



Nearshore fish abundance in an urban estuary is weakly associated with shoreline conditions across spatial scales

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ABSTRACT: Understanding the scale at which species respond to habitat characteristics can improve detection of effects from anthropogenic alterations to marine shorelines. Spatial context matters because habitat alteration may have more of an effect when prevalent throughout a region, depending on the spatial scale at which species experience changes in habitat value. In this study, we examined the associations of 4 highly motile fish species with shorelines that are altered via shoreline armor. We sampled fish for 4 yr in the Salish Sea, Washington, USA, and used model selection to evaluate the weight of evidence for associations between fish abundance and shoreline armor extent within hierarchically nested spatial scales. We evaluated species that inhabit nearshore waters under different contexts during their life histories because we expected different associations with armor between them. Of the species that are beach-associated at multiple times during their life histories, surf smelt showed no association with armor while Pacific herring showed a negative association, particularly at larger spatial scales. Of the species that pass through nearshore habitats during outmigration to the ocean, juvenile Chinook and chum salmon both showed slightly positive associations with armor presence, but these associations were not strong. The stronger association we observed in herring suggests that they may avoid areas with greater armor presence throughout a region. Distributions of anadromous species during migration are likely governed by other factors. This work highlights the importance of maintaining ecological context when considering future research aimed at understanding the impacts of shoreline armor on fish populations.

KEY WORDS: Multiple spatial scales · Pacific salmon · Forage fish · Nearshore · Habitat associations · Shoreline armor · Salish Sea

1. INTRODUCTION

Anthropogenic modifications of coastal landscapes often change the abiotic and biotic characteristics of the impacted area (Bulleri & Chapman 2010, Cook-Patton et al. 2014). Modifications can promote diver-

sity and enhance ecosystem function (Lepofsky et al. 2021), or they can disrupt function and transform nearshore habitats in ways that reduce the degree to which ecosystems can support valued species (Brown et al. 2018). The effects of modification can vary across taxa, and this taxonomic variation is often a

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function of the spatial scale of the alterations. For instance, a small localized patch of shoreline modification may decrease productivity for infauna that are relatively site-attached or spend the entirety of critical life stages within small areas, while having less of an effect for species with wider ranges (van Diggelen 2006). Low connectivity between subpopulations can also limit the impacts of local habitat degradation to the overall population (Fischer & Lindenmayer 2007). Understanding the relationship between scale and the response of different species to habitat change—especially within the context of local conditions—can provide insights into the cumulative impact of anthropogenic modifications for ecologically and culturally valuable species.

The scale dependency of habitat modification impacts may be relevant when landowners armor marine shorelines. Armor refers to structures (e.g. seawalls, bulkheads, rip-rap) that reduce or prevent natural erosion of shorelines and protect upland development (Griggs 2005). This disruption of the sediment supply changes the profile of the waterline, resulting in beaches with coarser sediment, smaller backshore width, and reduced intertidal area (Dugan et al. 2008, Bulleri & Chapman 2010, Ruggiero et al. 2010). The effects of armor can extend into the adjacent subtidal environment and can influence the integrity of associated biotic communities in nearshore habitats (Seitz et al. 2006, Bilkovic & Roggero 2008, Kornis et al. 2018). Conversely, restoration via armor removal is a popular and effective restoration strategy for reinstating geomorphic processes and revitalizing ecosystem function (Toft et al. 2021). Understanding the impacts of armor, and its removal, is a priority interest for developed coastal communities.

Several studies have indicated that shoreline armor influences the adjacent nearshore fish community (Gittman et al. 2016, Munsch et al. 2017). For instance, armor may alter the prey field (Toft et al. 2007, Partyka & Peterson 2008, Heerhartz & Toft 2015, Munsch et al. 2015) because reduction of beach area means less space for organic material to accumulate (Heerhartz et al. 2014), resulting in a lower abundance and diversity of intertidal invertebrates (Sobocinski et al. 2010, Des Roches et al. 2022). Additionally, distributions of small fish shift deeper due to loss of shallow-water habitats (Toft et al. 2007, Munsch et al. 2016, Kornis et al. 2017), but the extent to which armor affects nearshore fish is largely unknown (Francis & Kinney 2018). This is, in part, because fish can be highly motile, and species that swim large distances will inevitably experience shoreline habitat differently than species that are more res-

ident or site-attached. Moreover, the length of discrete stretches of armored shoreline can be small, relative to both the shoreline length of an estuary and the amount of shoreline used by wide-ranging species. Therefore, evaluating habitat associations for fishes while considering the context under which they inhabit the nearshore, and how that might dictate the scale at which they respond to habitat cues, is important to assess the impacts of shoreline armor on nearshore nekton.

Fish response to armor may be driven, in part, by the extent to which flexible behaviors that facilitate avoidance of armored shorelines occur during different life histories (Lowe & Peterson 2014). For example, Francis et al. (2022) evaluated how local subtidal abundances of 2 species of Pacific salmon and 2 forage fish species varied among short (<30 m) segments of different shoreline type, being either armored, natural in upper intertidal habitats, or restored (i.e. armor has been removed). They found that the abundance of the 2 forage fish species varied by shoreline type, among other factors, while the abundance of salmonids was not associated with shoreline type. One potential reason for the different responses to shoreline structure between forage fish and salmonids is their different life histories: salmonids migrate to the open ocean and may respond to habitat mosaics that occur at larger spatial scales. Many forage fish hatch on or near shore, linger close to spawning grounds initially, and then move offshore but do not generally move directionally along a nearshore pathway (Penttila 2007). In contrast, anadromous salmon undergoing migration may have less opportunity to avoid exposure to degraded habitats because their movements are restricted, relative to fishes that are able to move freely between nearshore habitats during some periods of their life history.

Our objectives for this study were centered on understanding how fish species with different life-stage-specific movement ecologies respond to armor presence locally and as compared to armor extent characterized at larger spatial scales. Specifically, we sought to understand whether the patterns of association between fishes and shoreline armor varied between scales of ecological function, and we did so by evaluating the relationship between armor extent and fish abundance in adjacent habitats at multiple spatial scales of armor context. We conducted this work in the Washington State boundaries of the Salish Sea, USA, where 29% of shorelines have some form of armor (MacLennan et al. 2017). The Salish Sea, spanning the USA and Canada, is a valuable model system for exploring the effects of armoring

because it contains urban, urbanizing, and wilderness areas that provide opportunities to contrast types of shoreline that fish may encounter. We hypothesized that armor would have a negative effect on fish abundance and that this effect would be stronger when observed at larger spatial scales, as the cumulative impacts of armor may increase when shifting from local to regional extents (Peterson & Lowe 2009, Dethier et al. 2016, Kornis et al. 2017). We also hypothesized that life history differences would amplify or determine responses to habitat quality at different spatial scales, so we evaluated abundances of species representing 2 life histories. We predicted that the effect of armor presence on fishes that are beach-associated at various times during their life histories would be stronger than the effect on juvenile anadromous fishes, which would be more constrained in their ability to select for high-quality habitats during their outmigration.

2. MATERIALS AND METHODS

We collected and analyzed a 4 yr time series of *in situ* fish count data collected in nearshore subtidal zones at 12 sites throughout the southern Salish Sea to examine how patterns of fish abundance relate to shoreline armor presence. We collected these data during periods when we expected peak fish presence, at sites that are characterized by different degrees of armor extent across multiple hierarchically nested spatial scales. We used statistical analyses with fish count as a response variable to identify associations between fish abundance (represented by count) and amount of shoreline armor at a subset of spatial scales, then conducted a comparative analysis to evaluate whether the subset of scales we selected had influenced our conclusions about the nature of these associations. We further asked how those associations, if any, differ between species representing different life histories.

2.1. Study sites

This study builds on field sampling described by Francis et al. (2022), which was focused on local effects of armor (and restored shorelines) on local fish abundances. We used the same sampling protocol and the same sampling sites, but added additional sites and years of study. Our field sampling program targeted juveniles of 2 resident species, Pacific herring *Clupea pallasii* and surf smelt *Hypomesus pretio-*

sus, and 2 anadromous species, Chinook salmon *Oncorhynchus tshawytscha* and chum salmon *O. keta*. Pacific salmon (*Oncorhynchus* spp.) are iconic within this region and they, along with forage fish, provide key linkages within the local marine food web (Ford & Ellis 2006, Fox et al. 2018, Sobocinski 2021). We selected sampling sites that covered a broad spatial area to maximize our ability to characterize fish abundance across these diverse nearshore habitat conditions (Fig. 1). When selecting sampling locations, we considered accessibility, the proximity of shoreline types

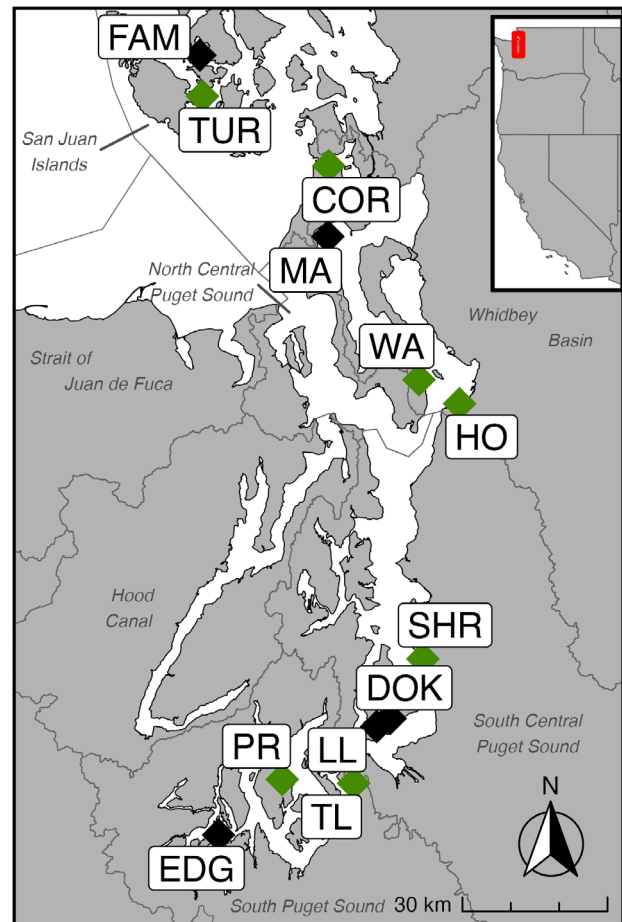


Fig. 1. Study area and sampling sites. Three-letter codes represent core sites (FAM: Family Tides; TUR: Turn Island; COR: Cornet Bay; SHR: Seahurst Park; DOK: Dockton Park; EDG: Edgewater Beach) that were sampled monthly from April to September over 4 yr. Two-letter codes represent supplemental sites (MA: Maylor Point; WA: Waterman Preserve; HO: Howarth Park; LL: Lost Lake; TL: Titlow Park; PR: Penrose Point) that were sampled in June during the last 2 yr. Sites with a green square have eelgrass present. Labels in italics are PSNERP (2010) basins of the southern Salish Sea that are represented in the analyses. Inset shows the location of the study area in Washington State, on the US west coast

within a littoral drift cell, and bathymetry. Our sites were most often characterized by wide, gradually sloping, mixed-sediment beaches, although our northernmost sites, in the San Juan Islands, contained pocket beaches within rocky shorelines. Half of our 12 sites contained eelgrass (*Zostera* spp.), which is an important foraging habitat for both Pacific salmon and forage fish (Kennedy et al. 2018, Rubin et al. 2018, Chali-four et al. 2019). We determined eelgrass presence from the Department of Natural Resources Submerged Vegetation Monitoring Program website (<https://www.dnr.wa.gov/programs-and-services/aquatics/aquatic-science/puget-sound-eelgrass-monitoring-data-viewer>) and confirmed via field observations (Fig. 1).

Of the 12 sites, we sampled 6 'core' sites monthly (April to September) in 2018, 2019, 2021, and 2022 (Francis et al. 2022), and 6 'supplementary' sites only in June of 2021 and 2022. Each site consisted of 1 armored, 1 restored, and 1 reference (natural in upper intertidal habitat) shoreline segment, except for Turn Island, which consisted of 2 reference and 1 armored segment. Restored shorelines were areas where armor removal had occurred within the last 3–10 yr. We included reference shorelines because full recovery of biological processes in restored marine ecosystems can take decades (Borja et al. 2010) and therefore fish associations with recently restored shorelines may be different from natural or armored shorelines. Shoreline segments within a site were all approximately 30 m long and of variable distance to each other, within the same littoral drift cell (within about 1 km). By doubling our survey effort with supplementary sites in June for the last 2 yr of sampling, we increased spatial coverage and the power to detect an effect of shoreline armor during the likely period of seasonal peak abundances of target species. More details about site characteristics and sampling effort are available in Table S1 in the Supplement at www.int-res.com/articles/suppl/m750p105_supp.pdf.

2.2. Field methods

We sampled fish using a boat-towed lampara net at 3 depth stations directly offshore from each shoreline segment. The net, which is similar to a purse seine, measured 37 m long at the surface and 35 m long at the bottom with a maximum 4.6 m depth and mesh size ranging from 48 mm at the ends to 6 mm in the central bunt. The shallowest station was approximately -1 m depth relative to Mean Lower Low Water (MLLW), the middle station was approximately -3 m depth (re. MLLW), and the deepest sta-

tion was 50 m directly offshore from our -3 m depth station. Straight-line distances between shallow and deep stations were typically between 50 and 120 m, the exception being Maylor Point, which had a maximum distance of 224 m (Table S1). Our target sampling window was between tide heights of $+1.5$ to $+0.5$ m (re. MLLW). Each month during the sampling period, we set a lampara net from a boat once per depth station (nested within shoreline type) at a site and then identified every fish captured to the lowest taxonomic group possible and counted the number of individuals of each species. We additionally measured body lengths for the first 20 individuals of each species to assess the size distributions within our sample. All procedures were conducted with appropriate state and federal permits, and all fish were immediately returned to the water after sampling.

We summarized the number of individuals representing each target species captured in each lampara net set for focal species by site and by month within the sampling interval. We additionally report catch per set by depth station, summarized across sites and sampling occasions, and summaries of the lengths of individuals by species captured at each depth station.

2.3. Spatial analyses

To characterize the extent of shoreline armor within the southern Salish Sea, we obtained data from the Beach Strategies Geodatabase (MacLennan et al. 2017). Construction of the database, under the Puget Sound Nearshore Estuarine Research Program (PSNERP), involved mapping armor extent throughout the region based on known data, with ground-truthing in priority areas. First, we updated the 'Beach Strategies' geospatial data layer (Esri shapefile) to reflect armor removal projects that occurred at our sampling sites since the database was last updated in 2016. Within the Dockton site, a restoration project occurred directly adjacent to our shoreline segments in 2020, so we made a second updated armor extent shapefile, with that segment of armor removed, to use for analysis with catch data post-2020. We did not update this shapefile with any other documented armor removal segments since 2016 because we did not observe the extent of these restoration projects first-hand, which is useful for accurate updates to the armor shapefile. There is also evidence for unpermitted and under-documented new armored structures in the region (Whitman 2022), so a marginal amount of armor presence and absence cannot be accounted for.

We used a Garmin® GPSMap 740s® chartplotter to acquire site and station geocoordinates at each shoreline type for each site, then used the 'sf' package version 1.0-12 (Pebesma et al. 2023) in R (R Core Team 2021) to generate a centroid point to represent each site as a whole. We snapped centroids to the nearest shoreline feature at each site, then created circular buffers around the points, with radii corresponding to 10 concentric spatial scales (100, 300, and 500 m, and 1.2, 3, 5, 7, 10, 15, and 20 km) chosen to represent the range of habitats that fish experience, from local to landscape. We evaluated 1.2 km specifically because that distance incorporates all shoreline segments within our most widely spread core site (Cornet Bay). Notably, this means that scales less than 1.2 km should be considered 'within-site'. Because of the proximity of some sites, some buffers overlapped between sites at spatial scales larger than 1.2 km. We additionally created a 'basin' scale by cropping the updated armor shapefile to the PSNERP Puget Sound Basins (PSNERP 2010), which represent the semi-distinct water bodies within the region. We calculated percent armored shoreline at each hierarchically nested spatial scale by dividing the length of armor by the length of shoreline within each buffer at each site. Finally, we repeated this procedure for calculating the percent of armored shorelines within PSNERP basin boundaries.

2.4. Statistical analysis

Our objective was to evaluate how local abundance of our focal species was related to the presence of shoreline armor across spatial scales. In an ideal analysis, we would embed the geographic computation of percent armor into a single statistical model given a spatial scale and identify the spatial scale at which the relationship between shoreline armor and fish abundance is strongest for each species. However, these computations are slow (made even slower by the need to integrate over the random effects of sampling sites) and are not guaranteed to converge. For that reason, we conducted our analysis using 2 less computationally demanding steps. In Step 1, we identified plausible alternative models that each represent armor presence differently, some including percent surrounding armor, then performed standard multi-model inference. In this step, models that included percent armor were evaluated as 3 different versions, where each version included percent armor within a different spatial scale (500 m, 1.2 km, and 10 km), chosen to span a range of relatively local to larger dis-

tances. This allowed us to identify whether model selection supports including the term for percent shoreline armor for any species at any scale, while also limiting the number of models we evaluated within our model selection process, which is important to prevent overfitting (Burnham & Anderson 2002). In Step 2, we evaluated whether our model selection results were robust to the choice of these 3 *a priori* spatial scales by calculating effect sizes for the full model evaluated at a wider range of spatial scales. This second step revealed whether other spatial scales yielded markedly different estimated coefficients for effect sizes of the percent armor parameter from those included in the model selection analysis.

For both Step 1 and Step 2, we used generalized linear mixed models with sample catches of fish summed across the 3 depth stations sampled at each shoreline as a response variable. Because our count data were overdispersed, we built our models with a negative binomial likelihood function and a log link where the number of individuals of a given species summed across the 3 depth stations y on a given day i is a function of mean μ and an overdispersion parameter k :

$$y_i \sim \text{NegBinom}(\mu_i, k) \quad (1)$$

We selected several predictor variables that were not central to our hypothesis but that we expected to account for local variation in fish abundance. We included a fixed effect of year (categorical with 4 levels: 2018, 2019, 2021, and 2022) to account for annual variation in abundance. We included a quadratic term for day of year (continuous, scaled around zero) to account for a natural peak abundance of juvenile salmonids during outmigration and peak abundance of forage fish given the selectivity of our net and their spawning phenology. In addition, we accounted for variation among sampling sites by assuming that there were differences in sampling sites related to presence of eelgrass and latent effects. Eelgrass was represented by the term 'veg' (categorical with 2 levels: present or absent). Latent site effects were modeled as random effects, with a mean of 0 and an estimated standard deviation σ . Together, these covariates comprise the base model, following the notation of Gelman & Hill (2006):

$$\log(\mu_i) = \text{site}_{j[i]} + \beta_2 \text{year}_i + \beta_1 \log(\text{day of year})_i + \beta_3 \log(\text{day of year})^2_i + \beta_4 \text{veg}_i \quad (2)$$

$$\text{site}_j \sim \text{Normal}(0, \sigma^2) \quad (3)$$

where observations were represented by sampling event i and intercepts varied by group (site) j . Here,

year_{*i*} is a row vector containing 0s and 1s to indicate the year the sample was taken, and β_1 is a column vector of the estimated effect sizes for each year. The estimates for β_2 and β_3 are slopes indicating the effect size for the continuous values associated with $\log(\text{day of year})$ and $\log(\text{day of year})^2$, the inclusion of which enables a dome-shaped relationship that accounts for a natural peak in abundance that approaches zero at the beginning and end of the season. We tested the full analysis with different functional forms, one symmetric (untransformed) and one with a longer right tail (log transformed), and there was no clear difference in model fit among them. We chose to use the form with the longer right tail because of the biology of our focal species, particularly salmon, which exhibit a rapid initial release and then distribute slowly thereafter. Finally, veg_i takes the value 1 if vegetation is present and 0 if absent, and β_4 indicates the effect size associated with the presence of aquatic vegetation.

We then built models to represent the effects of shoreline armor by adding predictors to the base model. The first of these included a fixed effect of shoreline type (categorical with 3 levels: armored, restored, or reference). We included this predictor variable because the study design intentionally included sampling at these 3 shoreline conditions within each site. Additionally, including local shoreline condition might reveal the relative importance of the spatial extent of local versus regional armor on fish densities. To address this second purpose, we examined the estimated coefficient for shoreline condition in any well-supported model that included local shoreline type, to confirm that the model support stemmed from an estimated armor effect relative to reference or restored shoreline types. The next 3 models included a continuous term for percent shoreline armor, each at a given scale (500 m, 1.2 km, or 10 km). The final 3 models included both the shoreline type term and the percent armor term, with a separate model evaluated for each of the 3 scales of percent armor. We provide the full equation for each model in Table S2. We inspected the independent variables for multicollinearity using the 'ggpairs' function in the 'GGally' package version 2.2.1 (Schloerke et al. 2024). The only significant correlation was between the day of year and quadratic day of year terms, which does not affect our conclusions because these are not the primary variables of interest.

In Step 1, we compared the 8 different models for each of the 4 focal species using Akaike's information criterion corrected for small sample sizes (AICc) (Akaike 1973, Hurvich & Tsai 1989, Burnham & Anderson 2002). We followed common practices to

identify the set of candidate models that are supported by the data. For non-nested models, we used the rules of thumb from Burnham & Anderson (2002) whereby models with $\Delta\text{AICc} < 2$ cannot be dismissed from consideration because they have similar degrees of support from the data, models with $\Delta\text{AICc} > 10$ are not supported by the data, and intermediate levels of ΔAICc represent a continuum of model support. However, following Leroux (2019), we applied additional procedures when pairs of models had $\Delta\text{AICc} < 2$, but one model was more complex than the other. This is necessary to remove 'uninformative parameters', and by extension, models that are not well supported compared to others. Here, the more complex model is dismissed if it has a higher ΔAICc than a simpler version of that model, the log likelihoods are virtually identical, and the standard errors for the additional parameters overlap zero. Collectively, these 'warning signals' indicate when the additional parameters do not improve model fit and should be interpreted as unimportant (Leroux 2019). For instance, if the base model had ΔAICc of 0, and an alternative model had ΔAICc of 1 and a log likelihood that is not significantly higher, the latter would be dismissed because it is a more complex version than the simpler base model but did not have an improved model fit. For our Step 2, we fit the full model with both the shoreline type and percent armor term for each species, using a different spatial scale to calculate percent armor in each model. We fit all of our models using the 'glmmTMB' package version 1.1.7 (Brooks et al. 2023) in R version 4.3.0 (R Core Team 2021), extracted summary statistics using the package 'AICcmodavg' version 2.3.2 (Mazerolle 2023), and conducted diagnostics for the models with the lowest AICc value for each species using the package 'DHARMA' version 0.4.6 (Hartig & Lohse 2022) and 'performance' version 0.12.0.8 (Lüdecke et al. 2024). The equations for the models with the lowest AICc values and the results of the diagnostic tests are given in Text S1 and Figs. S4–S8, respectively. Code to reproduce this analysis is available at https://github.com/e-bish/Armor_Across_Scales.

3. RESULTS

3.1. Sampling summary

Over the 4 yr of field sampling of our target species, we caught 942 Chinook salmon, 2456 chum, 815 her-ring, and 303 surf smelt. Fish distribution within our sampling stations was often patchy, and sometimes

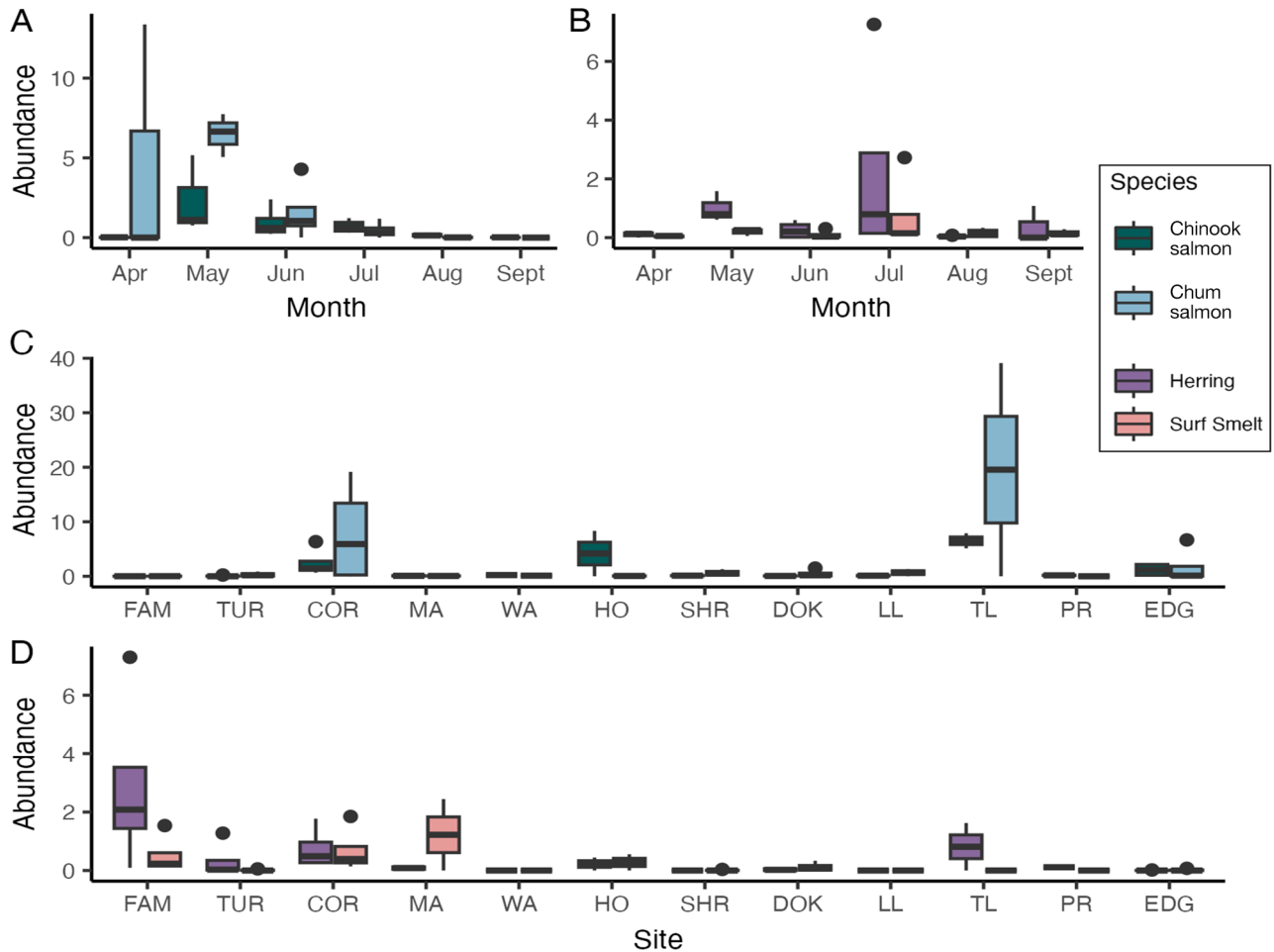


Fig. 2. Trends in catch across 4 survey years. Abundance is represented by the number of individuals captured in a single lampara net set and varied by month (April to September) for (A) anadromous salmonids and (B) intertidal spawning forage fish. Catch for all species was highly heterogeneous because all of the target species exhibit schooling behavior. Abundance also varied by site, ordered from north to south (see Fig. 1), for (C) salmonids and (D) forage fish. Boxes represent the interquartile range (25th to 75th percentile) of the data, the horizontal lines within the boxes represent medians, and the vertical lines represent the extent of the data (box boundaries $\pm 1.5 \times$ the interquartile range). Values outside of this range are represented as solid points

we caught large schools. Average catch rates varied by month, and these patterns were different for each species (Fig. 2). Average catch per set was greatest in May for both salmonid species and remained elevated through July (Fig. 2A), while there was no discernable seasonal pattern of mean catches for the forage fish (Fig. 2B). Average catch rates varied between locations but did not indicate any spatial gradient (Fig. 2C,D). For salmonid species, average catch rates were greatest at our shallowest depth station, while for forage fish, average catch rates were greatest at the middle depth station (Fig. S1). There was no apparent difference in mean fish size among the 3 depth stations for any species (Fig. S2), and few differences in size between sites except at Family Tides and Turn Island, where herring were generally smaller than at other sites (Fig. S3).

3.2. Percent armor by scale and site

Patterns of armor extent at a given scale varied between our sampling sites (Fig. 3), providing important contrasts to detect differences at the spatial scales we chose for model selection. Across all sites, percent armor within a 500 m radius ranged from 0% at Maylor Point to 100% at Howarth Park. In comparison, there was less variability among sites with respect to percent armor at larger (10 km) scales, where sites ranged from 6.45% armor at Family Tides to 65.9% armor at Titlow Park. The highest percent shoreline armor occurred at different spatial scales at different sites; in some cases, the percent armoring was highest at small scales (i.e. 100–500 m; see Howarth Park and Titlow Park) and sometimes it was highest at large scales (i.e. 15 km to basin-scale; see

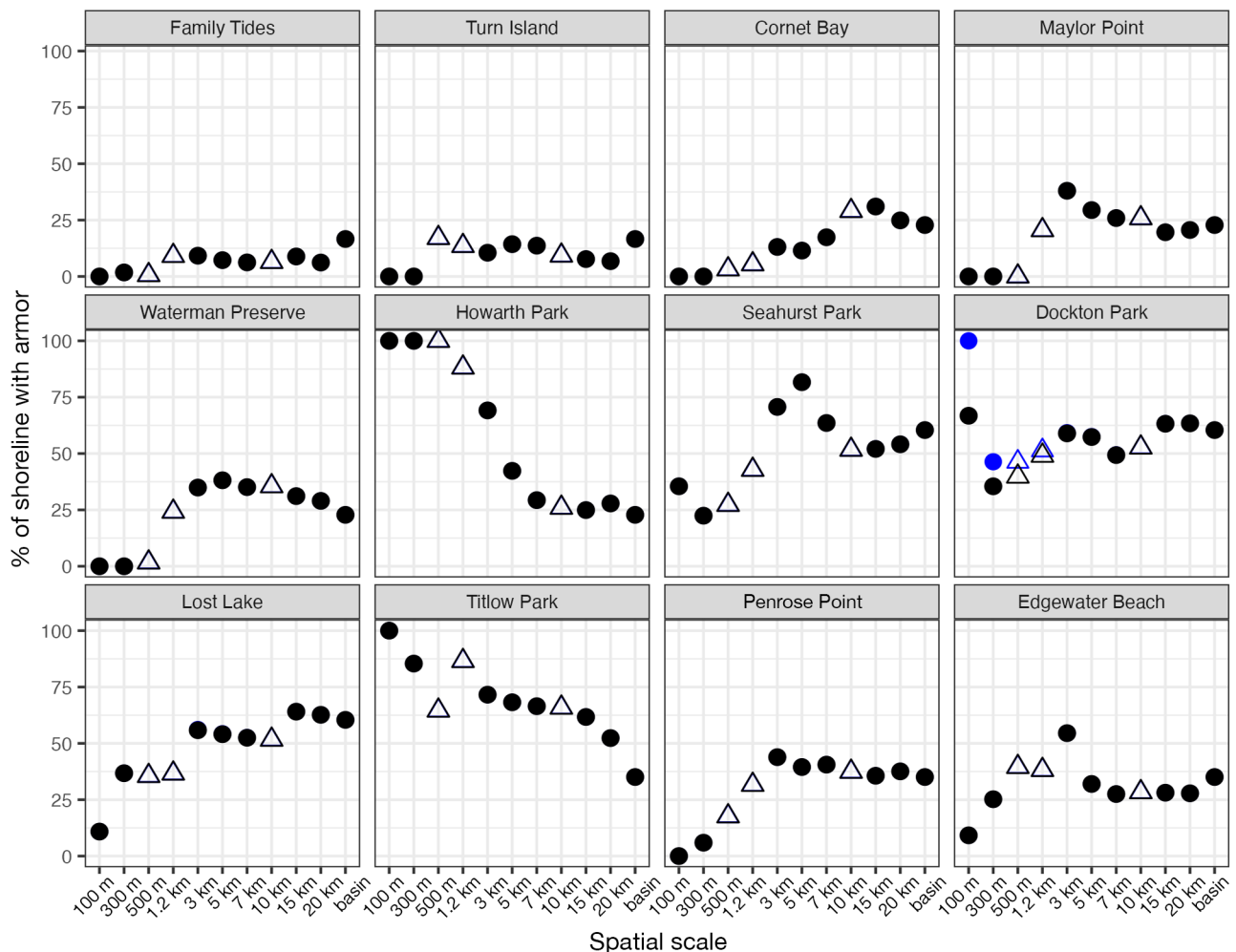


Fig. 3. Percent shoreline armor by spatial scale for each sampling site. Sites are ordered from north to south. At Dockton Park, the points in blue represent armor extent prior to a restoration project where 68 m of armor were removed in 2020. Hollow triangles represent the 3 spatial scales we used for model selection

Family Tides and Lost Lake). Armor was overall more prevalent in the central and southern extents of our study area compared to the northern sites (Fig. 3).

3.3. Model selection

Through AICc-based model selection, we found modest support for models that included regional percent armor as a parameter for every species except surf smelt at one or more spatial scales (see Tables 1 & 2). For Chinook salmon, the base model and the models that included percent armor at 500 m and 1.2 km scales were best supported by the data (Table 1). While the latter models had marginally more support, the weight of evidence is not strong enough to rule out support for the base model (Table 1). Moreover, the ΔAICc among models with different spatial scales were broadly

similar. However, among the well-supported models, the estimated effect size of percent armor was positive, contrary to our expectations. For chum, there was no support for the model that only included percent armor (Table 1). The only models that outperformed the base were the models that added shoreline type alone, and shoreline type with percent armor within a 10 km radius. However, as with Chinook salmon, the base model could not be entirely dismissed from consideration based on differences in ΔAICc . The estimated effect size for the armored shoreline type was of greater magnitude than the restored shoreline type (Fig. S4), indicating that the significance of the shoreline type variable was driven by armor presence rather than characteristics of restored shorelines. However, the effect size was positive, contrary to our expectations.

Model selection results for forage fish species also indicated only modest support for models containing

Table 1. Differences in model selection criteria (based on differences in Akaike's information criterion corrected for small sample sizes, ΔAICc) applied to counts of Chinook and chum salmon across 12 sites in the Salish Sea. We evaluated 8 candidate models, 7 of which built upon the base model that included covariates for year, day of year, vegetation presence, and a random effect of site. Additional parameters in more complex models included the % of surrounding shoreline with armor at a radius distance, and shore type (armored, restored, or reference). In this table, K represents the number of parameters estimated in the model, LogLik is the log-likelihood, and %armor effect size is the estimated parameter coefficient, displayed with its standard error (SE). Overall differences in AICc values between the base model and the models best supported by the data are small (≤ 2) so the base model cannot be dismissed from contention for either species. NA: not applicable

Model	K	LogLik	ΔAICc	%Armor effect size (SE)
Chinook salmon				
Base + %armor at 500 m	10	-389.61	0.00	0.61 (0.32)
Base + %armor at 1.2 km	10	-390.21	1.20	0.56 (0.36)
Base	9	-391.43	1.54	NA
Base + %armor at 10 km	10	-390.92	2.63	0.50 (0.49)
Base + %armor at 500 m + shore type	12	-389.27	3.55	0.62 (0.32)
Base + %armor at 1.2 km + shore type	12	-389.85	4.72	0.58 (0.36)
Base + shore type	11	-391.09	5.09	NA
Base + %armor at 10 km + shore type	12	-390.60	6.21	0.51 (0.50)
Chum salmon				
Base + shore type	11	-363.89	0.00	NA
Base + %armor at 10 km + shore type	12	-362.90	0.14	0.77 (0.55)
Base	9	-366.87	1.76	NA
Base + %armor at 500 m + shore type	12	-363.80	1.95	0.21 (0.51)
Base + %armor at 1.2 km + shore type	12	-363.84	2.03	0.14 (0.48)
Base + %armor at 10 km	10	-366.28	2.67	0.56 (0.53)
Base + %armor at 500 m	10	-366.86	3.83	0.08 (0.49)
Base + %armor at 1.2 km	10	-366.87	3.85	-0.03 (0.46)

a percent armor parameter at any of the spatial scales tested (Table 2), but the estimated direction of the effect was consistent with our expectations (i.e. a negative effect) across spatial scales. For herring, the model that included percent armor at 10 km and the base model had almost identical AICc values, indicating equal support for both. There was no support for models with shoreline type for either species, and effect sizes of the percent armor parameter were identical (and negative) between the models with and without the shoreline type parameters. For surf smelt, none of the more complex models outperformed the base.

We provide coefficient estimates and diagnostic results for the models with the lowest ΔAICc for all species in Figs. S4–S8. Notably, the standard deviations of the site random effects were large (Chinook = 1.33, chum = 1.52, herring = 1.81, surf smelt = 1.63), suggesting that latent differences between sites explained a high amount of variation in the data. The residuals of the models with the lowest ΔAICc values for each species showed no evidence of zero inflation.

3.4. Evaluating patterns across scales

We sought to confirm that the inferences made from model selection above were robust across spatial scales. For the 2 salmonid species, the estimated effect size was positive at nearly every scale, counter to our hypothesis, and relatively imprecisely estimated (Fig. 4). For surf smelt, estimated effect sizes were small (relative to precision) across all scales. For herring, there were slightly larger (negative) effect sizes at intermediate and broad (basin) spatial scales than at the scales we used in the model selection step. However, the differences in effect size were not so large that they would have likely led to a markedly different model selection outcome had we selected one of the scales with a larger effect size for model selection. That is, we likely would have reached a similar conclusion that there was modest support for models that include armor at these scales (Fig. 4).

4. DISCUSSION

Our findings suggest that the association between shoreline armor and the abundances of these nearshore fishes, namely juvenile salmon and forage fish, is generally weak, or absent, regardless of the scale considered. Furthermore, at a local scale, we did not detect a positive effect of restored shoreline type on fish abundance. We found modest support for models that associated fish counts with percent shoreline armor for Chinook salmon, chum salmon, and herring. We did not find a clear association between counts of surf smelt and percent shoreline armor. Varying the spatial scale at which we characterized the percent armor over more than 2 orders of magnitude, from 100 m to the basin scale, did not markedly change our conclusions. Distributions of fish in nearshore subtidal waters therefore do not appear to be primarily governed by the percent shorelines with armor. More work is needed to determine the contexts under which shoreline armor impacts salmon and forage fish.

Herring demonstrated the strongest evidence for an association between shoreline armor and counts, particularly at larger scales. However, in this analysis, we

Table 2. Differences in model selection criteria (ΔAICc) for models applied to counts of herring and surf smelt across 12 sites in the Salish Sea. Details as in Table 1. For herring, the AICc value for the base model is almost identical to the model that includes a percent armor parameter, indicating equal support by the data. For surf smelt, no model outcompetes the base model

Model	K	LogLik	ΔAICc	%Armor effect size (SE)
Herring				
Base + %armor at 10 km	10	-302.20	0.00	-1.03 (0.66)
Base	9	-303.30	0.10	NA
Base + %armor at 10 km + shore type	12	-300.65	1.14	-1.00 (0.61)
Base + shore type	11	-301.81	1.34	NA
Base + %armor at 1.2 km	10	-303.18	1.96	-0.28 (0.55)
Base + %armor at 500 m	10	-303.25	2.11	-0.17 (0.52)
Base + %armor at 1.2 km + shore type	12	-301.71	3.25	-0.25 (0.53)
Base + %armor at 500 m + shore type	12	-301.79	3.41	-0.11 (0.50)
Surf smelt				
Base	9	-235.63	0.00	NA
Base + %armor at 10 km	10	-235.11	1.06	-0.70 (0.71)
Base + %armor at 1.2 km	10	-235.47	1.77	-0.28 (0.48)
Base + %armor at 500 m	10	-235.55	1.92	-0.18 (0.41)
Base + shore type	11	-235.54	4.03	NA
Base + %armor at 10 km + shore type	12	-235.02	5.10	-0.71 (0.71)
Base + %armor at 1.2 km + shore type	12	-235.37	5.81	-0.28 (0.48)
Base + %armor at 500 m + shore type	12	-235.45	5.97	-0.18 (0.41)

did not distinguish between age classes of herring. We caught the most herring at our San Juan Islands sites (Turn Island and Family Tides), and these fish were almost all smaller individuals, within the size range associated with the age-0 size class in the nearby Whidbey Basin (Reum et al. 2013). We therefore caution that the weak negative association between herring and shoreline armoring could be a result of advection of young-of-year to these sites, which generally had the lowest amount of armor at wider scales. Alternatively, this association could be driven, in part, by cumulative landscape scale factors. Kornis et al. (2017) revealed that planktivore abundance in Chesapeake Bay was associated with landscape-scale factors, such as percent watershed cropland, percent of surrounding area with wetlands, and percent hardened shoreline. Additionally, Brook et al. (2018) found that planktivores were less abundant near armor in an estuary with low urbanization, but positively associated with armor in estuaries with moderate and high levels of urbanization, suggesting basin-level effects not captured simply by a shoreline armor variable. The present results agree with previous findings by Francis et al. (2022), and together they warrant further exploration of herring abundance associations with landscape-scale variables, including upland conditions, in the Salish Sea. We did not find an association between surf smelt and percent shore-

line armor, and previous work has also shown that planktivore response to armor can be variable among species (Kornis et al. 2017). Whether forage fish are avoiding armored shorelines or not, our results align with conclusions that species with relatively resident and relatively transient life histories exhibit different responses to coastal urbanization (Lowe & Peterson 2014).

The correlation between local salmon abundance and percent armor was weak but positive, opposite of our expectations, suggesting that local abundance is a product of multiple behavioral and ecological processes. These outcomes align with those of Francis et al. (2022), who concluded that other environmental factors likely govern local salmonid abundances more than shoreline type (armored, restored, or reference). Sampling more sites and over 2 additional years provided further support for these conclusions. The anadromous species represented here may be limited in

their ability to avoid armor because these fish are compelled to travel through armored areas during their migration from river mouths to the open ocean, while some resident motile species have flexibility to avoid large swaths of armored shorelines at different periods of their life history. For instance, salmon leaving the Puyallup River enter the Salish Sea in a highly urbanized area; the next 5 km of shoreline is 83% armored, and the entire east side of Central and Whidbey basins until Deception Pass near Cornet Bay is 40% armored. The San Juan Islands contain less armor relative to any other basin within the southern Salish Sea, but this region also contains the fewest salmon-bearing streams, and our sites were within areas that generally have low probabilities of salmon occurrence (Beamer & Fresh 2012).

We may have seen a stronger response in more species had we sampled closer to shore (Toft et al. 2007, Munsch et al. 2014, 2016). There may be a zone of influence, extending only a relatively small distance from the armored shoreline, in which habitat quality is altered, and perhaps our sampling stations were outside of that zone. For example, Kornis et al. (2018) found that the influence of armor was less pronounced when sampling extended farther from the beach. Future research could investigate whether impacts of armor are more apparent closer to shore and the distance at which those impacts begin to

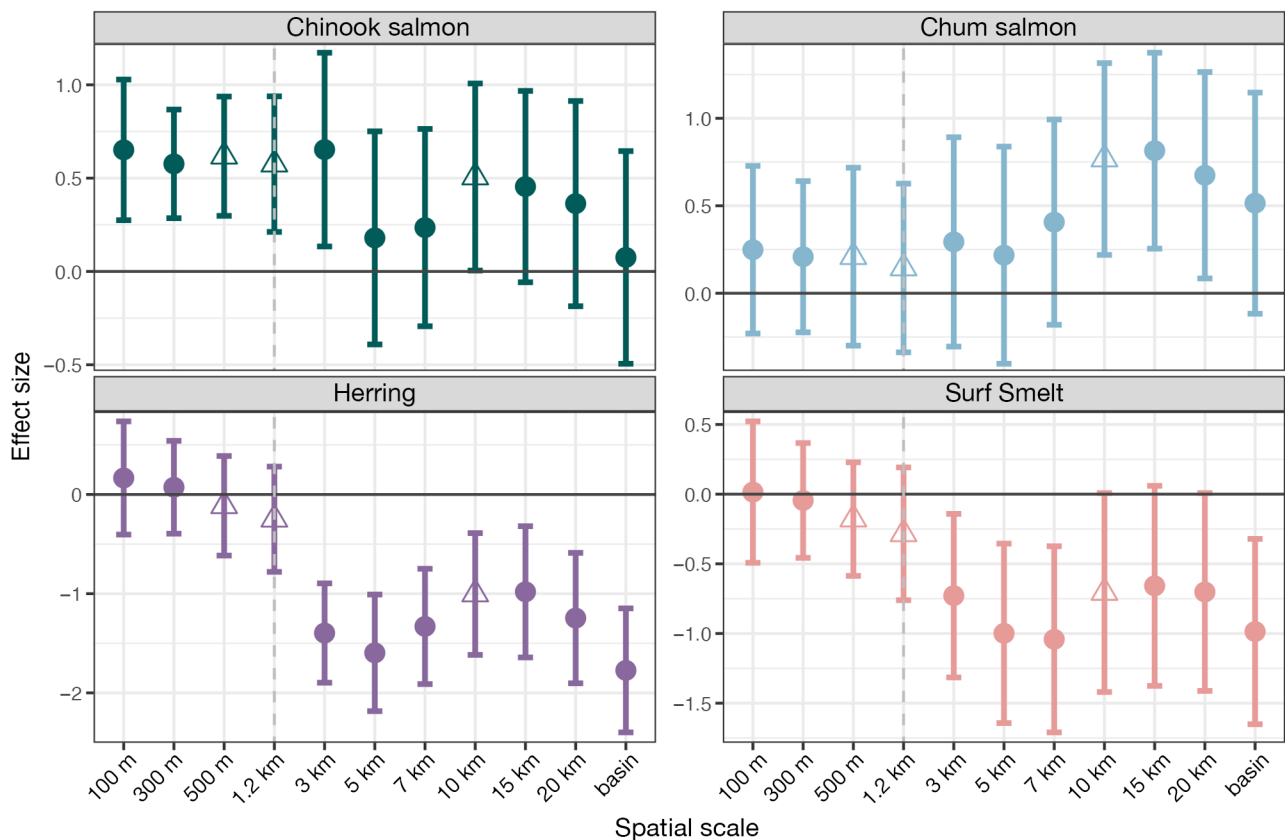


Fig. 4. Effect sizes of the percent armor coefficient. Values are shown with standard error, and hollow triangles represent the 3 spatial scales we used for model selection. Spatial scale represents the radius of an area within which shoreline armor was characterized, using the sample site as a centroid point. The horizontal line marks an effect size of 0. The gray dashed vertical line represents the divide between within-site scales (<1.2 km) and larger scales (>1.2 km)

attenuate. Coupled with habitat use studies to better understand the distance to shore at which specific life history stages are most often found, such insights could reveal the importance of armor for fish use relative to other human modifications. Future research may also involve the application of causal statistics (e.g. structural equation modeling; Maruyama 1997) or the development of a base model that accounts for the expected pattern of habitat use given wild and hatchery release sites and movement patterns. Ultimately, however, associations between fishes and armor may be easier to detect in species with higher site fidelity that are beach associated throughout the entirety of their life history.

We acknowledge other plausible hypotheses for why salmon might not have a negative association with armor. Armored shorelines are typically associated with steeper bathymetry as a result of sediment deficit and wave scour (Seitz et al. 2006, Toft et al. 2007, Dugan et al. 2011). Increased depth adjacent to armored shorelines may provide refuge from avian predators and therefore attract fish. Our sampling

occurred in nearshore waters, but did not extend up to the water line, while previous work has demonstrated that armor mediates habitat shifts for smaller individuals (Munsch et al. 2015). We may have sampled just offshore of shallow waters preferred by juvenile salmon at reference and restored shorelines. Another non-mutually exclusive alternative possibility is that armor is truncating the shallow water zone and therefore fish were pushed into deeper water where we were more likely to encounter them with the lampara net. We hypothesized that salmon would prefer unarmored shorelines that support a greater abundance and diversity of terrestrial insects, a prey item for smolts exiting natal estuaries (Morley et al. 2012, Woo et al. 2019), over armored intertidal zones that support fewer terrestrial insects as a result of reduced terrestrial vegetation (Sobocinski et al. 2010). Terrestrial invertebrates are more energy dense than marine invertebrates (Duffy et al. 2010), but in the absence of terrestrial prey, salmon may simply consume more marine-derived prey to offset the energy deficit (Woo et al. 2019). As smolts grow

and move farther offshore, insect prey becomes a less important food source (Bollens et al. 2010, Duffy et al. 2010, Davis et al. 2020), and our sampling stations were in this transition zone. Even still, lack of high-quality terrestrial prey could have a negative impact on outmigrating salmonids, particularly smaller individuals that inhabit shallow waters.

Our study had several limitations, and the absence of strong armoring effects is not conclusive. Distributions of target species are very patchy, even at fine scales, owing to their propensity to form schools and shoals. Our sampling gear was not sufficiently large to sample the entire volume of water at a site, and on several occasions, although large schools were observed, they were not captured in our net deployment. Either more intensive sampling or the adoption of multiple sampling methods (e.g. acoustic monitoring, shallow-water beach seines, snorkel surveys close to shore, environmental DNA sampling) would reduce our sampling variance and improve power. We used count as a response variable, but did not measure demographic metrics, like growth and survival, that would provide more information about the process by which armor may affect populations. Salmon pass through a gauntlet of armored shorelines during outmigration, so while our study did not detect a negative impact on counts, there could be higher predation risk from larger piscivorous predators that are able to access smolts in deeper water closer to shore, or catch weight could be lower due to reduced productivity (Davis et al. 2018). Measuring other vital rates could reveal effects of armor on migratory fish in the nearshore.

We chose a conservative approach to statistical analyses to avoid making inferences that were not robust (Burnham & Anderson 2002). We defined alternative models, representing a subset of spatial scales, to test in advance of model selection. Had we included many spatial scales (and therefore, many alternative models) in the model selection step, we would have identified stronger effects of percent armor for herring. However, such a conclusion might have been a spurious one caused by random variability in our data. We believe that our 2-step approach is a useful one for future studies examining scale-dependent responses, as it admits uncertainty in the choice of relevant scale, while providing a post hoc check for whether any inference is highly dependent on the choice of scale.

There is evidence that armor design and placement could be a major determinant for how much armor affects nearshore fishes (Gittman et al. 2016, Dugan et al. 2018). In particular, armor that is more structurally

complex, e.g. with a higher surface area to volume ratio, may impact fish community composition less than armor with a completely vertical design (Bilkovic & Roggero 2008, Gittman et al. 2016). Further, when armor is higher on the shoreline, it has less of a direct impact on the slope of the beach and therefore more shallow water area is retained (Toft et al. 2014). The tide line also reaches the armor less often, which leaves more space in the intertidal for logs and wrack to accumulate, thereby having less of an effect on the ecology of intertidal species (Sobocinski et al. 2010, Heerhartz et al. 2014, Jaramillo et al. 2021). The Beach Strategies Geodatabase that we used to calculate armor extent in this study only gives patchy information about the type of armor and the elevation of armor placement on the beach. Future work to focus on the mechanism by which armor may impact nearshore fishes will provide information to better weigh the importance of armor design and placement, particularly as interest in armor installation will likely increase with increasing rates of sea level rise (Beasley & Dundas 2021).

Taken together, these findings suggest that a combination of fine-scale *in situ* observations and landscape-scale land use analyses will ultimately improve our understanding of how nearshore fishes respond to shoreline habitat modifications. New insights into the factors that constrain the movements of estuarine fishes will strengthen our understanding of how human modifications to nearshore habitat features may affect population dynamics of ecologically and socioculturally important species like salmon and forage fish. Development of a more nuanced understanding of how fishes experience the environment at different scales will provide decision makers with important information about the circumstances under which armor removal may provide benefits for target species.

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