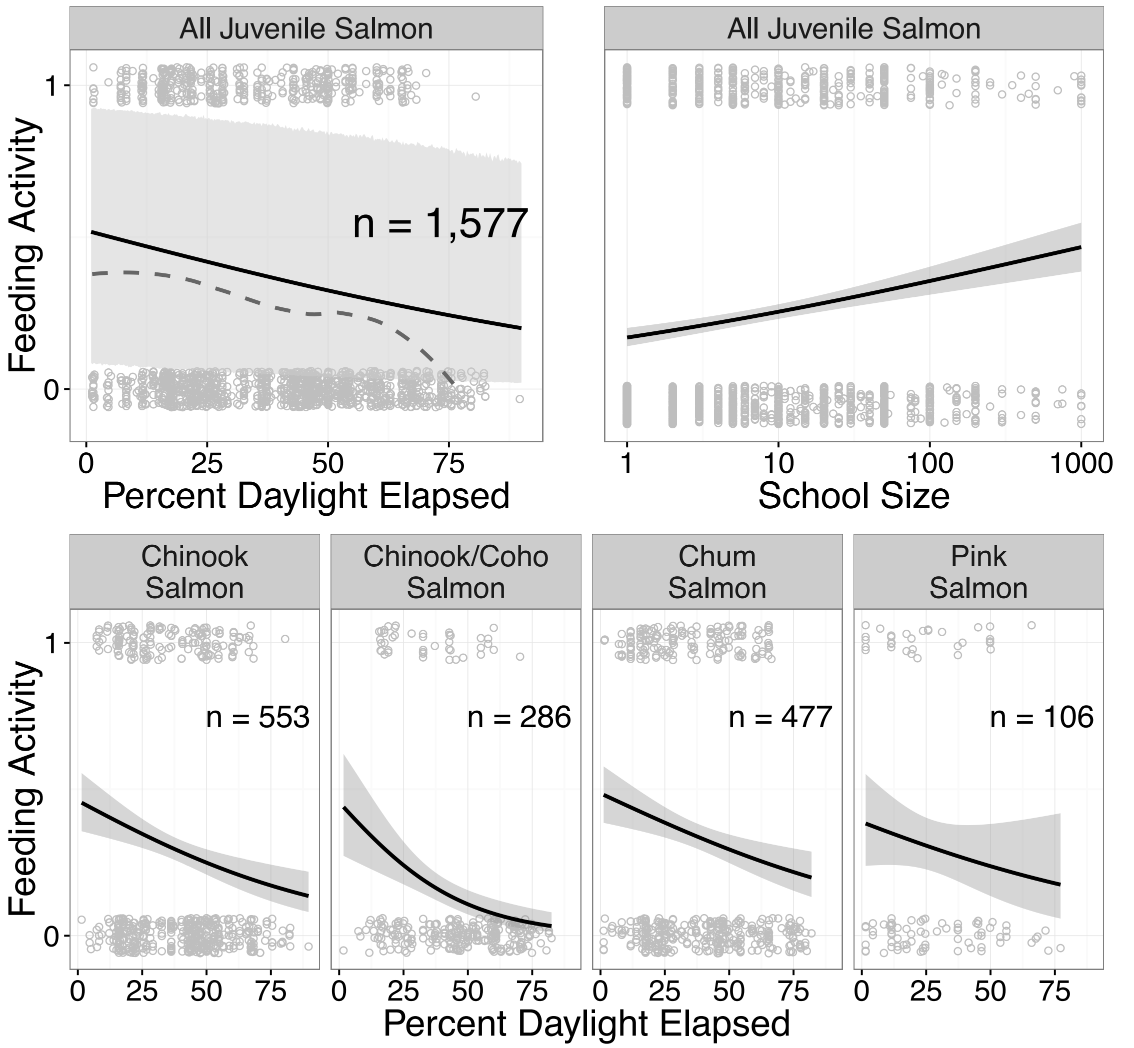

Figure 3. Feeding activity vs. predictor variables. Grey circles indicate raw data (1 = feeding activity present, 0 = feeding activity absent) and are vertically offset for clarity, black lines indicate model predictions, and shadings indicate 95% confidence intervals. Top left: Feeding activity vs. daylight elapsed for all salmon observations combined. Black line indicates the GLMM predicted values for the mean school size of 42 salmon. Dashed grey line indicates local regression (loess) on raw data. Top right: Feeding activity vs. log-transformed school size GLM for all salmon observations combined. Bottom: Feeding activity vs. daylight elapsed GLM separated by taxa observed a minimum of 100 times.

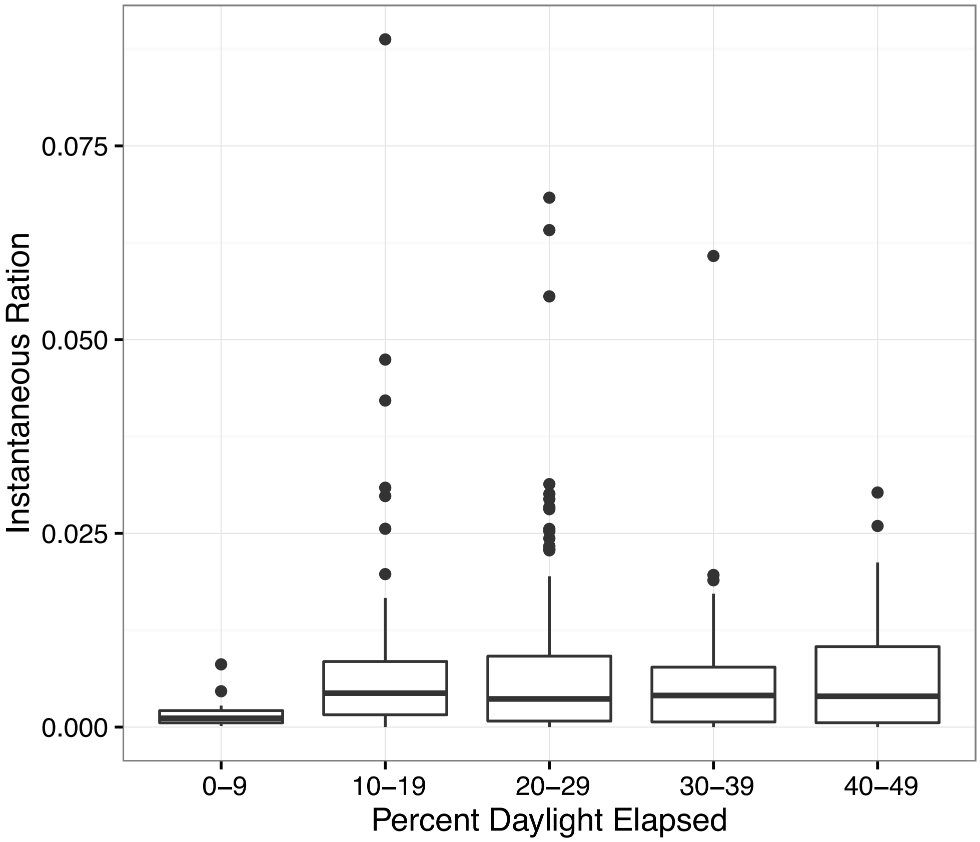

Figure 4. Instantaneous rations of juvenile salmon compared to time of capture.

Table 1. Summary statistics of mixed effect models. Parameter estimates, standard errors (SE) and p values are reported for fixed effects, and variance and standard deviations (SD) are reported for random effects. Fixed effects for the diet model indicate periods of percent daylight elapsed, which are compared to the baseline period of 0-9 percent.

Model	Fixed effect	Parameter estimate	SE	p	Random effect	SD
Feeding activity (primary)	Intercept	-3.663	0.745	8.79 x 10-7	Salmon taxa	1.247
	Daylight elapsed	-0.016	0.004	1.10 x 10-4	Site	0.458
					Dataset	1.014
Feeding activity (ancillary)	Intercept	-1.344	0.607	0.027	Salmon taxa	0.223
	Daylight elapsed	-0.018	0.009	0.034	Site	0.342
					Dataset	0.218
Instantaneous ration	Intercept	0.137	0.071	0.248	Salmon species	0.029
	10 –19	0.043	0.025	0.081	Site	0.023
	20 – 29	0.063	0.025	0.012	Dataset	0.092
	30 – 39	0.066	0.026	0.011		
	40 – 49	0.052	0.027	0.055		

Chapter Six: Effects of shoreline armoring and overwater structures on estuarine fish: opportunities for habitat improvement

SH Munsch, JR Cordell, JD Toft

Abstract

Nearshore ecosystems are increasingly recognized as critical habitats for fish of cultural, ecological, and economic significance. These ecosystems are often densely inhabited by juvenile fish, highly productive, and refuges from predation, leading ecologists to characterize them as nurseries. However, nearshore ecosystems are being transformed globally to support demands of growing coastal populations. Many shorelines are modified by armoring (e.g., seawalls, riprap) to minimize erosion, and overwater structures (e.g., piers, docks) to facilitate waterfront use. These modifications affect the ecology of nearshore systems by restructuring, eliminating, and shading shallow waters. Here, we review literature examining effects of armoring and overwater structures on coastal and estuarine fishes, and discuss how research and management can coordinate to minimize negative effects. Along armored shorelines, fish assemblages differed from unarmored sites, fish consumed less epibenthic and terrestrial prey, beach spawning was less successful, and fish were larger. Under large overwater structures, visually-oriented fish were less abundant and their feeding was impaired. Shade from overwater structures also interrupted localized movements of migratory fish. Thus, shoreline modifications impaired habitats by limiting feeding, reproduction, ontogenetic habitat shifts from shallow to deeper waters, and connectivity. Research suggests that restoring shallow waters and substrate complexity, and minimizing shading underneath overwater structures, can rehabilitate habitats compromised by shoreline modifications. Threats to nearshore fish habitats will increase as growing coastal populations and rising sea levels

increase demands for shoreline infrastructure. Our ability to assess and rehabilitate nearshore fish habitats will be enhanced by: focusing research attention on metrics that directly indicate fish habitat quality; implementing and evaluating shoreline features that repair compromised habitat functions within human-use constraints; collating natural history knowledge of nearshore ecosystems; and embracing the socio-ecological nature of habitat improvements by educating the public about conservation efforts and fostering appreciation of local nearshore ecosystems. Actions to reduce impacts of shoreline modifications on fish are feasible when they align with societal goals, such as improving flood protection and providing spaces that facilitate recreation, education, and connections between people and nature.

Introduction

People have modified waterfronts for millennia. Ancient Alexandria, founded 331 BCE, was a prototype for the modern port city: its engineers built harbors featuring wharves and brick seawalls that allowed ships to support the largest trade center in the world (Schwartz 1980; Lawler 2005). Shoreline infrastructure dates at least to 2300 BCE, when people created docks in present-day India by excavating and lining basins with bricks (Rao 1973). Waterfront civilizations have long prospered from aquatic resources and trade, and are now major components of the global economy, supporting not only international trade but a diversity of local industries such as tourism and real estate. Currently, 44% of all people live within 150 km of shore and many of the world's largest cities are on the coast (Ross 1995; Small and Nicholls 2003; Small and Cohen 2004).

People have introduced waterfront infrastructure throughout the world, and shorelines are often modified by armoring, the replacement or shielding of natural shoreline substrates with hard and resistant materials to minimize erosion and protect infrastructure (e.g., seawalls, riprap; Bulleri & Chapman 2010), and overwater structures that shade waters below (e.g., piers, docks) (Fig. 1). Widespread modification to shorelines is concerning because estuaries and coasts provide ecosystem services (e.g., cultural resources, food, flood protection, recreation) worth tens of trillions of US dollars annually Costanza et al. 1997; Temmerman et al. 2013). Fish are an important component of these services, as many shallow ecosystems are thought to provide nurseries for fish of cultural, ecological, and economic significance.

Nearshore ecosystems and their fish habitats warrant protection, but their management is complex. Fish are mobile and not easily observed, and evaluating fish habitats requires that we understand the benefits of habitat features, functions, and processes. Furthermore, many shorelines are extensively modified, centuries removed from natural, and their restoration outcomes uncertain. Economic or social pressures may disincentivize restoration, and shoreline ecosystems may be managed more pragmatically as novel socio-ecological systems (Hobbs et al. 2013; Miller & Bestelmeyer 2016). Research attention has recently focused on effects of shoreline modifications on fish, and how to rehabilitate impaired habitat functions (Fig. 2). In addition, the US Government is initiating policies that require ecosystem goods and services are accounted for in federal decision making (White House 2015). Thus, it is timely to consider how we can develop waterfronts to achieve triple "wins" (Elliott et al. 2016) that benefit ecology, particularly in the context of fish, as well as economy and human safety.

Here we review literature examining effects of shoreline armoring and overwater structures on coastal and estuarine fish assemblages, and suggest how research and management can coordinate to minimize negative effects in relation to constraints and opportunities of human use. We focused on ecology influenced by disturbances directly along the shoreline, and do not review studies of subtidal artificial reefs. In this review we refer to "management" as policies and decisions that determine ecological functions of nearshore waters by controlling or mitigating disturbances caused by shoreline modifications. We attempted a thorough review of the literature in estuarine and coastal systems, and drew from relatable freshwater literature when the focal literature was lacking. We collated studies from our own inventory and the first 400 search results from Google Scholar for the following terms: "fish shoreline armoring," "fish shoreline bulkhead," "fish shoreline riprap," "fish shoreline seawall," "fish shoreline dock," "fish shoreline 'overwater structure,'" and "fish shoreline pier." Some locations (e.g., Hudson River, Puget Sound) and fish (e.g., Pacific salmon [*Oncorhynchus* spp.]) were disproportionately common in the literature, and we thus referred to them often despite our attempt to present a broad synthesis.

Shallow Waters and Anthropogenic Pressures

Nearshore ecosystems provide vital functions for fish. Ecologists have long recognized that shallow areas support high productivity, high densities of juvenile fish, and low densities of predators (Beck et al. 2001; Able 2005). Shallow waters and their associated biogenic and geomorphic structures often limit the presence or effectiveness of larger predators, and provide diverse terrestrial, epibenthic, and planktonic prey (Simenstad, Fresh & Salo 1982; McIvor & Odum 1988; Paterson & Whitfield 2000). Juveniles of many fish species use shallow areas, especially in estuaries, before moving offshore as adults (Deegan 1993; Able 2005). Shallow habitats have conventionally been assessed as nurseries by measuring output of juveniles to adult populations (Beck et al. 2001; Dahlgren et al. 2006); however, we can more directly assess habitats by examining specific processes and dynamics that facilitate fish development. Ecologists have recently advocated for a sophisticated conceptualization of habitat value whereby networks of shallow areas benefit juveniles by providing access to appropriate resources (e.g., food, refuge) or environments (e.g., hydrodynamics, salinity, temperature) as they develop (e.g., Sheaves et al. 2015; Nagelkerken et al. 2015). These discussions underscore the importance of connectivity that allows fish to access habitat networks, and warn that conventional abundance metrics may overlook more direct components of habitat quality. Thus, the value of fish habitats will be better understood by examining processes and dynamics that support fish development (Simenstad & Cordell 2000; Sheaves et al. 2015).

The functions of nearshore fish habitats are threatened by shoreline armoring. Armoring is common along many of the world's shorelines (e.g., 14% of USA, Gittman et al. 2015), and studies in many locations have reported that armoring influences the composition of localized fish assemblages (Peterson et al. 2000; Clynick 2006; Toft et al. 2007; Bilkovic & Roggero 2008; Strayer et al. 2012; Lowe & Peterson 2014; Munsch, Cordell & Toft 2015a; Balouskus & Targett 2016; Torre & Targett 2016). Armoring has been associated with reduced metrics of assemblage integrity (e.g., diversity, richness, function) along Biloxi Bay and Davis Bayou (MS; Peterson et al. 2000), within marinas along the northwest coast of Italy (Clynick 2006), along the James River (VA [bulkheads, but not riprap]; Bilkovic & Roggero 2008), and along Delaware Coastal Bays (DE; Balouskus & Targett 2016, Torre & Targett 2016). Scuba surveys in Elliott Bay (WA) indicated that abundances of demersal species varied between armored shorelines and sediment-nourished beaches, and these fish appeared to select for substrates that were provided by the engineering of the shoreline (Munsch, Cordell & Toft 2015a). Some of these fish used the substrate directly, for example to hide from predators (e.g., flatfish [Pleuronectiformes] burrowed in sand), suggesting that armoring can affect the availability of substrate as a habitat resource. However, the biophysical mechanisms by which armoring affects localized abundances of species often remain elusive. Given that effects on fish assemblages have been documented in many systems, it is likely that many of the world's armored shorelines support non-historic fish assemblages.

Armoring may also affect the availability and consumption of fish prey. Epibenthic (e.g., Morley et al. 2012) and terrestrial (e.g., Dugan et al. 2008; Sobocinski, Cordell & Simenstad 2010) invertebrate production is disrupted along armored shorelines, presumably because armoring displaces or severs connections to their habitats. Armoring can also reduce prey production by narrowing beaches and limiting the accumulation of wrack that produces invertebrates (Heerhartz et al. 2016; Dethier et al. 2016). Impacts on prey availability can then lead to reduced prey consumption. Juvenile Chinook salmon (*O. tshawytscha*) along armored shorelines in central Puget Sound consumed fewer insects (e.g., chironomids; Toft et al. 2007). Also within Puget Sound, juvenile chum salmon (*O. keta*) along armored shorelines of the Duwamish River estuary (WA; Morley et al. 2012) and Elliott Bay (Munsch, Cordell & Toft 2015b) consumed fewer epibenthic harpacticoid copepods, their dominant prey during early estuarine migration (Salo 1991). Instead, chum salmon fed primarily on plankton, raising concerns that they may have switched to prey that were more difficult to detect, more evasive, or lower in energy content (Munsch, Cordell & Toft 2015b). Thus, armoring in productive systems may affect diet composition rather than total consumption, although consumption rates (i.e., per unit time) have yet to be quantified. Studies of armoring effects on estuarine fish diets appear to be limited to Puget Sound, but there is evidence that effects occur elsewhere; for example, largemouth bass (*Micropterus salmoides*) in Matsuyama, Japan consumed less benthic prey in lakes with greater portions of their shorelines armored (Doi et al. 2010). Overall, armoring may impair habitats by requiring that fish feed suboptimally, for instance on taxa that offer lower bioenergetic returns or that inhabit areas that expose consumers to predators.

Armoring may also affect other processes such as reproduction and ontogenetic habitat shifts. Intertidal areas are often used for spawning (DeMartini 1999), and armoring may limit the availability of spawning habitat (Rice 2006; Penttila 2007; Balouskus & Targett 2012). Compared to smooth cordgrass (*Spartina alterniflora*) shorelines, Atlantic silverside (*Menidia menidia*) in Roosevelt Inlet (DE) deposited fewer eggs along bulkhead and riprap shorelines (Balouskus & Targett 2012). In addition, surf smelt (*Hypomesus pretiosus*) embryo mortality was greater along an armored shoreline in Puget Sound where air temperature, substrate temperature, light intensity, and air dryness were greater than an adjacent natural shoreline (Rice 2006). Furthermore, a graded intertidal zone can support ontogenetic habitat shifts whereby fish use deeper habitats as they grow (Munsch, Cordell & Toft 2016). These shifts are hypothesized to occur because predators are uncommon in extreme shallows, larger fish are less vulnerable to predation, and fish balance the safety of shallows with other benefits of maximizing habitat use (e.g., foraging in less spatially-constrained environments). However, juvenile salmon in Puget Sound were proportionally larger along deep armored shorelines compared to shallow beaches, suggesting that armoring created waters inappropriately deep for smaller fish (Munsch, Cordell & Toft 2016). In general, intact intertidal zones provide shallow depth gradients and habitat complexity that appear to support fish habitat functions and processes (e.g., predator refuge, prey production, reproduction, ontogenetic habitat shifts) that are compromised by armoring.

Overwater structures (e.g., piers, docks) are another type of infrastructure that threaten fish habitats. Overwater structures, particularly those that are large, low to the water, and supported by dense pilings create dark environments and high-contrast shadow edges. Many fish are visually-oriented and sudden decreases in light can reduce their performance of visual tasks (e.g., feeding; Ali 1959), which may cause them to avoid areas under overwater structures. Trapping along the Hudson River and New York-New Jersey Harbor estuaries showed that abundance and diversity of young-of-the-year fish such as silver perch (*Bairdiella chrysoura*), striped bass (*Morone saxatilis*), and seaboard goby (*Gobiosoma ginsburgi*) were lower under piers compared to pile fields and open areas (Able, Manderson, Studholme 1998; Duffy-Anderson et al. 2003). Additionally, sonar surveys along the Hudson River estuary indicated abundances of small pelagic fish such as anchovies (*Anchoa mitchilli*) and Atlantic silverside were lower under a large urban pier as compared to unshaded areas (Able et al. 2013). Larger predators such as striped bass aggregated in shaded areas at the pier's edge, raising concerns that they may exploit these areas to ambush smaller fish. An additional study in the Hudson River estuary found that abundances of small nektonic fish were lower under piers and piling fields during the day, but not night, suggesting that both piling structures and shading can affect fish distributions (Grothues, Rockovan & Able 2016). In Puget Sound, preliminary reports suggested that juvenile Pacific salmon avoided shade created by piers (Heister & Finn 1970; Southard et al. 2006). Building on these observations, more widely published snorkel surveys indicated that fish including salmon were less abundant in shaded areas and often aggregated next to shading (Toft et al. 2007; Munsch et al. 2014). In addition, overwater observations showed juvenile salmon swam to avoid shade cast by a dock (Ono & Simenstad 2014). Together, these studies generated concern that overwater structures interrupted the seaward migrations of anadromous salmon, and suggested that areas under piers provided poor fish habitat. In contrast, areas under a comparatively narrow pier and bridge that casted less intense shadows in the estuary of Rio Formoso (Brazil) were inhabited by greater abundances and a different trophic structure of fish than sunlit mangrove roots, probably because the piling structures provided a unique prey field (Pereira et al. 2016). Thus, it appears that overwater structures can reduce habitat connectivity and accessibility if they cast intense shade that impairs vision.

Studies have shown empirically that overwater structure shading can reduce feeding. A series of experiments in the Hudson River estuary found that visually feeding winter flounder (*Pseudopleuronectes americanus*) and tautog (*Tautoga onitis*) fed less and experienced negative growth rates when caged under large piers (Duffy-Anderson & Able 1999; 2001), and that shade rather than pier pilings (i.e., unshaded piling fields) affected feeding (Able, Manderson & Studholme 1999). A similar experiment along the Hudson River estuary showed that Atlantic tomcod (*Microgadus tomcod*) were able to feed under piers, but fed and grew more in unshaded areas (Metzger, Duffy-Anderson & Able 2001). In addition, snorkel surveys indicated that juvenile salmon under piers in

Elliott Bay were less likely to be observed feeding (Munsch et al. 2014). Overwater structures may also affect prey availability. Harpacticoid copepods and gammarid amphipods that are common in the diets of juvenile salmon were less abundant on seawall substrate (i.e., the primary intertidal substrate) under piers in Elliott Bay (Cordell et al. In Press), probably because shading diminishes the viability of their algal prey. Effects were different in the Hudson River estuary where invertebrates under piers were smaller but more abundant, resulting in similar prey biomass available under and adjacent to piers (Duffy-Anderson & Able 2001). Overall, piers may reduce habitat value by impairing small-scale (e.g., habitat shifts) and large-scale (e.g., migrations) connectivity, reducing or altering prey assemblages, reducing prey detection, and, (potentially) increasing predation risk.

Opportunities to Improve Modified Fish Habitats

Nearshore fish habitats can be rehabilitated along waterfronts within constraints of human use (see Dyson & Yocom 2015 for designs in urban systems) (Figs. 3 & 4), and there is growing, experimental interest in designing shoreline features to mitigate negative effects of modifications. Detrimental effects of armoring and overwater structures generally fall into categories of connectivity and accessibility, prey availability, predation risk, and reproduction (Table 1). These habitat attributes may be repaired by shoreline features that add complexity to the substrate, replicate or restore low-gradient beaches, add backshore vegetation, and mitigate overwater structure shading.

Table 1. Categories of habitat attributes and examples of assessments to examine them.

Habitat attribute	Assessment examples

Connectivity & accessibility	• Do physical or behavioral (e.g., shade avoidance) barriers prevent fish from accessing appropriate resources or environments? • Are there continuous shallow waters along shore? • Do areas of low predation risk overlap with profitable foraging patches?
Prey availability	• Are appropriate prey available? That is, how do prey assemblages and fish diets compare to more pristine conditions? • If prey availability differs, do fish consume alternatives, and at what costs (e.g., energy content of prey, evasion capability of prey)? • Is the prey assemblage appropriate for all juvenile phases? That is, does the prey field allow for ontogenetic diet shifts?
Predation risk	• Is refuge from predators available? In particular, is there a shallow depth gradient available to provide predator refuge or mediate ontogenetic habitat shifts? • Are substrates or biogenic structures appropriate for the fish assemblage (e.g., sand that enables burrowing, eelgrass and kelp that provide cover)? • Do habitat features attract predators or create environments that are advantageous for predators?
Reproduction	• Are appropriate substrates available for beach spawning? • Are currents (or lack thereof) appropriate for larval fish?

Along shorelines with moderate human-use constraints where true restoration is impractical, the natural intertidal grade can be replicated to create connected shallow areas. One approach is to construct waterfronts using nature-based materials to avoid or minimize the use of armoring (i.e., “living shorelines”). To date, research has focused primarily on fish assemblage responses (e.g., composition, abundance). For example, In addition, breakwaters were created by subtidal oyster reefs in Mobile Bay and Mississippi Sound (AL) as an alternative to shoreline armoring (Scyphers et al. 2011). These breakwaters inconsistently mitigated erosion but supported greater fish densities, particularly many demersal species, and different fish assemblages relative to adjacent unaltered sites of eroding coastline. Similarly, oyster reefs deployed in Caillou Lake (LA) had minimal effect on erosion but increased the densities of some fish species (hardhead catfish [*Arius felis*], gulf menhaden [*Brevoortia patronus*], Atlantic croaker [*Micropogonias undulates*], black drum [*Pogonias cromis*], and red drum [*Sciaenops ocellatus*]; La Peyre et al. 2014). In addition, a shoreline constructed of marsh plantings and a low-profile breakwater along Pine Knoll Shores (NC) supported greater abundances and diversities of fish (e.g., mullets [Mugil spp.], pinfish [*Lagodon rhomboids*], spot [*Leiostomus xanthurus*]) relative to bulkhead and even natural marsh shorelines (Gittman et al. 2016). In Biscayne Bay (FL), fish assemblages differed between natural mangrove and riprap-mangrove shorelines (Peters, Yeager & Layman 2015). A similar study in Delaware Coastal Bays indicated that a riprap-sill shoreline provided fish (e.g., Atlantic silverside, silver perch) density and diversity more similar to a reference smooth cordgrass shoreline than a conventional riprap shoreline (Balouskus & Targett 2016). These results are encouraging, and there are other potential benefits of nature-based approaches that have yet to be fully evaluated, such as refuge from predation and increased foraging opportunities.

In a highly urbanized application, a steep riprap shoreline along Elliott Bay was replaced by two shoreline types that created shallow, low-gradient waters: a sediment-nourished pocket beach with backshore vegetation and a habitat bench composed of compacted substrate in front of conventional concrete infrastructure (Toft et al. 2013). These waterfronts were robust to erosion and supported greater densities of larval fish and juvenile salmon. In addition, salmon were generally observed feeding along the habitat bench and pocket beach more often than along riprap and pre-enhanced shorelines. Relative to the pre-enhanced riprap shoreline, the beach and habitat bench supported greater production of juvenile salmon prey, particularly epibenthic harpacticoid copepods and amphipods, and terrestrial aphids. The pocket beach and habitat bench provided graded intertidal waters that supported ontogenetic habitat shifts in juvenile salmon from shallow to deeper waters that were not observed along shorelines where armoring eliminated shallows close to shore (Munsch, Cordell & Toft 2016). In a less urban area, restoring a seawall shoreline to a beach increased abundances of invertebrates inhabiting supratidal and vegetated tidal elevations within one year. Invertebrates at lower tidal levels, however, responded slower, suggesting that ecological responses may require several years depending on tidal elevation (Toft, Cordell & Armbrust 2014). Although not tested in the context of fish, a habitat skirt in Vancouver (Canada) similar to the habitat bench in Elliott Bay also created a graded intertidal area and supported habitat for invertebrates (Slogan 2015). Thus, restoring or replicating low-gradient shorelines may create corridors with greater prey availability and the opportunity for juvenile fish to select appropriate depths for refuge from predation.

Along shorelines where habitat improvements are constrained by human use of water and land, prey availability may be enhanced by increasing the complexity of armoring substrate. Although not evaluated in the context of fish prey, cavities (i.e., rock-pool mimics) in a seawall of Sydney Harbour (Australia; Chapman & Blockley 2009) created habitat for invertebrates. Compared to uniform seawalls, textured seawalls in Elliott Bay produced greater abundances of juvenile salmon prey such as harpacticoid copepods and chironomids, although invertebrate responses varied among years (Cordell et al. In Press). An additional, untested approach to increasing prey availability is to plant vegetation that overhangs seawall faces and facilitates insect "fallout" to waters below.

Overwater structure shading can be mitigated along shorelines to improve habitat connectivity for fish that avoid dark areas. A study in Puget Sound found that juvenile salmon swam closer to a dock when areas underneath were illuminated by fiber optic and halogen lighting systems, although the authors questioned the practicality of using electronics vulnerable to marine environments (Ono et al. 2010). Currently, a more pragmatic solution is to integrate light penetrating surfaces (LPS) into overwater structures that passively transmit light. A pilot study in Elliott Bay suggested that LPS (e.g., glass panels, metal grating, skylight) mitigated shading and improved accessibility for juvenile salmon under a large urban pier (Cordell et al. In Press). Subsequently, as part of a seawall re-build, a LPS migration corridor for juvenile salmon was constructed using glass blocks along Elliott Bay's urban waterfront (Cordell et al. In Press). Other, less tested options to mitigate shading include: increasing the height of overwater structures relative to water levels; decreasing overwater structure widths, particularly near shore; orienting overwater structures perpendicular to the sun's arc; using reflective materials or paint; and avoiding dense pilings (Nightingale & Simenstad 2001). In addition to facilitating large-scale movements, enhanced lighting under piers may also benefit fish by facilitating localized searches for food, habitat features, or conspecifics, allowing visually-oriented fish to detect predators and prey, and improving the production of epibenthic prey under piers.

Overall, there is great potential to reduce negative impacts of shoreline modifications through innovative waterfront features. It is important for management and research to coordinate the development, implementation, and evaluation of these features so that waterfronts can be designed to benefit fish within constraints of human use. By continuing to monitor innovative and experimental approaches to improve nearshore fish habitats, we can maximize their utility and application in diverse settings.

Moving Forward: Filling Knowledge Gaps & Adjusting Practices

There is still much to learn from evaluating shoreline habitats. Firstly, we need to understand why fish select for shoreline attributes by expanding habitat assessments to include a greater focus on metrics that directly indicate fish habitat value (Sheaves et al. 2015). Studies conventionally evaluate habitat using abundance metrics, which can imprecisely measure habitat quality because (1) abundance is only loosely correlated with true habitat value conferred by dynamic functions and processes (Sheaves et al. 2015), and (2) fish are mobile and may be locally abundant only temporarily, such as juvenile salmon along migration routes (Simenstad & Cordell 2000). Habitat features may simply aggregate fish without benefitting them, or attract fish to habitat mosaics of poor quality (similar to the contentious management role of artificial reefs). Ecologists can more directly assess habitat quality and fitness by examining capacity features that promote fish production (e.g., preferred prey availability, appropriate physical conditions), habitat accessibility (e.g., tidal flooding, continuous appropriate environments), and realized function (e.g., growth, feeding behavior; Simenstad & Cordell 2000). Given that we know shoreline modifications affect fish assemblages in many locations and that assessing nearshore biota is becoming feasible on large scales (e.g., emergence of environmental DNA sampling; Kelly et al. 2016), it is increasingly important to connect patterns in community composition to specific attributes so that habitat improvement efforts can address determinates of habitat quality directly. In particular, our understanding would benefit from manipulative studies (e.g., enclosing fish near shore) to verify localized costs (e.g., bioenergetics, predation) of occupying modified shorelines and (2) tracking studies to (a) examine habitat selection as it relates to shoreline modifications and (b) quantify any costs of absorbing change (e.g., opportunity costs, time and energy searching for appropriate habitats).

Our ability to manage nearshore fish habitats is also limited by gaps in our knowledge of natural history. Natural history encompasses the fundamental traits of organisms – what they are, how they behave, and how they interact with their environments and other biota (Tewksbury et al. 2014). In fish, this understanding is often incomplete (Able 2016), in part because studies typically use capture-based methods that preclude or degrade information on behavior and habitat use. Natural history information can guide local habitat improvements and place these efforts in the broader context of conserving fish populations, for example by empirically understanding: (1) species, life history stages, and life history types that use shallows directly next to shore; (2) quantitative food webs, accounting for ontogenetic diet shifts and prey selection; (3) habitat features that produce prey, provide protection from predators, or facilitate reproduction; and (4) the contribution of juveniles in nearshore waters to the ultimate production of the species (Beck et al. 2001). Natural history information is often collected passively (e.g., byproduct of research, local ecological knowledge) and should be disseminated (e.g., FishBase; Tewksbury et al. 2014) at incremental cost to existing studies into accessible media to make linkages between shoreline modifications and habitat values more intuitive (e.g., providing helpful "starting points" for investigations).

Future efforts to improve habitats will benefit from adaptive management and empirically verifying fish responses to habitat change. Firstly, the outcomes of habitat rehabilitation need to be documented by measuring impacts on fish rather than assumed. In situ metrics that relate to fitness (e.g., growth, survival) are ideal, but often impractically laborious to study; however, we can still evaluate habitat improvements through short-term studies that measure localized responses (e.g., bioenergetic estimates of growth, behavior). Secondly, it is important to incorporate adaptive, experimental management and learning in habitat improvement efforts by defining ecological objectives, monitoring thresholds, and actions triggered from thresholds, to ensure that fish benefit from these investments and inform future efforts (Fischman & Ruhl 2016). For example, a study may (1) set an objective to increase consumption of preferred prey by a specified amount for given fish species, (2) create habitat for prey by restoring a shoreline or implementing a habitat enhancement, (3) monitor fish diets before and after restoration or enhancement, and (4) if fish do not increase consumption of preferred prey, discuss projective alternatives such as whether to perform additional restorative measures or to increase consumption of a secondary prey item. Similar to our recommendations to disseminate natural history knowledge, management would benefit from documenting and communicating outcomes of habitat improvements in accessible media so that future efforts can employ and refine their methods. Thus, we can avoid "carrying out ecological modifications which are neither guaranteed to be necessary or successful but rather which make society (including ecologists) feel as though something is being done" (Elliott et al. 2016).

Managing Socio-Ecological Systems

Efforts to improve nearshore fish habitats should embrace their socio-ecological roles and leverage untapped appreciation for local nearshore ecosystems. Restoring or enhancing shorelines can improve fish habitats and create desirable public locations that foster appreciation for local ecosystems (e.g., Toft et al. 2013, 2014). Restored and recreated shorelines along urban parks such as Harlem River Park (New York City), Randall's Island Park (New York City), and Olympic Sculpture Park (Seattle) enhance recreational spaces, provide educational opportunities (e.g., organized events and kiosks that teach the public about local ecology [Fig. 5]), and connect people with "nature" in urban landscapes (*sensu* Hobbs et al. 2013). Exposing people to local ecology is important to create accountability between people and their local shoreline ecosystems. In particular, taxpayers that fund habitat improvement projects and property owners considering ecologically-conscious decisions about their own shorelines (e.g., Scyphers, Picou & Powers 2015) should understand the purpose of their investments. To our knowledge, fish responses to habitat rehabilitation along urban recreational shorelines have only been evaluated at Olympic Sculpture Park (Toft et al. 2013; but see preliminary work by Reid et al. 2015), and we consider such efforts great opportunities for further research because they align goals to create spaces that are desirable for fish and society.

Building on this, managers should target triple "wins" that benefit ecology, economy, and human safety (Elliott et al. 2016). As changes in climate, sea level rise, land subsidence, and sediment supply increase risk of flooding, nature-based coastal defenses provide potentially cost effective and ecologically beneficial alternatives to conventional shoreline infrastructure (Temmerman et al. 2013). In addition, many homeowners value the aesthetics and ecology of intact shorelines, but are misinformed about building costs, maintenance costs, and durability of different shoreline types, and armor their shorelines in response to damage caused by armoring on neighboring property (Scyphers, Picou & Powers 2015). Thus, homeowners may be incentivized to remove armoring along their shores through education about these costs, coordinated removal efforts among many adjacent properties, and subsidized construction of nature-based defenses and property insurance along shorelines at low risk to erosion. Another option is to provide tax breaks to property owners with ecologically functional shorelines (e.g., meeting criteria such as provision of intact shallow areas or intertidal substrates that produce fish prey), analogous to Leadership in Energy and Environmental Design (LEED) certifications for buildings. Shoreline restoration projects can also stimulate local economies by generating jobs and improving property values (Edwards et al. 2013; NOAA 2016). For example, a $10m project to restore shorelines along Lake Michigan is predicted to generate a return on investment of $66m, including increases of $12m in property values, $600,000 in annual tax revenue, and $1m in annual recreational spending (NOAA 2016). Thus, there is great potential to align ecological, economic, and human safety goals through shoreline rehabilitation projects.

Conclusions

Shoreline infrastructure modifies much of the world's coastal zone and drives change in the ecology of fish. This may impair the viability of habitats in ecological time and select against shoreline-oriented life histories in evolutionary time (i.e., reducing biocomplexity, *sensu* Schindler, Armstrong & Reed 2015). Our goal should be to avoid a no-net loss paradigm that "supports a degraded status quo" (Wilson, Mugerauer &

Klinger 2015) by striving for shoreline ecosystems that appeal to people and benefit fish. Habitat enhancement (Toft et al. 2013), ecological engineering (Bergen 2001), and educational efforts often require only a fraction of project budgets when building shorelines or replacing dilapidated infrastructure, yet they provide habitat functions while maintaining, and potentially improving, the value of shorelines to society. Many urban waterfronts are so removed from natural ecosystems that return to historical conditions is impractical (Hobbs et al. 2013), and urban settings provide experimental systems to develop modern habitat features that function within the constraints of waterfront use by people. Given uncertainties of climate change, it will be critical to progress from conventional waterfronts dominated by large, impervious surfaces that impair fish habitats, provide little protection from flooding, and create precarious situations of sea levels rising against built shorelines (i.e., costal squeeze; (Doody 2004; Cheong et al., 2013; Temmerman et al. 2013).

An updated management framework should: (1) empirically verify fish responses to shoreline modifications and habitat improvement, focusing greater attention on metrics suggestive of habitat quality and fitness; (2) develop and evaluate shoreline features that repair compromised habitat functions within human-use constraints; (3) collate regional knowledge of natural history to streamline habitat improvement efforts; and (4) embrace the socio-ecological role of habitat improvements by targeting ecosystem services and leveraging appreciation for nearshore ecosystems. More broadly, the research and management community should consider that the value of nearshore ecologists and habitat managers lies in their abilities to guide habitat improvements, connect people to nature, and elucidate natural history that may be poorly represented by metrics conventionally used to assess scientific output (e.g., publications, grant revenue).

By the 8th century, the metropolis of Ancient Alexandria entered a dark age. Much of its original waterfront is now underwater, as Roman engineers were unable to construct a waterfront resilient to earthquakes, tsunamis, and subsidence (Lawler 2005). Modern shorelines are built similarly, leaving coastal civilizations vulnerable to environmental stressors and burdened by maintenance costs of conventional infrastructure (Temmerman et al. 2013; Scyphers, Picou & Powers 2015). Given current challenges of climate change, sea level rise, and increasing coastal populations, we should move beyond millennia-old, unsustainable designs and invest in shoreline ecosystems that benefit fish and people over the long term.

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Figure 1. Top: A highly modified shoreline within an urban landscape. Bottom left: a shoreline modified by seawall armoring. Bottom right: a shoreline modified by a pier and floating docks.

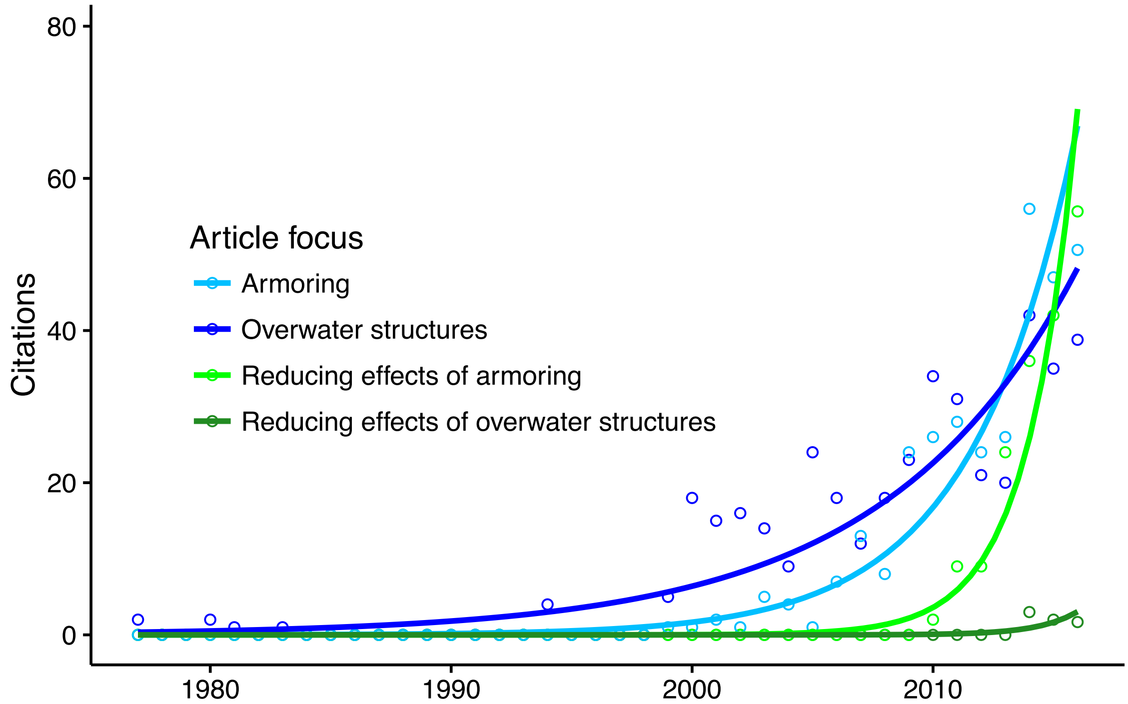

Figure 2. Time series of interest in research examining effects of shoreline modifications on fish, and reducing negative effects. Citations were counted using Google Scholar.

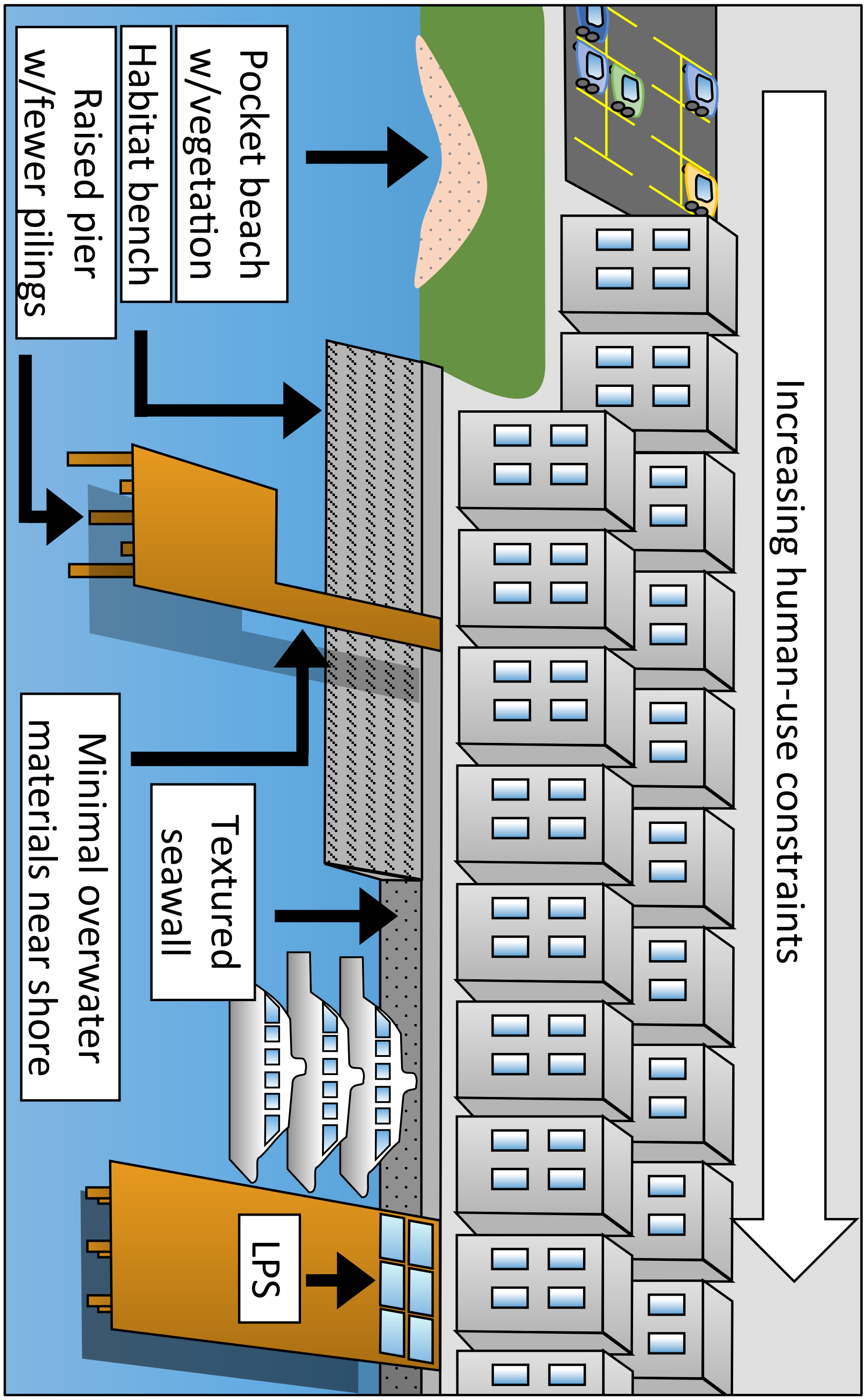

Figure 3. Schematic illustrating how shorelines features can improve nearshore fish habitats within constraints of human use. Shoreline features are described more thoroughly in Fig. 4. LPS: Light penetrating surfaces.

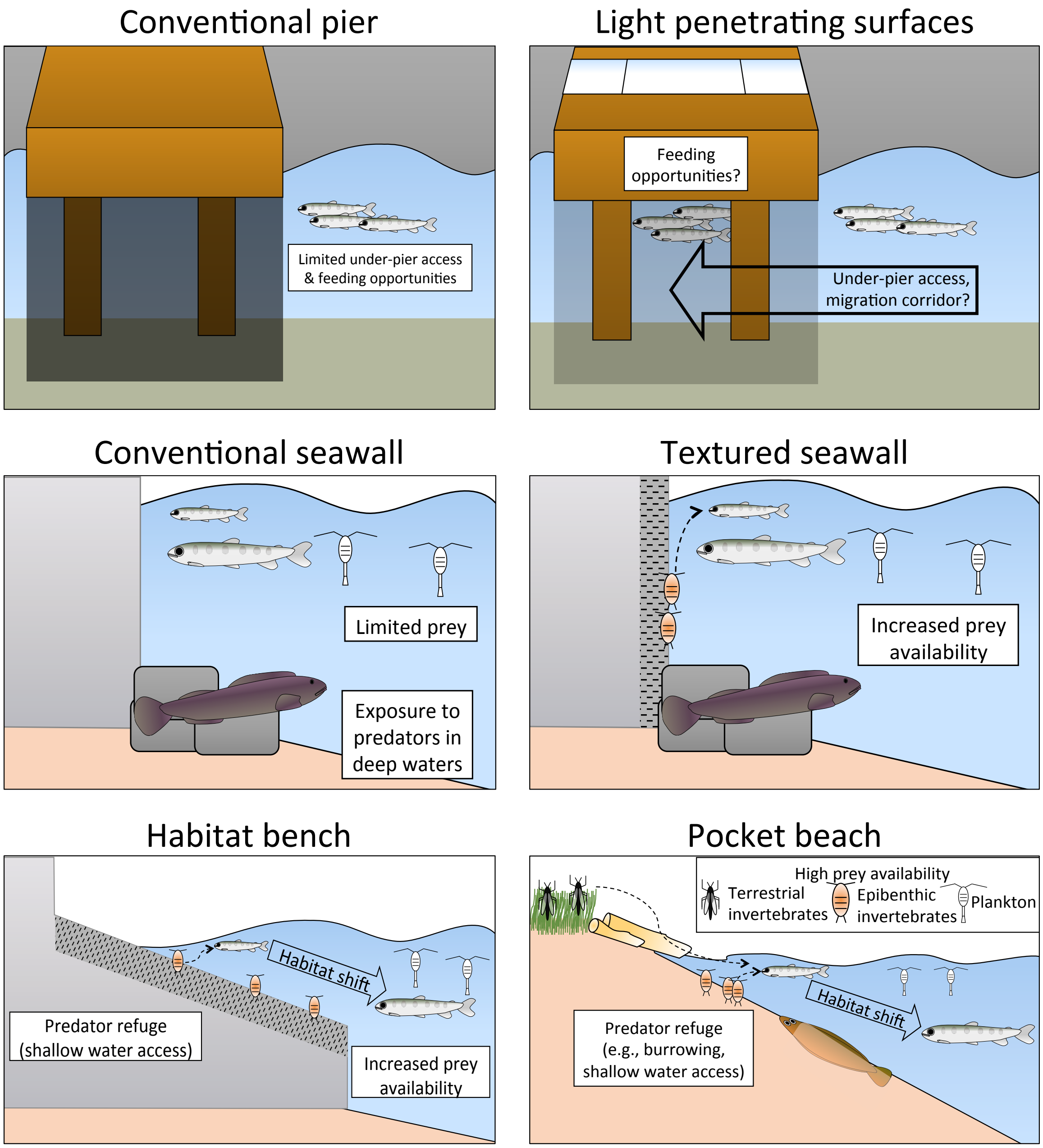

Figure 4. Conceptual models describing how fish habitats are affected by shoreline armoring, and how habitat improvements aim to mitigate negative effects. Question marks indicate conjectural (i.e., untested) habitat improvements. Habitat shifts: ontogenetic transitions from extreme shallows to deeper waters.

Figure 5. Kiosk along the downtown Seattle (WA) waterfront describing the local nearshore ecosystem and why a beach provides better habitat than the previous armored shoreline.

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Synthesis

Nearshore ecosystems support important fish habitats. The nexus of terrestrial, benthic, and aquatic realms can create shallow, structured waters that assemble prey and limit larger aquatic predators. Fish in Puget Sound aggregate in these shallows where they feed frequently, school, and select from a diversity of microhabitats (e.g., depths, substrates), often "considering" real-time information about their environment and themselves. The resources and environments provided by shallow waters support niches for residents and transient juveniles, benthic and pelagic species, and fish that transition habitats and diets as they grow. Thus, they enable choices, evolutionary adaptations, and processes that maximize fitness by facilitating growth and avoiding predation.

Shoreline modifications affect the ecology of fish by eliminating, restructuring, and shading nearshore waters. In our primary research, we found that armoring and overwater structures affected the assemblage composition, abundance, diets, behavior, and size distribution of fish. Our literature review indicated that similar effects occur in other systems, and that shoreline armoring also impairs spawning. These changes degrade habitat functions and processes such as the provision of prey, connectivity, predator refuge, ontogenetic habitat shifts, and reproduction. Despite likely impairment to their habitats, fish continue to use highly modified shorelines, including anadromous species that must migrate through developed areas. Given that shoreline modifications are common worldwide, it is plausible that the ecology and assemblages of many shallow waters differ from historical conditions and many fish habitats are compromised. Furthermore, as growing coastal populations and sea level rise increase demands to modify shorelines, we can expect negative effects to become more severe and widespread.

We can mitigate negative effects of shoreline modifications, including along waterfronts used by people. Ideally, we can restore shorelines (e.g., armoring removal) to re-establish lost ecological processes (e.g., beach formation and associated prey production) and habitat benefits (e.g., shallow sloping waters that allow fish to select appropriate depths). In many cases, true restoration is undesirable, but we may still mimic (e.g., nourished pocket beaches) or replicate (e.g., habitat benches) natural shoreline features that repair lost habitat functions. We can also avoid features known to degrade fish habitats (e.g., “living shorelines” that minimize armoring, piers that minimize overwater materials near shore). Along waterfronts where human uses constrain shoreline features, we must innovate and experiment to improve fish habitats. For example, we can construct piers using translucent materials, light areas under piers, add texture or relief to seawalls, implement “green” infrastructure (e.g., seawall tops that include or overhang vegetation), and recruit biogeneic structures (e.g., kelp eelgrass). Innovation, however, evokes a more fundamental question of what nearshore ecosystems we wish to support because novel shoreline features create non-historic ecosystems. Should we design waterfronts to recreate historical ecosystems, or to maximize other metrics (e.g., diversity, abundance)? Do our opinions change if non-historic ecosystems benefit species of conservation concern or if restoration is implausible? While we must continue to define management goals in highly impacted systems, there is clearly great potential to improve fish habitats along modified shorelines.

We can improve our ability to protect nearshore fish habitats by adjusting how we research and manage them. First, we must use incisive metrics to evaluate habitats. There are many studies that show fish abundances vary among shorelines with different features, but there are few that explain why. To protect habitat features, environments, or processes, we must know what they are and how they benefit fish. This requires us to go beyond catching fish; we must observe them underwater, collect their diets, and perform manipulative experiments. This will enable us to establish relationships between habitat attributes and determinants of habitat quality (e.g., growth, predation avoidance, reproduction).

Second, we must develop and test innovate shoreline features that allow us to improve nearshore fish habitats among a range of human-use constraints. Research is currently at a frontier in how to improve habitats along urban shorelines, and our understanding will benefit from an experimental approach that is willing to risk failures en route to developing ecologically-beneficial shoreline designs. It is important to scale localized pilot studies to larger stretches of shorelines (e.g., entire built waterfronts) to evaluate habitat improvements on scales that can rehabilitate meaningful portions of modified shorelines or target the full extent of extremely modified shorelines (e.g., urban centers).

Third, we must understand the natural history of nearshore ecosystems. That is, we must have a quantitative, empirical understanding of how fish use their habitats and why. Questions such as “what do fish eat?”, “what eats them?”, “how do fish avoid being eaten?”, “when do fish feed?”, “where, within nearshore ecosystems, do fish occur?”, “what are the symbiotic relationships in a given nearshore ecosystem?”, “what physical environment does a fish need", "how does nearshore habitat quality affect overall fitness?", and "what is the contribution of a given nearshore ecosystem to the overall population of a species" lead us to ask perceptive research questions and contextualize management decisions. Datasets that provide this information in quantitative terms are often characterized by high ratios of signal to noise. As shown in this dissertation, long-term, large datasets can be used to elucidate natural history attributes of nearshore ecosystems because they allow us to find signals within noise. Similar to evaluating habitats using incisive metrics, a more in-depth understanding of natural history requires that our observations go beyond catching fish.

Fourth, we should seek to align objectives to improve shorelines for fish and people. Restoring or enhancing shorelines can benefit people directly by creating recreational and educational spaces, improving property aesthetics and value, or increasing resilience to flooding. Natural and semi-natural shorelines are venues for socializing, exercise, weddings, photography, field trips, camping, bird-watching, tide pooling, and science camps. Local communities may embrace proposals to improve fish habitat if the benefits to people are clearly communicated. Ideally, shorelines created by habitat improvement efforts will reconnect people with natural shorelines and show them why we should invest in the protection of nearshore ecosystems.