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Evaluating responses of marine nearshore communities to anthropogenic pressures

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Abstract

Evaluating responses of marine nearshore communities to anthropogenic pressures

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Coastal ecosystems are changing and causing impacts to the ecology of marine species. Understanding these consequences is essential for ensuring that natural resource management remains effective under changing environmental conditions. In my dissertation, I sought to understand marine species' responses to anthropogenic impacts within an urbanized estuary. Two themes within my research included how patterns change across scales of biological organization and how motile species distribute across a mosaic of nearshore habitats. In Chapter 1, I asked how the abundance of two Pacific salmon and two forage fishes varied as a function of the extent of armored shorelines and examined how patterns of association vary across spatial scales of armor presence. In Chapter 2, I evaluated the diversity of fish assemblages across the Salish Sea in nearshore areas adjacent to different shorelines with variable urbanization contexts. In Chapter 3, I synthesized information about Chinook salmon interactions with nearshore habitats to evaluate habitat quality in the context of nearshore juvenile outmigration. In Chapter 4, I evaluated the robustness of the current management strategy for Dungeness crab to stressors identified by managers of the Washington State fishery in the Salish Sea. Ultimately, this body of work informs resource management strategies to promote recovery for the region and urbanized estuaries worldwide.

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DEDICATION

To the waters and winds of the Salish Sea

INTRODUCTION

The biophysical features of marine coastlines shape species distributions and community structure. For example, rocky intertidal habitats support assemblages that typically depend on the hard rock substrate for settlement and protection from wave energy, while assemblages at sandy beaches support more benthic infauna that use softer sediments for burrowing (McLachlan, 1996; Schiel, 2004). The effect of the physical composition of shorelines extends into the neighboring nearshore environment, where subtidal fish distributions depend, in part, on factors like distance to shore, depth, and vegetation cover (Sharpe et al., 2019; Toft et al., 2007). The nearshore, defined from the Mean Low Water line to the 100m depth contour, provides critical habitat for a suite of culturally and economically significant species globally (Beck et al., 2003; Bizzarro et al., 2022). This zone is transforming, however, as human development changes the landscape of coastlines, thereby altering habitat conditions and the ecological processes that depend on them (Bulleri & Chapman, 2010; Crain et al., 2009).

Humans have been fundamentally altering coastal ecosystems since time immemorial. For example, historical evidence from around the world, including Japan, Sardinia, Hawaii, and shows that early inhabitants enclosed coastal lagoons to trap fish and maintain access to them for food (Beveridge & Little, 2002). By ~3500 years ago, coastal communities in the northeast Pacific were similarly cultivating the nearshore landscape by building clam gardens (Toniello et al., 2019). Indigenous people in this region also modified coasts by placing cedar and hemlock boughs in intertidal areas during periods of herring spawn to collect eggs and constructing weirs on tidal flats to catch adult herring (Williams, 2021). With colonization, industrialization, and increased human populations worldwide, the scale and intensity of coastal impacts have accelerated (Lotze et al., 2006). Wetland filling, dredging, shoreline armoring, and other forms of development have transformed nearshore habitats, altering both their physical structure and environmental conditions (Johnston, 1981; Lee et al., 2006).

Intensified coastal development affects species that inhabit the marine nearshore through multiple pathways that act cumulatively. As coastal modification has intensified, its cumulative effects have increasingly altered the habitats that support marine nearshore species. Habitat impacts may result from the direct conversion or loss of habitat area, such as through fill or structure placement, but can also extend beyond the modified area (Crain et al., 2009). For example, overwater structures can reduce light availability in adjacent habitats, affecting photosynthetic submerged aquatic vegetation (Crain et al., 2009). Conversely, additions of structures can provide new habitat for introduced and invasive species to colonize, sometimes leading to novel ecosystems (Hobbs et al., 2013). Besides direct changes to habitat, species also face threats related to reductions in water quality, due to excess nutrients and pollutants, and overexploitation, which can lead to changes in food web structure due to removal of key species (Brown et al., 2018; Crain et al., 2009). Exploited species, in particular, are vulnerable to a suite of stressors associated with human activity because they experience habitat change and harvest simultaneously (Brown et al., 2018).

These impacts extend to a significant proportion of species inhabiting the marine nearshore for at least part of their life history. In the Northeast Atlantic, 92% of fish species are thought to be affected by human activity in the coastal zone and 42% are thought to be affected by coastal

development directly (Brown et al., 2018). Globally, human impacts to marine coastal environments are already 50% greater than impacts to other ocean ecosystems (Halpern et al., 2025). This is concerning given that total human impacts on all ocean ecosystems are projected to increase by 2.2-2.6 times in the next 30 years (Halpern et al., 2025).

Coastal restoration and fishery management are primary solutions to these cumulative impacts. Ecological restoration addresses these impacts because it involves humans assisting in the recovery of ecosystems which are degraded, damaged, or destroyed (Society for Ecological Restoration International Science & Policy Working Group, 2004). Fishery management addresses these impacts by implementing control rules that garner reasonable trade-offs between social-ecological objectives, which typically include sustainable harvest (Punt, 2010). To quantify these objectives and progress towards them, restoration and management have traditionally considered habitat and population status relative to a baseline state. Early restoration ecology, with its roots in the 1980s, focused on rebuilding biodiversity, and aimed to restore specific community structure or composition that historically existed before a major perturbation (Higgs et al., 2014). For example, in North America baseline conditions are often considered as prior to European colonization. Fishery management often uses historical information about the population size and variability to establish the relative health of a given stock (McClenachan et al., 2024).

Yet increasingly, the combined impacts of global change may prevent the return to historical conditions. Consequently, restoration ecology has evolved to emphasize re-establishing ecological functions and processes, rather than specific species assemblages (Higgs et al., 2014). Ecological restoration with a focus on resilience theory seeks to re-establish the ability for natural systems to maintain desired functions in the face of future change or disturbance (Campbell et al., 2009). Sometimes a new stable state or new combinations of species might be a desired result of restoration (Dudney et al., 2018). The restoration ecology field is also increasingly recognizing that desired outcomes should consider the multiple values and knowledge systems within social-ecological systems (Volpe et al., 2024).

Effective restoration requires understanding how species respond to a range of habitat conditions, in order to promote desired functions. Yet, important uncertainties remain about the mechanisms underlying these relationships and the ecological scale that they occur. We often know how species respond to individual habitat features but understand less about how species respond to habitat mosaics within a landscape (Boström et al., 2011; Sheaves, 2009). This limits our ability to prioritize restoration actions between those targeted at fine-scale species responses and those addressing broader-scale species distributions. We also know that the diversity of biological traits represented by species within an ecosystem influences ecosystem functioning, and habitat heterogeneity can support diverse functional groups. However, marine ecosystem monitoring typically focuses on the identities of species present rather than their functional traits, so the effects of different habitat types on local diversity of traits are understudied in the marine environment.

Effective fisheries management requires evaluating whether historical management approaches remain robust under changing conditions. Existing fishery management frameworks may be robust under the historical range of variability, but as conditions depart from historical norms,

there is increasing uncertainty in how effectively management will continue to meet objectives (Perry et al., 2010; Pinsky & Smith, 2026). Different management frameworks have different adaptive capacity, and some may be more robust to particular stressors than others (Melnychuk et al., 2014). Strategies like dynamic closures rather than relying on fixed seasons may be implemented to increase adaptability to meet management objectives in the face of increasing stressors that affect population vulnerability to overharvest (Holsman et al., 2019). Assessing the effects of current management structures on fisheries facing novel population states in response to shifting environmental conditions and human impacts can inform whether amendments to the management strategies will increase population resilience and maintain resource access.

Collectively, these uncertainties limit our ability to design restoration actions that support ecological function and to implement management strategies that remain effective under changing environmental conditions. These challenges are prevalent within the southern Salish Sea (herein referring to the inland marine waters of Washington State), which serves as a model system for examining the response of nearshore communities to stressors associated with coastal development. This large fjordal estuary hosts an array of nearshore habitat types and a variety of urbanization contexts. For example, one of the primary human impacts within this region is shoreline armor (Sobocinski, 2021), which refers to any structure, including bulkheads, seawalls, and riprap revetments, installed by landowners to prevent erosion of their properties and to preserve upland area (Griggs, 2005). However, when armor limits sediment supply to the beach and alters wave patterns thereby increasing scour, the adjacent intertidal habitat becomes narrower, deeper, and coarser (Ruggiero et al., 2010; Shipman, 2010), which then alters the composition of the adjacent biotic community (Gittman et al., 2016; Munsch et al., 2017). Yet the extent to which armor affects nearshore communities is still largely unknown, making it challenging to mitigate potential impacts (Francis & Kinney, 2018).

This dissertation enhances understanding of nearshore ecological communities and to support restoration and management in a changing world. In Chapter 1, I asked how the abundance of two Pacific salmon and two forage fishes varied as a function of the extent of armored shorelines in the Salish Sea and examined how patterns of association change across spatial scales of armor presence. The purpose of this chapter was to identify the elements of different life histories that facilitate, or suppress, species' response to habitat modification, to inform restoration planning in a heterogeneous landscape. In Chapter 2, I evaluated the functional trait diversity of fish assemblages across the Salish Sea in nearshore areas adjacent to different shorelines with variable histories of shoreline armor. The purpose of this chapter was to improve our understanding of how environmental and habitat features shape the structure of nearshore communities and illustrate the impacts of human encroachment and restoration activities in critical ecosystem boundaries. In Chapter 3, I synthesized information about juvenile Chinook salmon interactions with nearshore habitats to evaluate our understanding of what makes high quality habitat for this species and life stage. The purpose of this chapter was to refine the definition of quality habitat for a particular species to understand the features of nearshore habitats that should be prioritized for restoration. Finally, in Chapter 4, I evaluated the robustness of the current management strategy for Dungeness crab to stressors identified by staff involved in management of Salish Sea fisheries. The purpose of this chapter was to support co-managers in the region who have identified the need for a re-evaluation of the status quo management strategy, given anticipated changes in the fishery due to human stressors and environmental

change. Ultimately, this work informs restoration and resource management strategies to promote recovery for the region and for urbanized estuaries worldwide.

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Chapter 1. NEARSHORE FISH ABUNDANCE IN AN URBAN ESTUARY IS WEAKLY ASSOCIATED WITH SHORELINE CONDITIONS ACROSS SCALES

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1.1 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 four highly motile fish species with shorelines that are altered via shoreline armor. We sampled fish for four years 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 armor on fish populations.

1.2 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 diversity and enhance ecosystem function (Lepofsky et al. 2021), or 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 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 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. 2015b) 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 resident 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 two species of Pacific salmon and two forage fish species varied among short (<30m) 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 two 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 than more resident fish. 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 United States 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 two 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.

1.3 METHODS

We collected and analyzed a four-year 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.

1.3.1 *Study sites*

This study builds on field sampling described in 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 resident juvenile Pacific herring (*Clupea pallasii*) and surf smelt (*Hypomesus pretiosus*) and juvenile anadromous 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 (Figure 1). When selecting sampling locations, we considered accessibility, the proximity of shoreline types within a littoral drift cell, and bathymetry. Our sites were most often characterized by wide, gradually sloping, mixed-sediment beaches, though 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, Chalifour et al. 2019). We determined eelgrass presence from the Department of Natural Resources Submerged Vegetation Monitoring Program website and confirmed via field observations (Figure 1).

Of the 12 sites, we sampled 6 "core" sites monthly (April - September) in 2018, 2019, 2021, and 2022 (Francis et al. 2022), and 6 "supplementary" sites only in June, 2021-2022. Each site consisted of an armored, restored, and reference (natural in upper intertidal habitat) shoreline segment, except for Turn Island which consisted of two reference and one armored segment. Restored shorelines were areas where armor removal had occurred within the last 3-10 years. 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 two years 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.

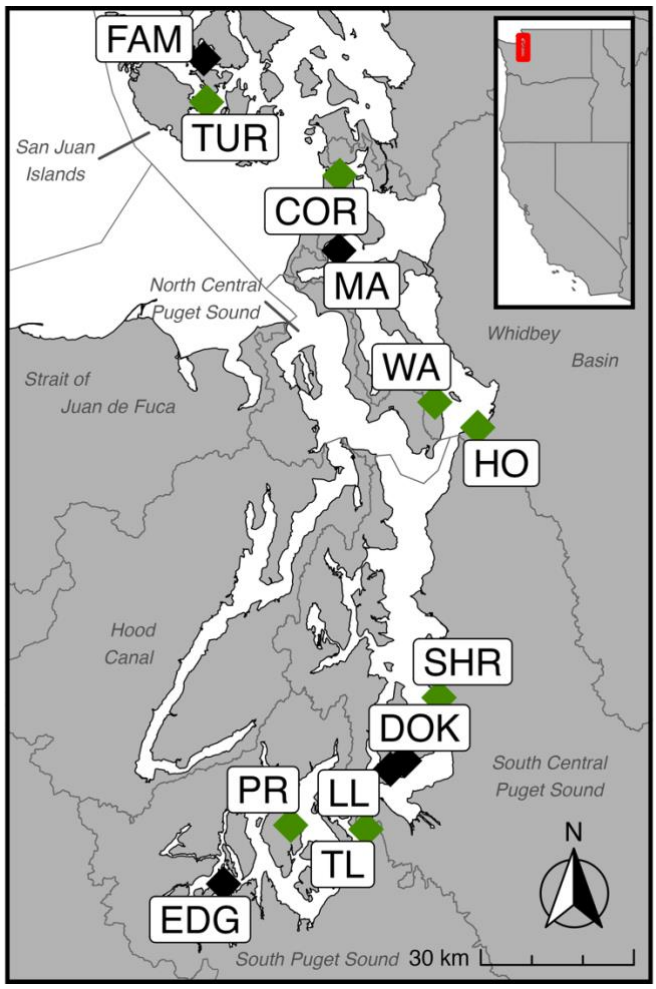

Figure 1. Map of the study area and sampling sites. Three letter codes represent core sites (FAM = Family Tides, TUR = Turn Island, COR = Cornet Bay, SHR = Seahurst Park, DOK = Dockton Park, EDG = Edgewater Beach) that were sampled monthly April - September over 4 years. Two letter codes represent supplemental 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 years. Sites with a green point have eelgrass present. Labels in italics are PSNERP (2010) basins of the southern Salish Sea that are represented in the analyses.

1.3.2 *Field methods*

We sampled fish using a boat-towed lampara net at three 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 station was 50m directly offshore from our -3 m depth station. Straight-line distances between shallow and deep stations were typically between 50 – 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 +0.5m (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.

1.3.3 *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 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 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 (100m, 300m, 500m, 1.2km, 3km, 5km, 7km, 10km, 15km, 20km) chosen to represent the range of habitats that fish experience, from local to landscape. We evaluated 1.2km specifically because that distance incorporates all shoreline segments within our most widely spread core site (Cornet Bay). Notably, that means scales less than 1.2km should be considered “within-site”. Because of the proximity of some sites, some buffers overlapped between sites at spatial scales larger than 1.2km. 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.

1.3.4 *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 two less computationally demanding steps. In step one, 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 (500m, 1.2km, and 10km), chosen to span a range of relatively local to larger distances. 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 two, 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 (GLMMs) with sample catches of fish summed across the three 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 three depth stations $\boldsymbol{y}$ on a given day i is a function of mean μ and an overdispersion parameter k.

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

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 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 and Hill (2006):

$$log(\mu_i) = site_{j[i]} + \beta_1 year_i + \beta_2 \log(day\ of\ year)_i + \beta_3 \log(day\ of\ year)_i^2 + \beta_4 veg_i \quad (2)$$

$$site_j \sim Normal(0, \sigma^2) \quad (3)$$

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(day of year) and log(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 three 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 (either 500m, 1.2km, or 10km). 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 Information Criterion (AIC) corrected for small sample sizes (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 and Anderson (2002) whereby models with $\Delta AIC_c < 2$ cannot be dismissed from consideration because they have similar degrees of support from the data, models with $\Delta AIC_c > 10$ are not supported by the data, and intermediate levels of ΔAIC_c represent a continuum of model support. However, following Leroux (2019), we applied additional procedures when pairs of models had $\Delta AIC_c < 2$, 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 ΔAIC_c 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 ΔAIC_c of 0, and an alternative model had ΔAIC_c 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 AIC_c 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). Code to reproduce this analysis is available at https://github.com/e-bish/Armor_Across_Scales.

1.4 RESULTS

1.4.1 *Sampling summary*

Over the four years of field sampling of our target species, we caught 942 Chinook salmon, 2,456 chum, 815 herring, and 303 surf smelt. Fish distribution within our sampling stations was often patchy, and sometimes we caught large schools. Average catch rates varied by month, and these patterns were different for each species (Figure 2). Average catch per set was greatest in May for both salmonid species and remained elevated through July (Figure 2A), while there was no discernable seasonal pattern of mean catches for the forage fish (Figure 2B). Average catch rates varied between locations but did not indicate any spatial gradient (Figure 2C and 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 (Figure S1). There was no apparent difference in mean fish size among the three depth stations for any species (Figure S2), and few differences in size between sites except at Family Tides and Turn Island where herring were generally smaller than at other sites (Figure S3).

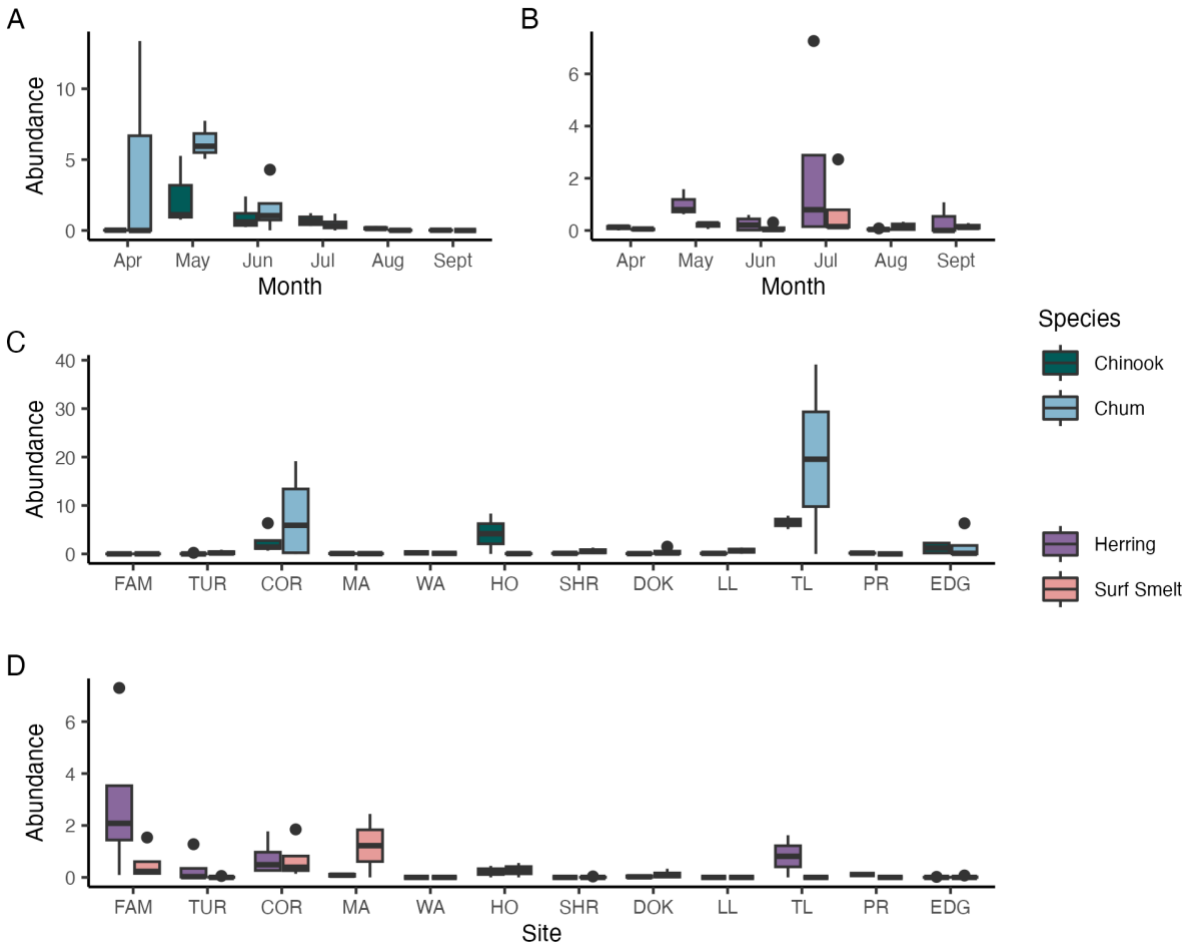

Figure 2. Trends in catch across four survey years. Abundance is represented by the number of individuals captured in a single lampara net set and varied by month (April - September) for anadromous salmonids (A) and intertidal spawning forage fish (B). Catch for all species was highly heterogeneous because all of the target species exhibit schooling behavior. Abundance also varied by site, ordered from north to south, for salmonids (C) and forage fish (D). Boxes represent the interquartile range (the 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 ± 1.5 * the interquartile range). Values outside of this range are represented as solid points.

1.4.2 *Percent armor by scale and site*

Patterns of armor extent at a given scale varied between our sampling sites (Figure 3), providing important contrasts to detect differences at the spatial scales we chose for model selection. Across all sites, percent armor within a 500m 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 (10km) 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., 100-500m;

see Howarth Park and Titlow Park) and sometimes it was highest at large scales (i.e., 15km - basin; see Family Tides and Lost Lake). Armor was overall more prevalent in the central and southern extents of our study area versus the northern sites (Figure 3).

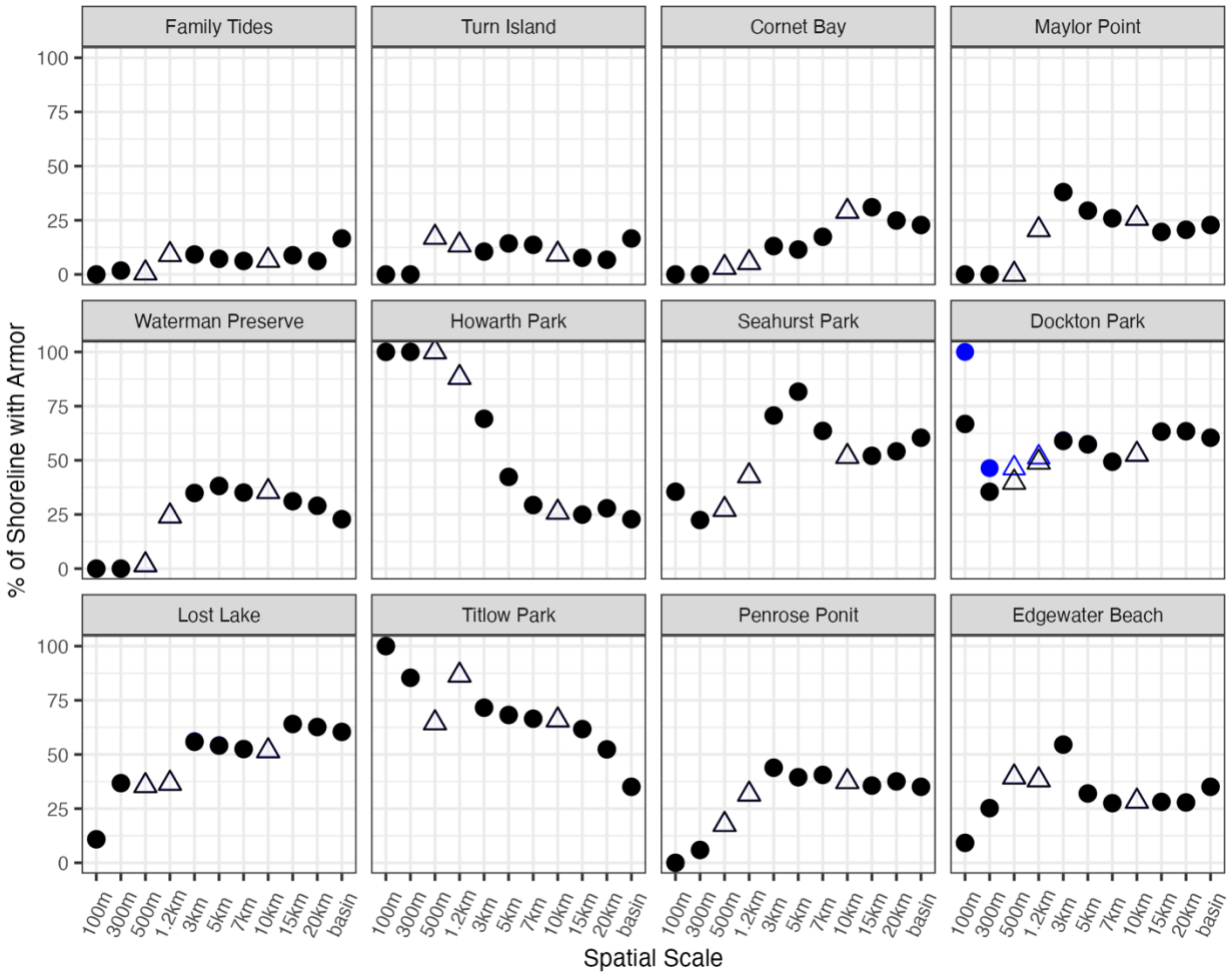

Figure 3. Percent shoreline armor by spatial scale for each sampling site. Sites are ordered from north to south. At Dockton Park (DOK), the points in blue represent armor extent prior to a restoration project where 68 meters of armor were removed in 2020. Hollow triangular points represent the three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

1.4.3 *Model selection*

Through AIC_c-based model selection, we found modest support for models that included regional percent armor as a parameter for every species but surf smelt at one or more spatial scales (Tables 1, 2). For Chinook salmon, the base model and the models that included percent armor at 500m and 1.2km 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 ΔAIC_c 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 10km radius. However, as with Chinook salmon, the base model could not be entirely dismissed from consideration based on differences in ΔAIC_c. The estimated effect size for the armored shoreline type was of greater magnitude than the restored shoreline type (Figure S4 in the Supplement), 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 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 10km and the base model had almost identical AIC_c 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 ΔAIC_c for all species in Supplementary Material 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 ΔAIC_c values for each species showed no evidence of zero inflation.

Table 1. Differences in model selection criteria (ΔAIC_c) 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 AIC_c 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.

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

Table 2. Differences in model selection criteria (ΔAIC_c) for models applied to counts of herring and surf smelt 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). For herring, the AIC_c value for the base model is almost identical to the model that includes a percent armor parameter, indicating equal support by the data. No model outcompetes the base for surf smelt.

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

1.4.4 *Evaluating patterns across scales*

We sought to confirm that the inferences made from model selection above were robust across spatial scales. For the two salmonid species, the estimated effect size was positive at nearly every scale, counter to our hypothesis, and relatively imprecisely estimated (Figure 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 (Figure 4).

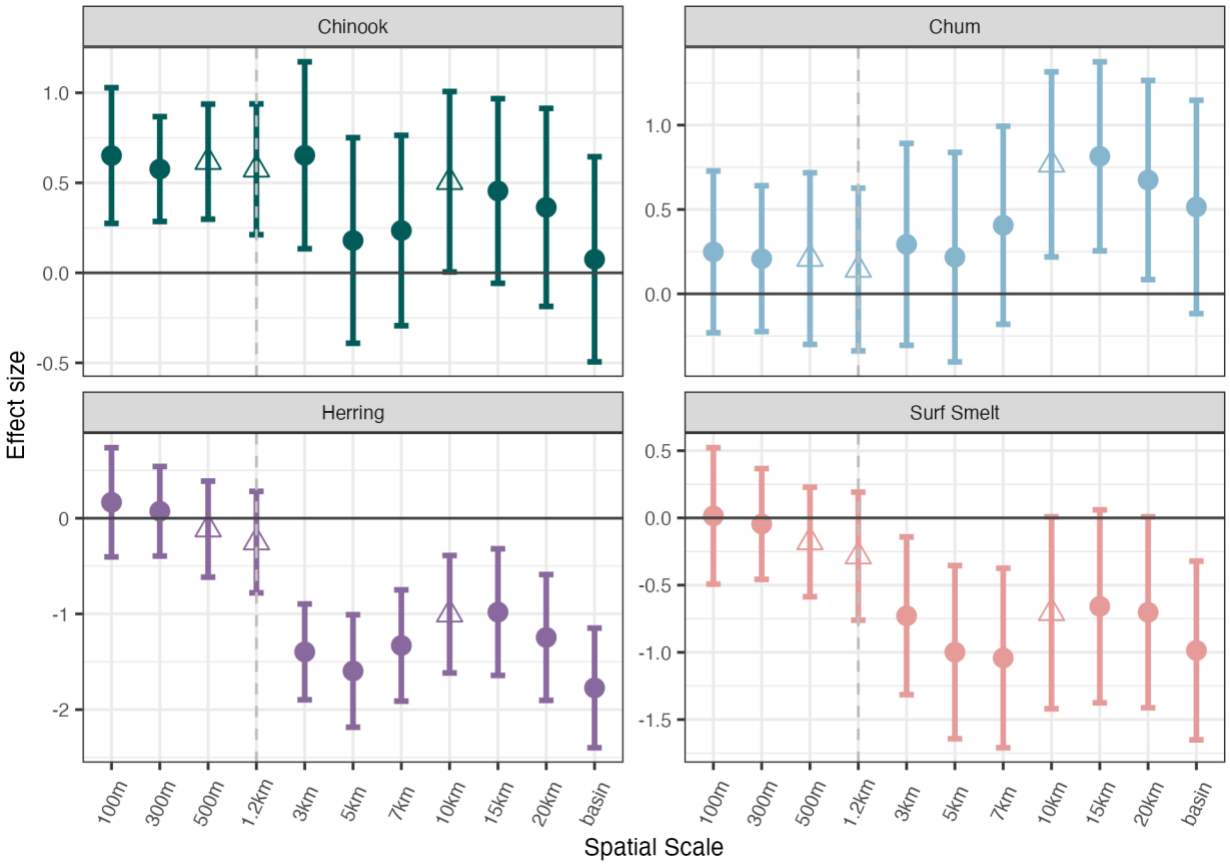

Figure 4. Effect sizes of the percent armor coefficient. Values are shown with standard error, and hollow triangular points represent the three spatial scales we used for model selection. Spatial scale represents the radius of an area within which shoreline armor has been characterized, using the sample site as a centroid point. The gray dashed vertical line represents the divide between within-site scales (<1.2 km) and larger scales (>1.2km).

1.5 DISCUSSION

Our findings suggest that the association between shoreline armor and the abundances of these nearshore fishes, 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 two orders of magnitude, from 100m 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 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 shoreline 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 two 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 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 by developing 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. 2015b). 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 less 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 based prey could have a negative impact on outmigrating salmonids, particularly smaller individuals that inhabit shallow waters.

There were several limitations to our study, 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 at several occasions large schools were observed, but 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 two- 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 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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Chapter 2. SPATIAL VARIABILITY IN SPECIES AND FUNCTIONAL DIVERSITY OF NEARSHORE FISHES EXCEEDS VARIABILITY RELATED TO SHORELINE ARMOR IN AN URBANIZED ESTUARY

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2.1 ABSTRACT

One important measure of biodiversity is functional diversity within a given assemblage, because it provides information about the collective roles that species play in an ecosystem. The expressed functional diversity of an assemblage can be thought of as realized niche space occupied by species present, shaped in part by characteristics of the available habitat. Assessing functional traits can therefore provide some indication of the ecological significance of different habitat features, and how habitat modification may impact community structure. Here, we assessed the functional diversity of fish across the Salish Sea, Washington, USA adjacent to shorelines of different degrees of anthropogenic impact via shoreline armor. We found differences in assemblage composition between shorelines from northern and southern sites, for example Pacific herring and Pacific tomcod were more abundant at northern sites, while three-spined stickleback were most abundant at southern sites. However, we found no equivalent trend in functional diversity between these groups, nor did we find any variation in metrics of taxonomic or functional diversity among coastal fish assemblages based on shoreline condition (natural, armored or restored). Although we detected some local variation in species richness, functional richness, and functional evenness, these differences did not appear to be structured by broader spatial context. This work represents the first broad-scale assessment of the functional diversity of fishes in the Salish Sea and informs our understanding of the degree to which nearshore fish assemblage structure varies in response to shoreline conditions within an urbanized estuary.

2.2 INTRODUCTION

Biodiversity of fishes in coastal ecosystems varies in association with habitat features (Pasquaud et al., 2015; Valesini et al., 2004). At a broad scale, climate determines the potential range of species present in a given region (Manel et al., 2020; Tittensor et al., 2010). The diversity of the regional assemblage is then determined, in part, by the mosaic of habitats present (Connell & Irving, 2008; Kovalenko et al., 2012; Tuya et al., 2011). This is because the various features of

local habitats support different ecological niches, and the biological traits of individual species determine which niches they inhabit (Mason et al. 2005; Wiens 2011; Koutsidi et al. 2020). Higher habitat complexity typically supports greater diversity, but other factors, like connectivity between areas and frequency of disturbance, also play a role (Altman and Whitlatch 2007; Sheaves 2009; Bishop et al. 2017; Henderson et al. 2022). Understanding the diversity of niches supported by a coastal ecosystem can therefore provide some indication of the influence of habitat condition on ecological function (Villéger et al., 2010).

One common method used to quantify the range of available niches in an ecosystem is functional diversity analysis (Mason et al. 2005; Laureto et al. 2015). This technique assigns biological traits to species present in a community and then measures dissimilarity within communities found in an ecosystem, which can then be compared among communities. It can describe community structure and indicate how environmental factors influence available niche space (Mouchet et al. 2010; Götzenberger et al. 2012; Mason et al. 2013). For example, environmental disturbance, upland urbanization, and in-water development along marine shorelines are known to impact the functional diversity of coastal fish communities (Dolbeth et al., 2016; Mouillot et al., 2013; Shaffer et al., 2018; Villéger et al., 2010). These impacts tend to result in coastal communities that have more generalist species that are adapted to exploit multiple habitat types (Bilkovic & Roggero, 2008; Henderson et al., 2020; Shah Esmaeili et al., 2022). In examining the representation of traits within a region, we can generate hypotheses about the mechanisms by which different habitat contexts influence ecosystem function (Hillebrand et al., 2008; Mouillot et al., 2011; Sobocinski et al., 2010). For example, fishes in natural tidal wetlands exhibit traits associated with full water-column use, whereas fishes in diked marshes exhibit traits indicative of bottom avoidance, leading to hypotheses that dikes may primarily impact these fish communities via changes to sediment composition, abiotic conditions near the sediment, or availability of benthic prey (Lechêne et al., 2018).

The Salish Sea faces challenges emblematic of developed estuaries worldwide and hosts an array of nearshore habitat types with variable human impacts that may be altering the ecological niches available to fish (Simenstad et al., 2011; Dethier et al., 2016a, 2017). Fish play important roles in marine ecosystems by providing key forage for upper trophic levels, recreational and commercial fishing opportunities, and nutrient cycling, among other services that are impacted by changes in community structuring due to altered niche space (Villéger et al., 2017). In the Salish Sea, there is significant interest in developing tools to prioritize shoreline habitats for conservation and restoration efforts to support nearshore ecological function. Yet, in this region there has been no assessment of the functional diversity of fishes at a broad scale, and therefore coastal ecologists lack an understanding of the associations between different local habitat conditions and the ecological niches available to fish communities. This gap in knowledge limits our ability to identify anthropogenic pressures that impair coastal ecological function, and our ability to manage them (Kelley et al. 2018).

One of the main anthropogenic impacts facing Salish Sea coastlines is shoreline armor. Armor consists of hard substrate, such as bulkheads or riprap revetments, installed along the shoreline to prevent erosion (Griggs, 2005). Installation of armor changes the physical characteristics of the beach, resulting in reduced diversity and abundance of benthic infauna and invertebrates in intertidal zones (Sobocinski et al. 2010; Dethier et al. 2016b; Des Roches et al. 2022; Laurino et

al. 2022). Shoreline armor is a common feature of developed coastlines, and its impacts on intertidal biota and substrate are well documented (Gittman et al., 2016a), but less is known about the extent to which these impacts extend into subtidal environments (Munsch et al. 2017; Francis and Kinney 2018). Previous work suggests that the taxonomic composition of subtidal fish communities is altered by shoreline armor (Munsch et al., 2015; Gittman, et al., 2016b), and that species responses to armor vary between functional groups (Toft et al., 2007; Bilkovic & Roggero, 2008; Bishop et al., 2024; Brook et al., 2018; Kornis et al., 2018), but these studies have not assessed the effects of armor on functional trait diversity.

There are several pathways by which shoreline armor may alter functional trait diversity in adjacent habitats. For instance, larger fishes are more likely to be observed inshore at armored shorelines compared to natural shorelines because armor often creates steeper shorelines with increased water depth (Kornis et al., 2018). Because armor increases wave scour and thereby produces coarser substrates, there can be reduced densities of species with flat body shapes that associate with sandy substrate in the presence of armor (Toft et al. 2007; Munsch et al. 2015). Armoring also reduces the diversity of terrestrially-derived prey, and alters benthic prey communities (Kornis et al., 2017; Sobocinski et al., 2010), both of which may favor fish species with some feeding strategies over others. In addition to the above causal pathways, the magnitude of species response to armor may differ among functional groups. For example, vertical distribution in the water column is thought to mediate the strength of relationship between a given species and benthic sediment characteristics (Toft et al. 2007; Munsch et al. 2015; González-Sansón et al. 2022) so demersal species are likely to have a stronger response to changes in sediment grain size than pelagic species. Similarly, migration behavior is thought to mediate the strength of the relationship between a given species and local habitat conditions, because resident and transient species are likely to exhibit different degrees of response to local habitat quality (Lowe and Peterson 2014; Bishop et al. 2024). Comparing the ecological niches available between shorelines with and without armor fills a gap in our understanding of potential cumulative anthropogenic effects on nearshore fish communities.

In this study, we evaluated the functional diversity of fish at shorelines throughout Puget Sound and the San Juan Islands, in the Washington State, USA portion of the Salish Sea, that are representative of the region and subject to variable anthropogenic pressures. We asked which traits dominate nearshore assemblages in this region, and which traits make the greatest contributions to functional diversity metrics. We then examined the extent to which the functional diversity of nearshore fishes varies between shorelines in an urbanized estuary. We specifically hypothesized that shoreline armor modifies the functional diversity of the assemblage. We expected that, relative to natural shorelines, armored shorelines would be associated with fish assemblages dominated by similar functional groups occupying fewer ecological niches. We also expected that if areas with more upland urbanization tend to have fewer functionally distinct species in adjacent subtidal habitats, then functional diversity would be lower at sites closer to urban centers.

2.3 METHODS

2.3.1 *Study location*

Puget Sound is a temperate fjordal estuary carved by glaciers. Its waters are generally calm, with landforms protecting most areas from ocean swell and wind-driven waves. The estuary has a distinct latitudinal gradient in geomorphology: shorelines in the south are primarily dominated by sandy sills backed by high bluffs, while shorelines in the San Juan Islands are dominated by rocky coasts. The central basin of the sound has the most urbanized shorelines, associated with larger cities including Seattle and Tacoma. Major river systems from the Cascade Mountains drain into the eastern shores, where tidal channels connect freshwater to the nearshore. The extent of the native eelgrass, *Zostera marina*, an ecosystem engineer that provides habitat for an array of species, has remained relatively stable at the regional scale in recent history (Shelton et al., 2017). Understory kelp, another habitat feature exploited by nearshore fishes, is also common though there has been no formal inventory of its distribution to date.

The current study is based on four years of field data, collected between 2018 and 2022, on nearshore fish assemblages across Puget Sound and San Juan Island shorelines (Francis et al. 2022; Bishop et al. 2024). We sampled at six sites, which we primarily chose for their ability to facilitate comparison among three different shoreline conditions (armored, restored, and reference shorelines that had no existing or historical armor) and assess the influence of eelgrass. Each sampling site therefore consisted of three unique shorelines representing different conditions within the same geomorphic drift cell (<1.2 km total distance between shoreline segments within a single site). The condition categories were “armored” with a bulkhead or riprap revetment in place, “restored” where armor had been removed, and “natural” which consisted of coastline unmodified by armor. Armor at these sites is typical of many armored sandy beaches in the Salish Sea; it is located high in the intertidal or above the high tide line. Half of the sites were adjacent to subtidal eelgrass beds (Table S1). Some sites are nestled within shallow embayments while others are more exposed to longer fetch and stronger tidal energy. Several are on public land while others abut private property (Table S1). Some are gradually sloping sandy beaches and some are on steep rocky coasts. The upland areas adjacent to Edgewater and Dockton are comprised of undeveloped forests and rural single-family homes, but these sites are within 8 miles by water of the cities Olympia and Tacoma, respectively. The area surrounding Turn Island and Family Tides is similar, though Turn Island is within 2 miles of Friday Harbor, a small city, and Family Tides is surrounded by some agricultural land. Conversely, Cornet Bay has primarily undeveloped forest land in its watershed and Seahurst Park is surrounded by urban development in the Seattle metro area. The 18 shoreline segments that comprised our six sites therefore represented a cross section of the nearshore habitats that are available to fishes in this region.

2.3.2 *Field Sampling*

Full sampling procedures for fish are described in Francis et al. (2022) and Bishop et al. (2024). Briefly, we used a 37-m long x 5-m deep lampara net, a modified beach seine deployed by boat, to capture fish in nearshore surface waters at the six sampling sites in 2018, 2019, 2021, and 2022. We sampled once per month at each site during April - September (Fig. 1, for further sampling details see Table S1 in Bishop et al. 2024). In 2021 and 2022, we measured surface water quality (temperature, salinity, and dissolved oxygen), using a handheld YSI-brand sensor, and turbidity, as Secchi depth, monthly at each shoreline. We sampled fish at three depth stations seaward of each shoreline, consisting of a shallow station at 1 m, a middle station at 3 m, and a deep station that was about 50 m offshore of the 3 m depth station. The distance from the shallow station to shore varied among sites based on local bathymetry but all shallow stations were within about 5 - 150 m of shore. Bottom depth at the deep stations ranged between - 3.75 and - 14.5 m relative to mean lower low water (Table S1). We counted the number of fish we collected of each species and measured the fork lengths of 20 randomly-selected individuals per species.

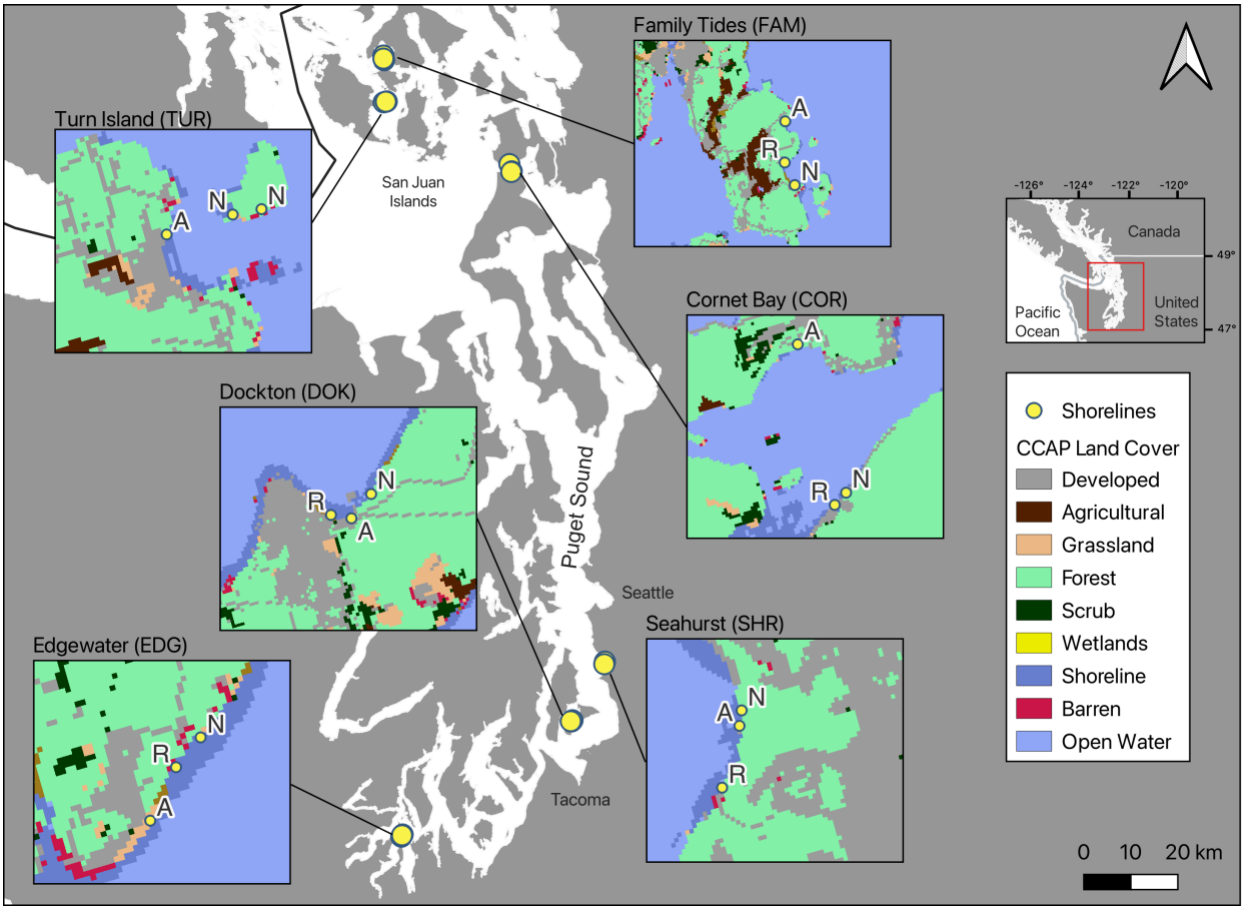

Figure 1. Study location in the Salish Sea, Washington, USA depicting sites where the nearshore fish community was sampled via lampara netting in 2018, 2019, 2021, and 2022. Sites are labeled with their respective abbreviations. Sites are comprised of 3 shorelines each, and shoreline labels correspond with shoreline condition categories, A = Armored, N = Natural, R = Restored. Inset base maps are displayed with simplified NOAA Coastal Change Analysis

Program (CCAP) land cover categories (National Oceanic and Atmospheric Administration Office of Coastal Management, 2016).

2.3.3 *Constructing the abundance matrix*

Fish catch was patchy, particularly at the deepest station and during the beginning and end of the sampling season. This patchiness resulted in part from capturing fewer bottom-associated species at deeper stations (Fig S1), and because early spring and late summer are the tail ends of the seasonal peak in abundance for juvenile Pacific Salmon (*Onchorhynchus* spp.), which constituted a large proportion of our overall catch. Some metrics of functional diversity require more unique species per sampling event than the number of axes retained for the functional trait space (described below), and high quality trait spaces typically require at least 3-4 axes (Maire et al. 2015). Because we caught fewer than 4 species during 95% of catch events, we aggregated catch data to meet this requirement for as many samples as possible.

Summing catch data across depth stations substantially decreased the proportion of samples with fewer than four species (to 80%), but not enough to conduct the functional diversity analysis. To address this, we also aggregated catch across time. Because our hypotheses were focused on the habitat characteristics of these sites, we chose to characterize the assemblage at each shoreline over periods that include seasonal peaks in abundance for some species rather than explore potential seasonal variability in functional diversity. We therefore calculated aggregated functional trait metrics for each site and year, summing over sample depths and months, which resulted in a much lower proportion (12.5%) of samples with fewer than four species present. We then divided this summed value by the sampling effort (number of net deployments) across all sampling days within a year at each shoreline, resulting in a catch per effort value associated with each shoreline for each year. The final abundance matrix consisted of abundance values for 42 unique species, where abundance is represented as total catch per effort at each shoreline in each year, across 72 samples.

2.3.4 *Functional trait assignments*

We selected 5 functional traits to represent the fish assemblage, based on each trait's potential linkages to nearshore habitat quality and prey availability given variable habitat (Table 1). To represent size, we selected mean fork length. To represent sediment association, we selected body transverse shape and vertical distribution. To represent response to prey field, we used feeding guild. Last, to represent the strength of response to local habitat conditions, we used migration behavior. Collectively, these traits characterize the interspecific variability of species present as we did not have sufficient data to select traits that could be assigned at the individual level to characterize intraspecific variability.

Table 1**.** Biological traits used to characterize the functional diversity of nearshore fishes in the Salish Sea, Washington, USA. Size, the only continuous trait, was calculated from field data, and all other trait values were assigned to species based on their description in FishBase, an information system that houses information on fish species worldwide. These five traits were selected to describe the interspecific variation among species based on the different ecological niches they occupy.

Trait	**FishBase Field Code** (if applicable)	**Type of variable**	**Units/Values**	**Definition/Relevance**	**Reference**
Size	N/A	Continuous	Mean fork length in mm	Body size relates to resource use	Baptista et al. 2014
Transverse shape	BodyShapeI	Categorical	eel-like, elongated, fusiform/normal, short and/or deep	Body shape relates to physical structuring in the water column and swimming performance	Villéger et al. 2017
Vertical distribution	DemersPelag	Categorical	benthopelagic, demersal, epipelagic, pelagic	Degree of dependence to substrate characteristics	Baptista et al. 2014, Luiz et al. 2013
Feeding guild	FoodI	Categorical	omnivorous, planktivorous, zoobenthivorous	Relates to position within the food web	Villéger et al. 2017
Migration behavior	AnaCat	Categorical	migratory, resident	Transfer of energy between areas and degree of association with local habitat	Kelley et al. 2018

We assigned trait values to each of the 42 species in the regional assemblage to create a 42 x 5 (species x trait) trait matrix. We calculated size for each species across all sampling events using measurements collected in the field. All other traits were categorical and extracted from FishBase (Froese & Pauly, 2024) using the package rfishbase (Boettiger et al., 2012) in R. FishBase is an information system that contains biological data about fishes from around the globe. We inspected the FishBase results for each species and adjusted values when necessary to ensure that trait data were representative of the life stage we encountered. For example, we only encountered lingcod (*Ophiodon elongatus*) as juveniles during sampling, so feeding guild data were adjusted to represent the juvenile life stage diet. Further details on trait assignments can be found in the Supplementary Material Table S2.

2.3.5 *Functional diversity analysis*

We built a functional trait space by converting the trait matrix into Gower's distances and then computing a Principal Coordinate Analysis (PCoA) on the resulting distance matrix. Gower's distance is a similarity measure that enables the use of both continuous and categorical data (Gower, 1971). We assigned equal weights to each trait and checked the quality of the functional trait space to confirm that the Euclidean distances calculated in the PCoA accurately reflected the original Gower's distances. We chose to retain the first 3 dimensions of the PCoA for the final trait space because this allowed us to retain samples with few species and maintain a sufficient space quality value (< 0.1, Maire et al., 2015).

We calculated metrics of alpha diversity, including functional richness, functional evenness, functional divergence, and functional dispersion, for each assemblage. Functional richness, evenness, and divergence, are independent measures of alpha functional diversity that cumulatively characterize the breadth of ecological niches occupied by species within an assemblage and the overlap in abundances of species occupying the functional trait space (Mason et al. 2005). Richness represents the proportion of the trait space occupied by the assemblage, and can indicate how efficiently an assemblage is exploiting that space (Mason et al. 2005). Evenness describes how regularly an assemblage is distributed in the trait space, indicating whether species with different functional roles are present in similar abundances (Mason et al. 2005). Divergence is a measure of the extent to which species with high abundances have similar functional traits, and can indicate the degree of potential competition between species with high abundances that use similar resources (Mason et al. 2005). Functional dispersion is a variation on functional richness that is less sensitive to outliers. Dispersion simultaneously accounts for the amount space occupied by the assemblage within the trait space, and the abundances of species (Laliberté & Legendre, 2010).

We used the metrics FRic, FEve, and FDiv, proposed by Villéger et al. (2008), to calculate functional richness, evenness, and divergence, respectively. These metrics are based on the distribution and abundances of species within the multidimensional functional trait space. Each metric describes the trait space estimated by the PCoA in a different way: FRic is the convex hull volume created by plotting all the species in the assemblage (Villéger et al., 2008), FEve describes how regularly the species are distributed within the space (weighted by abundances from the abundance matrix), and FDiv represents the divergence in the distribution of weighted abundances from the center of gravity within the space (Villéger et al., 2008). Evenness and divergence are both bounded between 0 and 1; high evenness suggests relatively equal resource use between functional groups and high divergence suggests that functional groups are highly specialized. We used FDis, proposed by Laliberte & Legendre (2010), which is the weighted distance of each species from the weighted centroid, to calculate functional dispersion. We conducted the functional diversity analysis using the package mFD version 1.0.7 (Magneville et al., 2024) in R for samples with more species than the number of axes retained from the PCoA ($n = 63$). For all other samples, ($n = 9$) we assigned a value of zero because doing so allowed us to maintain a balanced sampling design for permutation-based hypothesis tests.

2.3.6 *Statistical analysis*

Before evaluating whether functional diversity varied between shorelines, we explored spatial patterns in water quality metrics and examined species richness and community composition as traditional metrics of taxonomic alpha diversity. We describe water quality metrics and species richness with summary statistics, and summarized proportions of catch comprised of common species groups across all samples. We tested for the effect of interactions among shoreline type, site, and year on species richness using a permutational analysis of variance (PERMANOVA) test with 9999 unrestricted permutations of samples (McArdle & Anderson, 2001). To visualize differences between fish assemblages in each sample (representing location and year), we plotted nonmetric multidimensional scaling (NMDS) with Bray-Curtis distances calculated after performing a square-root transformation on the species abundance matrix to down weight the effect of species with high abundances. We were additionally interested in whether measures of water quality correlate to differences in assemblage composition. However, we did not collect water quality data during the first two years of sampling, so we constructed two separate ordinations: one with the full set of samples across samples collected in 2018, 2019, 2021, and 2022, and one with samples from only 2021 and 2022. We then averaged temperature, salinity, dissolved oxygen, and turbidity over the season for each shoreline for 2021 and 2022 and assessed the association between these metrics and samples in the second NMDS using the function envfit with 9999 permutations in the R package Vegan (Oksanen et al., 2022). This function conducts multiple regressions to assess the strength of correlations between explanatory variables and distribution of the samples in the ordination space.

Next, we summarized the prevalence of different functional groups within the fish assemblage and the extent to which each trait contributed to functional diversity metrics. We used the FD package version 1.0-12.3 (Laliberté et al., 2022) to determine the community-level weighted mean trait values in each sample (Lavorel et al., 2008). The community-weighted mean metric is commonly used in functional diversity analyses to characterize the dominant value within a sample for each trait (Ricotta & Moretti, 2011). Dominant traits, those associated with abundant species, have the highest influence on ecosystem function according to the mass-ratio hypothesis (de Bello et al., 2021), so comparing the composition of dominant traits among groups enables inferences about potential differences in ecosystem function. For size, the only continuous variable, the dominant trait value is calculated as the weighted mean fork length, where more abundant species have higher weight. For the categorical variables, the community-level weighted mean represents the most common value that we observed for each trait. We then summarized the relative abundance of community-level weighted mean trait values among samples grouped by shoreline, site, and year.

To evaluate the contribution of each trait to observed functional diversity, we started by calculating each of the four metrics of functional diversity using the entire abundance matrix, across all samples, to generate a single value per metric that represents the regional assemblage. We then calculated each functional diversity metric five more times, each time with a different trait omitted. We used these results to fit a series of linear models that each had a single response and predictor variable. The response variables were metrics calculated using the full set of traits, and the predictor variables were the same metrics, but with individual traits omitted. For these models, the R^2 value will equal 1 if the omitted trait has no contribution to the functional metric,

and will approach zero as the contribution of the omitted trait increases (Stuart-Smith et al., 2013). We then ranked the importance of each trait to each functional metric based on its contribution to the R^2 value.

We tested for differences in functional diversity metrics between shoreline conditions, sites, and years using PERMANOVA tests with 9999 unrestricted permutations of shorelines. We conducted these tests using the adonis2 function in R, which does not display results for both interaction terms and main effects when assessing marginal effects. We therefore tested models with all combinations of interactions, and finding no support for interaction terms, proceeded to tests for main effects. We used the package pairwiseAdonis to conduct follow-up pairwise tests for differences in group centroids (Martinez, 2020), and followed the PERMDISP2 procedure for testing for differences in distances from group medians (Anderson et al., 2006). We conducted statistical analyses using R statistical software version 4.4.2 (R Core Team, 2021), with the vegan package version 2.6-10 (Oksanen et al., 2022).

2.4 RESULTS

2.4.1 *Water quality species richness, and community composition*

During 2021 and 2022, the two years we collected water quality measurements, we observed minor spatial variations across all metrics at the site level, but no variation between shorelines within sites (Fig. S2). We observed temperatures between 7.8 and 19.4 degrees C, with higher average temperatures at the three southern sites (13.5 °C ± 2.87 standard deviation) relative to the northern sites (10.9 °C ± 1.77 sd). Secchi depth was roughly twice as high at Turn Island (6.23 m ± 0.98 sd) than Family Tides (3.27 m ± 1.46 sd), Cornet Bay (3.05 m ± 1.54 sd), and Dockton (3.16 m ± 1.2 sd). Dissolved oxygen varied between sites and years, ranging from 3.6 to 14.0 mg/L (mean 8.48 mg/L ± 2.74 sd), while salinity was the most consistent metric across space and time (19.5 - 42.4 ppt, mean 29.6 ppt ± 3.71 sd).

We caught nearly 14,000 individual fish over the course of sampling, of which 35.3% were Pacific salmon (*Onchorhynchus* spp.), 28.2% were surfperch (*Cymatogaster aggregata, Embiotoca lateralis,* or *Phanerodon vacca*), 20.3% were species typically associated with eelgrass communities (in the families Aulorhynchidae, Pholidae, Syngnathidae, or Stichaeidae), and 8.9% were forage fishes (*Ammodytes hexapterus, Clupea pallasii, Engraulis mordax,* or *Hypomesus pretiosus*). Shiner perch, *C. aggregata*, and three-spined stickleback, *Gasterosteus aculeatus*, were both observed at 17 out of the 18 different shorelines. We observed a minimum of 1 and a maximum of 25 species at a given shoreline in a given year. Species richness was about three times higher, and two times as variable across shorelines and over time, at Cornet Bay relative to all other sites. We observed an average of 14.20 (± 5.31 sd) unique species per sample versus an average of 5.75 (± 2.48 sd) unique species per sample across all others. The interaction between site and year was significant in the PERMANOVA (SS = 133.56, pseudo-$F(15) = 1.89$, $p = 0.040$), and while we did not have sufficient replication to follow up with pairwise tests, it appears that species richness was slightly lower at Cornet Bay in 2018 and 2021 and the number of species present in those years was similar to Turn Island. We also observed

different dominant species between sites, for example three-spined stickleback at Dockton and Pacific tomcod (*Microgadus proximus*) at Turn Island (Fig. S3).

Overall assemblage composition varied between samples correlated with warmer (envfit, R^2 = 0.19, p = 0.0285) and more turbid (R^2 = 0.29, p = 0.0035) conditions, generally in the south, compared to samples correlated with cooler and less turbid shorelines, generally in the north (Figure 2A & B). We did not find significant correlations for dissolved oxygen or salinity (Figure 2B).

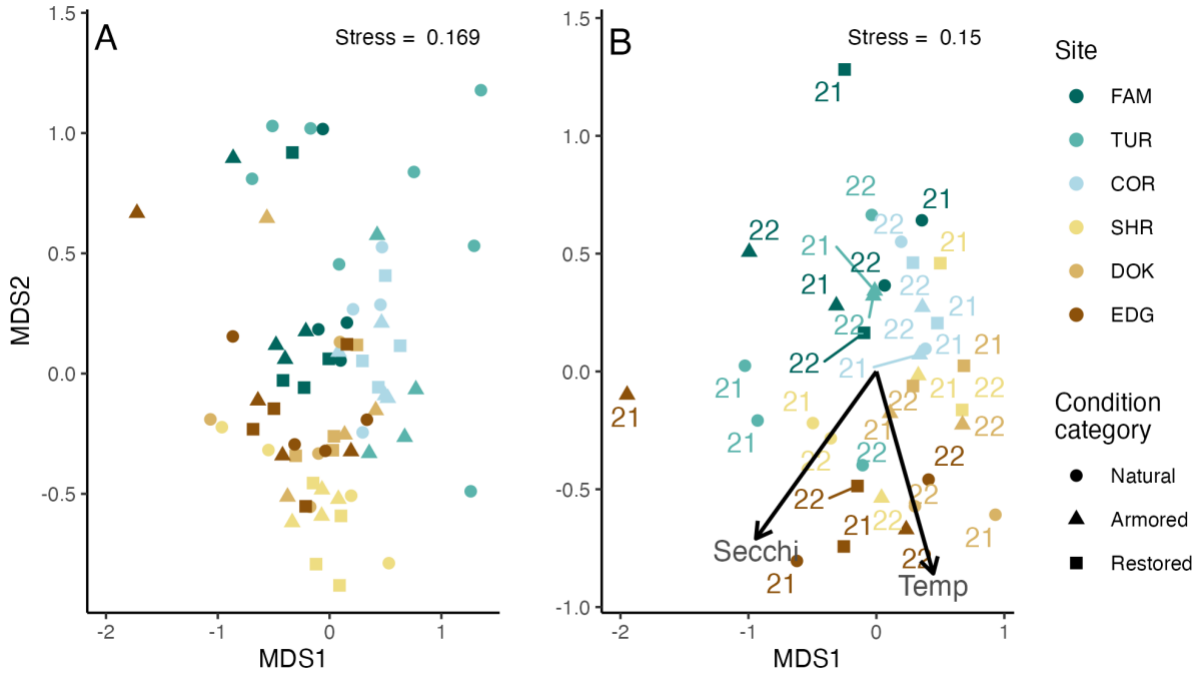

Figure 2. Non-metric Multidimensional Scaling (NMDS) ordination of nearshore fish assemblages in the Salish Sea, Washington, USA. This ordination was calculated using Bray-Curtis distances on an abundance matrix with samples from all years of field sampling (2018, 2019, 2021, and 2022; A) and with samples from only 2021 and 2022, when we also took water quality data (B). Points represent distinct shorelines and labels on the right plot signify sample year. Significant correlations with water quality metrics are displayed, with arrows pointing in the direction of increased values. Secchi indicates Secchi depth, and Temp indicates temperature. Sites are labeled in a north to south order.

2.4.2 *Functional group prevalence and contributions to functional diversity*

Traits did not appear to broadly differ between shoreline types, yet traits had different degrees of influence on functional diversity metrics. The community-level weighted mean for each of the five traits was similar among assemblages grouped by shoreline condition category (Fig. S4), and year (Fig. S5), although resident species were dominant in assemblages less often in 2022 relative to other years. There were generally more pronounced differences among sites (Figure 3). For example, Seahurst had larger fish, and higher abundance of eel-like body shapes, relative

to other sites, while Turn Island had higher abundance of pelagic and resident species, with less frequent dominance of short and / or deep species (Figure 3). Each of the individual traits contributed similarly to the richness and dispersion metrics of functional diversity, while the contributions of traits to evenness and divergence metrics were more variable (Table 2). Body transverse shape and feeding guild had the highest influence on evenness and divergence, indicating high variation in the abundances of species with different trait values, while body length had the lowest influence (Table 2).

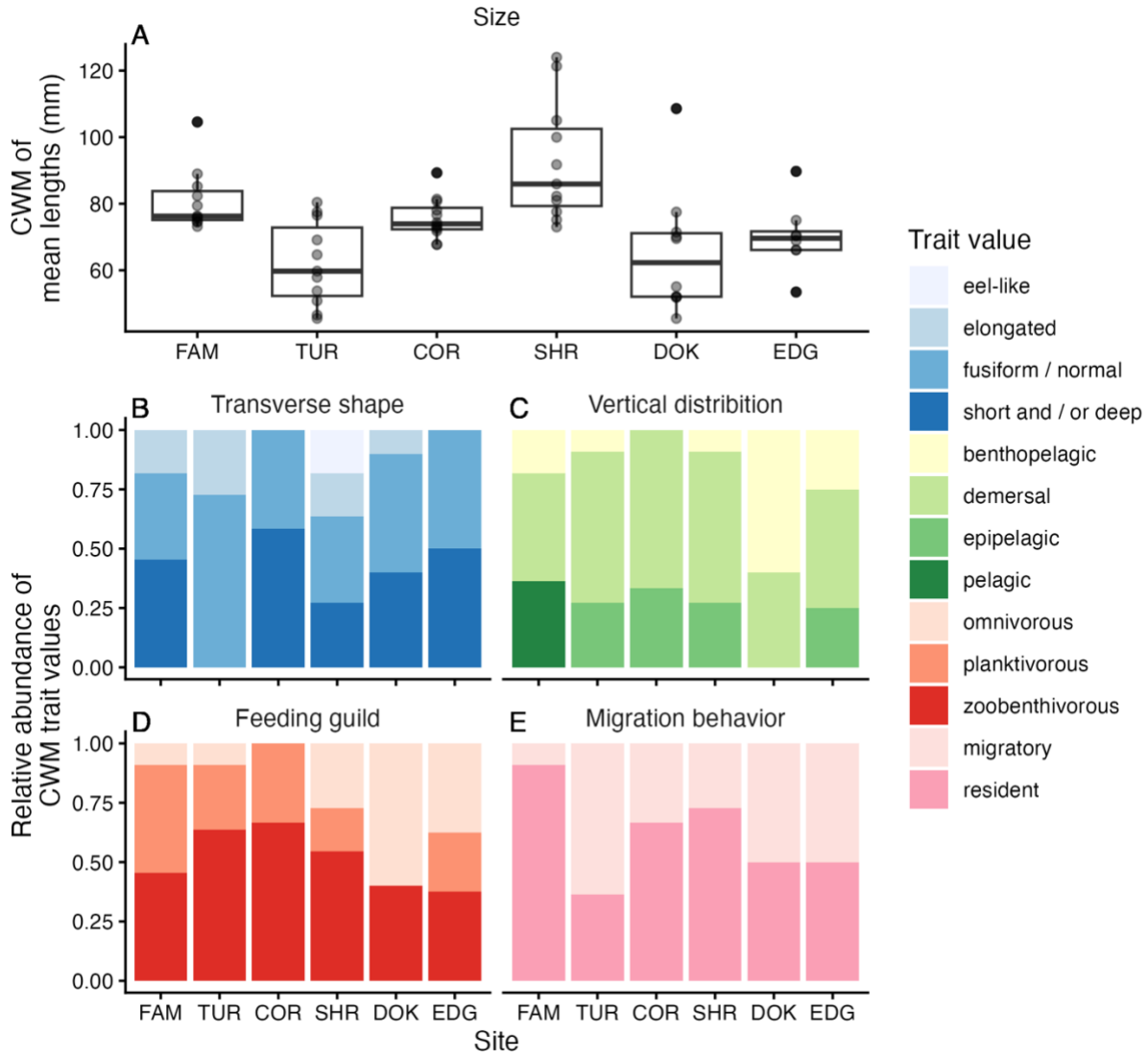

Figure 3. Community-level weighted mean (CWM) trait values associated with nearshore fishes in the Salish Sea, Washington, USA. Catch data for fish is summarized in samples, where each sample represents the summed catch at each shoreline segment for a given year (n = 44 FAM, TUR, and SHR, 48 COR, 40 DOK, and 32 EDG). In our study design, shoreline segments are hierarchically nested in sites, and this figure displays samples grouped by site. The CWM for size (A), the only continuous trait, is a weighted average of the mean fork length values for fishes in a given sample. CWM for the categorical traits (B-E) is the trait value with the highest

abundance in each sample and is displayed here as the proportion of samples when the CWM was a given trait value.

Table 2. The contribution of individual traits to the functional diversity of nearshore fish in the Salish Sea, Washington, USA. We measured the sensitivity of functional diversity metrics to omission of each trait by fitting a series of linear models, where each diversity metric, calculated for the entire regional assemblage with all five traits, was regressed against the same diversity metric calculated with one trait omitted. R^2 values are displayed for each model where a given trait has been omitted from the metric calculation. Lower rank indicates greater contribution to a given metric.

Omitted Trait	Richness	Rank	Evenness	Rank	Divergence	Rank	Dispersion	Rank
Size	0.96	4	0.51	4	0.77	5	1.00	5
Transverse shape	0.92	2	0.19	1	0.26	1	0.90	1
Vertical distribution	0.92	2	0.65	5	0.65	4	0.95	3
Feeding guild	0.81	1	0.40	2	0.45	2	0.92	2
Migration behavior	0.95	3	0.45	3	0.62	3	0.97	4

2.4.3 *Functional diversity comparisons*

Metrics of functional diversity varied spatially and temporally (Figure 4). Functional richness ranged between 0 and 0.16 across all samples (mean 0.03 ± 0.04 sd). The average functional evenness was relatively low (mean 0.40 ± 0.21 sd) relative to the maximum value of 1, although values for individual shorelines ranged between 0 and 0.70, while divergence values across all samples were generally high (mean 0.78 ± 0.31 sd) relative to the maximum value of 1. Dispersion ranged between 0 and 0.42 among all samples (mean 0.22 ± 0.13 sd). Samples assigned a value of zero were well distributed among different shorelines, sites, and years (Figure 4).

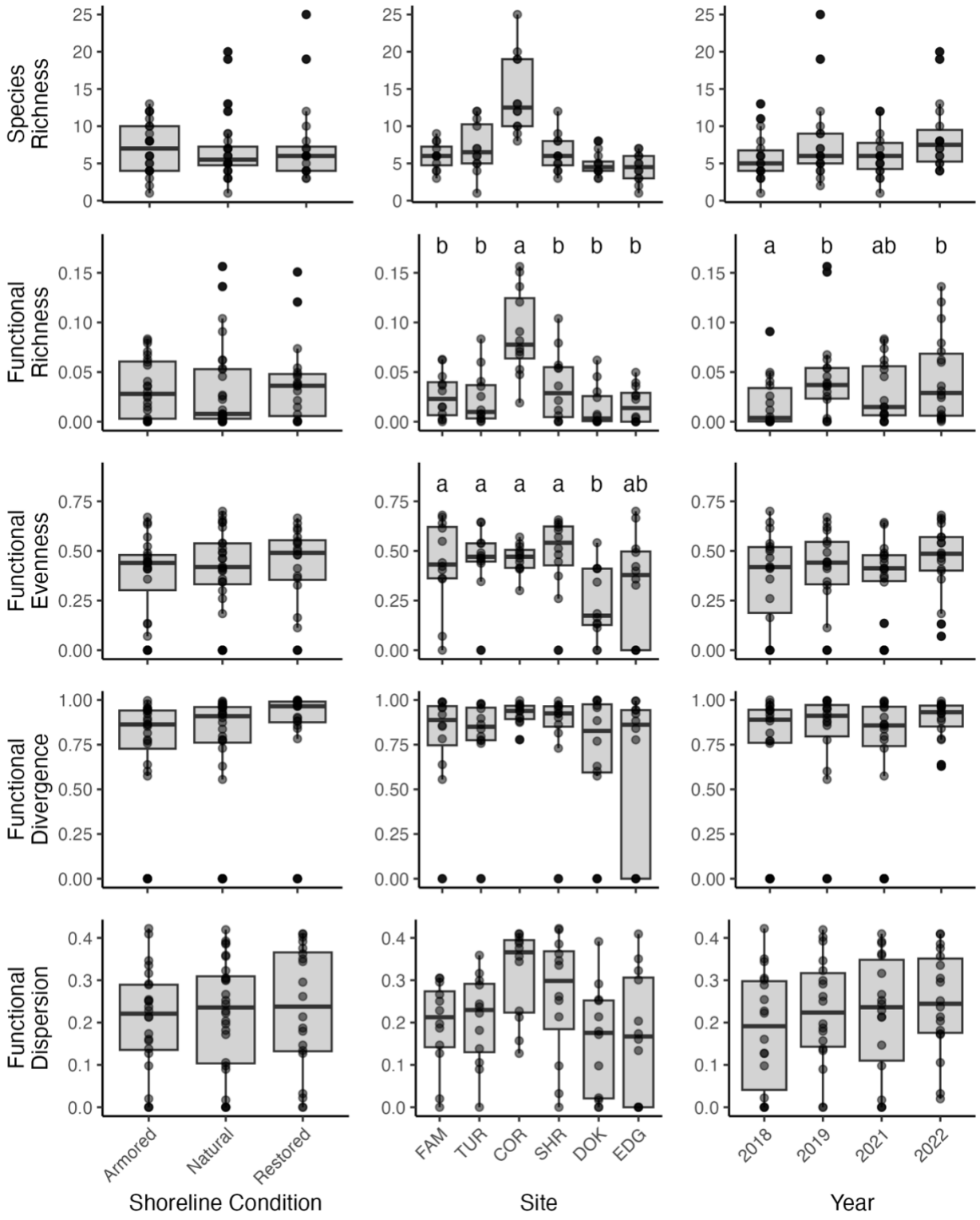

Figure 4. Functional diversity of nearshore fish assemblages in the Salish Sea, Washington, USA, where samples are grouped by shoreline condition category (left), site (middle) and year (right). Significant groupings from pairwise PERMANOVA tests are displayed with letters when present. Boxplots display the median value plus and minus the interquartile range, and points represent individual samples.

We observed some differences in functional diversity among sites and years. Richness was higher at Cornet Bay than at any other site (pairwise PERMANOVA $p < 0.01$), and significantly lower in 2018 than in 2019 or 2022 (pairwise PERMANOVA SS = 0.007, pseudo-F(1) = 5.082, p = 0.033 and SS = 0.006, pseudo-F(1) = 4.478, p = 0.042 respectively). We found significant differences in functional evenness (Fig. 4, Table 3) among sites: Dockton had significantly lower functional evenness than Family Tides (SS = 0.044, pseudo-F(1) = 5.771, p = 0.025), Cornet Bay (SS = 0.303, pseudo-F(1) = 16.244, p = 0.003), and Seahurst (SS = 0.364, pseudo-F(1) = 10.407, p = 0.0006). No other functional metrics were found to vary significantly among sites or through time (Table 3). We found no significant difference in any functional diversity metrics between shoreline condition categories (Figure 4, Table 3).

Table 3. Results of permutational analysis of variance (PERMANOVA) tests for differences in functional diversity metrics among nearshore fish assemblages in the Salish Sea, Washington, USA. Statistically significant p-values are displayed in bold, at an alpha level of 0.05.

		df	SS	Pseudo-F	p
Functional Richness	Shoreline condition	2	0.000	0.064	0.983
	Site	5	0.046	11.859	**0.003**
	Year	3	0.009	3.803	**<0.001**
	Residual	61	0.047		
	Total	71	0.102		
Functional Evenness	Shoreline condition	2	0.039	0.520	0.720
	Site	5	0.588	3.156	**0.043**
	Year	3	0.115	1.030	0.354
	Residual	61	2.274		
	Total	71	3.001		
Functional Divergence	Shoreline condition	2	0.160	0.855	0.519
	Site	5	0.748	1.601	0.270
	Year	3	0.388	1.385	0.241
	Residual	61	5.702		
	Total	71	6.969		

	Shoreline condition	2	0.007	0.211	0.899
Functional	Site	5	0.216	2.668	0.220
Dispersion	Year	3	0.043	0.874	0.392
	Residual	61	0.989		
	Total	71	1.256		

In addition to comparisons of mean levels, the magnitude of variability was also different among sites. There were eight-fold differences in the variability of functional richness and four-fold differences in the variability of other functional diversity metrics across sites between samples collected at different shorelines and in different years (Figure 4, Figure 5). The interannual variability of functional evenness was significantly lower at Cornet Bay, compared to Family Tides (PERMDISP $p = 0.029$), Dockton ($p = 0.028$), and Edgewater ($p = 0.003$). Cornet Bay also displayed the lowest interannual variation in functional divergence values, which were significantly lower than Dockton ($p = 0.004$) and Edgewater ($p = 0.011$). These differences were largely due to differences in temporal variability, as we observed no differences in variation among shoreline condition categories (PERMDISP $p > 0.05$).

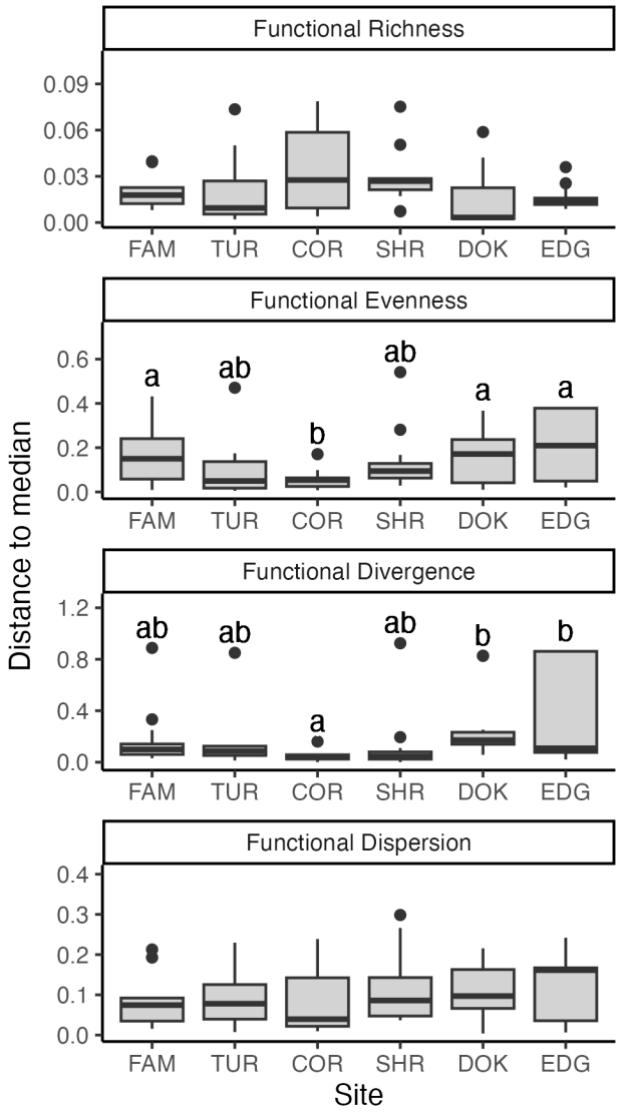

Figure 5. Variability in functional diversity metrics by site. Distance to median refers to the average Euclidean distance to the sample's spatial median in multivariate space. Boxplots show median value of all years (2018, 2019, 2021, and 2022) for each site and whiskers represent the interquartile range. Letters represent significant groupings (PERMDISP $p < 0.05$).

2.5 Discussion

Nearshore marine areas provide vital ecosystem services to coastal communities, including provisioning from fishery catch, water quality regulation, and aesthetic values (Buonocore et al., 2021). These services may be impaired if anthropogenic impacts to shorelines change the ecological niches available to nearshore species, for example by reducing heterogeneity or increasing competition. It is therefore important to understand how species occupy the available niches among different habitats and determine what, if any, habitat changes are likely to alter community structuring. Here, we found marked variation in assemblage composition among sites representing different habitats. Despite this, metrics describing the species occupation of the

ecological niche space, known as functional diversity, were not different among sites and there were few differences in functional diversity within these sites, at different shorelines. Specifically, contrary to our expectations, we found no differences between shoreline condition categories representing differing histories of armor presence, and few differences among sites close to and far from urban centers. Our results suggest that either similar ecological niches are available to nearshore fish at these different shorelines, or that differences in ecological niche space affect multiple functional groups similarly.

The relationship between species richness and functional diversity is complex and depends on environmental filters and biotic interactions that shape the assemblage (Mayfield et al., 2010; Stuart-Smith et al., 2013). Functional diversity can increase with species richness if species have unique traits or, conversely, if species have similar functional traits, then additional species will be functionally redundant (Rosenfeld, 2002). Among multiple metrics of functional diversity, both positive and negative relationships with species richness are common in the literature (Suárez-Castro et al., 2022). We observed the highest functional richness at the site with the highest species richness but found no differences among other sites. Cornet Bay is a very heterogeneous site, with both eelgrass and a dock, and is situated at a narrow passage between a geological basin with greater oceanic influence and one with greater estuarine influence, along a primary migration route, and these characteristics likely contributed to the high species and functional richness at this site. Given that other sites had differences in assemblage composition, this suggests that species at different sites were not functionally distinct, or that the functions they contributed did not substantially change the overall pattern in distribution of traits across ecological niches.

We found that groups of species in the Salish Sea with similar functional traits were not present in equal abundances (low functional evenness, sensu Mason et al. 2005). This suggests that resource availability is either uneven among the occupied ecological niches, or the resources in ecological niches that support fewer fish are underused in this system, which can result in decreased ecosystem productivity and allow opportunities for invasive species (Mason et al. 2005). We also found a high degree of differentiation between species in the functional trait space (high functional divergence, sensu Mason et al. 2005). Differentiation between species traits suggests that the community can inhabit a wide variety of ecological niches, rather than competing for resources in fewer niches (Mason et al. 2005). Assigning functional diversity metric values of zero to samples with low species richness may have biased our results if these cases were predominantly in one shoreline condition category, site, or year, or if zero was much smaller than any of the other calculated functional diversity metric levels for low species richness sampling events. The former case did not manifest because zeros were relatively well distributed between groups, and the latter case only occurred for functional divergence, but did not affect our conclusion that functional divergence was high. While we found some differences in functional evenness among sites, and higher variance across multiple metrics at some sites, there was no clear spatial trend that would indicate differences in ecological function related to shoreline condition or position within the estuary.

Our study had some limitations that may have reduced our ability to detect an association between functional trait diversity of nearshore fishes and shoreline habitat conditions. The style of net we used is efficient at sampling the fish community in surface waters offshore of the

intertidal zone, beyond the area that beach seines can sample. However, because it targets fish at the surface, it is less efficient at capturing demersal species present in waters deeper than five meters. Regardless, we caught more demersal species than pelagic species, so this sampling bias did not preclude us from using vertical distribution among the traits to compare shorelines in our analysis. Deeper stations were also farther away from armor and those areas may have been less directly impacted by any changes in sediment composition propagated by the structures. We were unable to test this in the current analysis because our data had too many zeros to disaggregate different depth stations, but future efforts could test alternative sampling methodologies to target the subtidal benthic community. Given that the impacts of armor may be highly localized, and our surveys took place offshore of the structures (up to 200 m offshore at deep stations), even our shallow stations may have been too far away to detect a strong effect (Kornis et al., 2018; Smith et al., 2021). We also assigned traits at the species level and therefore did not assess intraspecific variation between shorelines. This may have been particularly important for the body size trait, if distribution shifts in response to armor impacting the availability of shallow water habitat were occurring at the individual, rather than the species, level (Munsch et al. 2016; Kornis et al. 2018). We also limited this study to traits that we could assign post-hoc to species based on their availability in Fish Base for the life stages we observed. Traits not captured in our analysis, and direct measures of ecosystem function based on species productivities or metabolisms, for example, may reveal different insights.

It may not be surprising that we did not detect differences in the functional diversity of fish assemblages between armored and unarmored shorelines, or between sites near or distant from urban centers. While Russet-Rodríguez et al. (2023) found higher functional diversity of fishes at urbanized sites, the authors acknowledged that there were likely confounding factors, such as correlated differences in habitat and sampling depth. The strength of armor impacts are also context-dependent (Dugan et al., 2018), and the armor at our sampling sites was high in the intertidal zone. The ecological impacts of armor are thought to be stronger when armor is placed lower in the tidal frame (Toft et al., 2014), which may contribute to differences in the strength of effect of armor on nekton reported in other locations. The nature of these effects may also be different. Structural complexity is essential for habitat provisioning, and when armor changes the structural complexity of the shoreline there are likely to be consequences for fauna that directly interact with it, but if fish are not regularly interacting with the structure because it is largely out of the water or high in the intertidal zone, the consequences for the armor presence may be more related to its disturbance of intertidal communities and terrestrial subsidies (Toft et al., 2010). Within the Salish Sea, other work has found no association of urbanization with ecosystem function, measured as primary productivity and decomposition (Samhouri et al., 2022), which is consistent with our observation that there are few differences in ecosystem function among sites, as measured via functional diversity.

The shorelines in our study exist within a network of patches that comprise the nearshore habitat mosaic, and the size and arrangement of patches within the mosaic may be modulating the effect of shoreline type on fish communities. Different habitats provide different resources for nekton, and motile species will move between patches of different habitat types to seek prey resources and refuge from predators (Skilleter & Loneragan, 2002). Linkages between habitats therefore play an important role in determining survival and growth of species that rely on them (Gain et al., 2017; Grabowski et al., 2005). Species use is also a function of patch size, as the edges of

patches can function differently than the centers (Gittman et al., 2018; Skilleter & Loneragan, 2002). The mosaic of habitat types may be sufficiently connected so that local impacts of armor at our study sites is offset by niche space available in other tightly linked habitats. This could be one reason that while other work has found differences in the representation of different functional groups between armored and unaltered shorelines in salt marsh habitats (Kornis et al., 2017), we did not find a strong response among sites that occurred along highly connected sandy beaches and rocky coasts where fish to move freely between adjacent habitats. Future work could continue to explore the potential effects of armor in relation to linkages with other habitat types within the mosaic. Understanding the use of different habitats for different species will help determine ideal spatial arrangements and habitat patch sizes to target for conservation and restoration efforts.

Our findings support other work that has found differences in the dominant species between northern and southern oceanographic basins in the Salish Sea (Rice et al., 2012). Spatial differences do not appear to translate into significant differences in occupation of the ecological niche space. On the other hand, biological processes operate at different spatial scales, and we may not have observed fish at the same scale at which trait differentiation occurs. For example, at the shoreline scale of this effort (~30 m long segments), our results suggest that armor does not substantially affect niche breadth available to fish in subtidal habitats in this system. There may be enough movement of individuals between shorelines that the aggregate measures we used fail to reflect finer-scale differences in the available ecological niches. Alternatively, environmental filtering and trait responses to urbanization may be occurring at broader spatial scales, and we could have seen a stronger response had we compared our region to another. For instance, the strength of response to urbanization appears to be stronger when comparing between regions than between sites within regions (Teichert et al., 2018). Future work would benefit from an integration of additional spatial scales, to investigate the degree to which trait variation responds to environmental drivers across scales (Suárez-Castro et al., 2022). Our study lacked sufficient replication at the site level to statistically test for differences between sites aggregated by oceanographic basin or region, but this could be a focus of future work.

We conducted the first regional analysis of functional diversity in subtidal, nearshore fishes within the Salish Sea. This approach furthered our understanding of extent to which functional diversity varies spatially within a fjordal estuary where shorelines are subject to variable local conditions. The low variability of functional traits displayed by nearshore fishes within this area suggests that the functional traits of this assemblage are maintained even in the presence of shorelines that may be considered degraded based on their armored condition. Metrics of functional diversity could be tracked over time to serve as indicators of environmental change, particularly if human impacts on coastlines increase. Future work to explore other functional traits that relate to an expanded set of potential responses to habitat and environmental conditions, particularly intra-specific variability, may aid in developing priorities for restoration activities targeted towards coastal fishes and the ecosystem functions they support.

2.6 Data Availability Statement

Field data and code to reproduce the associated analyses are available in a public repository on Github at https://github.com/e-bish/Nearshore_Fish_Diversity.

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Chapter 3. EVIDENCE FOR JUVENILE CHINOOK SALMON ASSOCIATIONS WITH NEARSHORE MARINE HABITAT FEATURES

3.1 Abstract

The early marine phase is a critical period in the Chinook salmon life cycle, and there are increasing efforts to prioritize actions that support growth and survival for this species at this stage, including habitat restoration. However, our understanding of the physical features that comprise high quality nearshore marine habitat for Chinook salmon are often borrowed from other Pacific salmon species and other habitats, despite evidence that generalizations may not apply. Given this gap, efforts to restore nearshore marine habitat for the benefit of Chinook salmon may be misplaced or prioritized such that direct benefits for Chinook smolts are not maximized. I conducted a literature review to assess the extent and strength of known associations between juvenile Chinook salmon and physical features of nearshore marine coasts that are frequently considered during restoration projects. I then used this evidence to assess our current understanding of the features that comprise high quality habitat for juvenile Chinook salmon in the marine nearshore. I found few conclusive associations with specific habitat features, which individually appear to have little direct influence on habitat quality. Given that a comprehensive recovery strategy for Chinook salmon must inevitably consider trade-offs in size and placement of restoration activities and conservation areas, a better understanding of the ecological function inferred by different habitat types in the nearshore will help weigh these trade-offs.

3.2 Introduction

Chinook salmon (*Oncorhynchus tshawytscha*) have a complex life history, and decades of research have contributed to informing restoration techniques that are tailored to maximize growth and survival at different stages in their life cycle (Quinn 2018). Members of this species rear in freshwater, travel downstream through the estuary, then distribute widely in marine waters, making extensive use of nearshore habitats (Duffy et al. 2005). Restoration actions targeted at the earliest life stages, in freshwater, are well defined, and more recent work in estuaries has described habitat use in ways that support restoration prioritization (Hood et al. 2022; Chamberlin et al. 2022; Hall et al. 2023). However, once outmigrating Chinook salmon enter the coastal marine environment, it becomes more challenging to track their fine-scale movements and habitat preferences, so less is known about where to prioritize restoration actions targeted at the early marine phase. This is a critical gap because rapid growth during this phase is a primary driver of adult returns (Duffy and Beauchamp 2011).

Prioritizations for habitat restoration in the marine nearshore often group multiple Pacific salmon species together or assume that studies showing a response in a different species will translate to a similar result for Chinook salmon (Walsh et al. 2020). However, Pacific salmon species use

estuaries differently and pass through nearshore habitats at different rates (Thorpe 1994; Quinn 2024). For example, pink (*O. gorbuscha*) and coho (*O. kisstch*) salmon move rapidly to the ocean, while chum (*O. keta*) and Chinook salmon use estuaries and coastal habitats more extensively (Thorpe 1994; Quinn 2024). Pacific salmon also exhibit resource partitioning, where different species will target different prey (Romanuk and Levings 2005). For example, Chinook salmon diets are primarily comprised of insects, while chum eat a combination of insects, larvaceans, and copepods, and coho eat decapods and fish, based on research in in Willapa Bay, Washington, USA (Dumbauld et al. 2015). Because of these differences, descriptions of how one Pacific salmon species uses nearshore habitats may not apply to for others.

Even within a species, generalizations can be misleading. Chinook salmon have a diversity of life history pathways, which impacts their residence in nearshore habitats (Bourret et al. 2016). Hatchery and wild-origin Chinook salmon also use nearshore habitats differently (Beamer et al. 2024). Therefore, efforts to characterize salmonid use of nearshore environments that group species together could be missing critical nuances between species that are known to have different behaviors and partition resources differently.

Similarly, understanding of juvenile Chinook salmon habitat use in estuaries is often generalized to the marine nearshore. These habitats are frequently treated as interchangeable because they are tightly linked, and the transition between them can be gradual. Shipman (2008) distinguishes the following coastal geomorphic systems: rocky coasts, beaches, embayments, and river deltas. Here, I define marine nearshore habitat as including features of exposed rocky coasts and beaches, but not features unique to protected embayments and river deltas (e.g., distributary channels), which make up estuaries (Shipman 2008). Distinctions between the estuary and marine nearshore can be especially difficult to untangle in areas like the Salish Sea where, for example, Puget Sound is a fjordal estuary that contains both tidal estuaries and marine nearshore habitat. Not only that, but semi-enclosed and calm areas of nearshore marine habitat in Puget Sound are called “pocket estuaries” (Shipman 2008). Another complicating factor is that juvenile Chinook salmon exhibit complex movement patterns among habitats. Rather than progressing directly through estuary and nearshore environments out to the ocean, some outmigrating fish leave their natal estuaries, enter the marine nearshore, and then redistribute into non-natal estuaries where they continue rearing (Chamberlin et al. 2026).

There are some documented differences between juvenile Chinook salmon found along exposed marine coastlines that comprise the nearshore, and those in estuarine tidal deltas. For example, juvenile Chinook salmon in the marine nearshore are larger and consume more marine-derived prey than juveniles in estuaries (Duffy et al. 2005). In estuaries, juvenile Chinook salmon rear in tidal channels, consuming terrestrial-based foods while undergoing physiological transitions to adapt to the saltwater environment (Davis et al. 2020). Once individuals move into the marine nearshore, the open-water environment allows them to move more freely among coastal habitats, and they consume more crab, euphausiid, and fish prey (Davis et al. 2020). Given these differences, habitat use in estuaries is not necessarily indicative of how this species uses nearshore marine environments. Different habitat features might be more or less important to individuals as their vulnerability to predation changes and as they enter different foraging arenas (Wells et al. 2025).

Currently, restoration efforts in the marine nearshore aimed at improving coastal functions for Chinook salmon include actions that increase the availability of terrestrial prey and the area of aquatic vegetation. This commonly involves removal of shoreline armor (Dethier et al. 2016), often accompanied by beach nourishment and planting of coastal vegetation (Des Roches et al. 2024). These restoration practices have been shown to restore natural functions of beaches with direct benefits to forage fishes that rely on intertidal habitat for spawning (Penttila 2007). While juvenile Chinook salmon may benefit indirectly from this restoration via an increase in spawning habitat for their forage fish prey, few studies have demonstrated specific benefits of armor removal via changes in habitat use for Chinook salmon. In fact, recent studies that examined this issue found equivocal effects of armor presence on Chinook salmon abundance in subtidal water adjacent to armored shorelines (Francis et al. 2022; Bishop et al. 2024). Due to the generalizations that have been made from other species and habitats, the type of restoration often employed along marine coasts may not benefit Chinook salmon in the ways we expect, or in ways that are measurable using current metrics of restoration success.

Chinook Salmon have been intensively studied for decades, and there is a robust body of literature describing their associations with different habitats; yet the early marine phase of Chinook salmon is relatively understudied, and a general understanding of habitat associations in this key life phase is lacking. Therefore, I undertook a literature review to identify and synthesize the available literature relating specifically to Chinook salmon in the marine nearshore. My aim was to evaluate the extent of evidence in the literature relating physical features of nearshore habitats to juvenile Chinook salmon ecology, including their distributions and demographic variables. Specifically, I reviewed evidence on how the habitat features considered in habitat quality assessments (e.g., water depth and presence of submerged aquatic vegetation) or targeted for restoration (e.g., shoreline armor) influence the distribution, growth, and survival of juvenile Chinook salmon. With a more specific understanding of what high-quality nearshore habitat looks like for Chinook salmon, conservation and restoration efforts can be directed at enhancing features that provide the most support for their growth and survival during the early marine phase.

3.3 METHODS

3.3.1 *Literature search*

To identify relevant literature, I queried the database Web of Science core collection on March 31st, 2025 using the search terms (“nearshore” OR “marine” OR “coastal” OR “estuary”) AND (“chinook salmon” OR “Oncorhynchus tshawytscha” OR “pacific salmon”) AND (“habitat” OR “eelgrass” OR “armor” OR “rock”* OR “kelp”). I did not use any filters for language, article type, or geographic area. I scanned titles of all sources and excluded any that did not appear relevant to the present study, then scanned the abstracts of the remaining sources excluding any that were not relevant to Chinook salmon use of marine nearshore environments. When abstracts did not provide enough detail to determine if the source was relevant, I scanned the whole article. I also scanned the references in each of these finalist articles to identify potentially relevant technical reports and white papers. My initial search returned 978 unique sources, of which I scanned 311 abstracts and reviewed 186 full texts. I also scanned 62 manuscripts and technical

reports that were cited by records identified in the database search, or that I encountered while searching for full texts of records in the database search.

I screened sources for measures of Chinook salmon habitat associations, including measures of fish distribution, feeding habits, and demographic variables. I limited inclusion to articles that measured the direct associations of Chinook salmon to physical habitat attributes. For example, I included papers that measured predator avoidance behaviors of Chinook smolts in different habitats but not papers that described how different habitats might alter predator abundance. I did not consider biophysical features like temperature, salinity, or chlorophyll-a because this review focused on three-dimensional habitats that are targeted for restoration.

I excluded studies that grouped multiple salmonid species together or did not match the target life phase for this analysis. As noted above, Pacific salmon species have varied behaviors and my aim was to identify trends specific to Chinook salmon, rather than drawing conclusions from the behaviors of other species. I also excluded papers that were exclusively in freshwater or tidal marsh habitat characteristic of estuaries but included papers that sampled in low tidal deltas to capture preferences of juvenile Chinook salmon undergoing a transition into the marine environment. Determining a seaward limit for sources to include was complicated by the fact that the scale of different geographic regions informs the extent of the area considered to be nearshore. For example, the nearshore environment in Puget Sound is generally considered within a few hundred meters of shore, while "shallow" water sampling of juvenile salmonids off the Washington and Oregon coasts occurs up to 50 km offshore (Bi et al. 2007). I therefore relied on the size of the fish to determine if they matched the target life phase of this analysis and only included studies that examined fish that were, on average, smaller than 400 mm fork length.

3.3.2 *Data extraction*

For each source that met the inclusion criteria, I recorded the region, specific system within the region, the area type (e.g., nearshore versus lower estuary), the size range of the Chinook salmon in the study (if provided), the origin of the fish (hatchery versus natural), and the relevant habitat feature. I grouped relevant habitat features into three major categories: substrate and depth, submerged aquatic vegetation, and human development. I also recorded the metric used to measure the response to the habitat feature, and the direction of the effect on Chinook salmon

To clarify the nature of Chinook salmon responses to habitat features, I interpreted response metrics using categories of measures described by Simenstad and Cordell (2000). These measures, which were developed to evaluate the habitat's ability to support demographic performance, include: capacity, opportunity, and realized function. Capacity is related to the ability of a habitat to support salmon growth and survival, opportunity relates to the ability for salmon to access and benefit from the habitat, and metrics that measure realized function are direct measures of behavioral or physiological responses to the environment that benefit the fish (Simenstad and Cordell 2000).

In the review that follows, I summarized evidence that different habitat features are associated with capacity, opportunity, and realized function, in addition to fish distribution. Metrics of fish distribution, including occurrence, abundance, and density, are commonly used to assess habitat

quality and were therefore important to include in this review (Ciotti et al. 2025). These metrics should be interpreted with caution however, because density is not always positively associated with habitat quality (Van Horne 1983). For example, individuals may occupy one habitat not for its benefits, but to avoid another, lower quality habitat (Hodgson et al. 2020). In this review, I use Chinook salmon presence and density in the body of evidence to ascribe habitat quality, while giving greater weight to demographic variables. Demographic variables are more reliable measures for habitat quality because they address specific mechanisms by which habitat is supporting the growth and survival of individuals and populations (Van Horne 1983).

3.4 RESULTS

I found 38 sources that matched all inclusion criteria. Most of these sources were from United States and Canadian waters of the Salish Sea and the coastal waters of Washington and Oregon, USA. In what follows, I present results organized by the habitat feature evaluated in each source and discuss the strength of evidence that each habitat feature is associated with juvenile Chinook salmon distribution, capacity, opportunity, or realized function. A matrix of results from the literature search is available in the Appendix.

3.4.1 *Depth and substrate*

Depth

High quality habitat for Chinook salmon includes a variety of water depths, because Chinook salmon smolts distribute into different depths based on their size class. With respect to distribution, in the Skagit basin of Washington State, lampara netting revealed a negative association between abundance and depth for fishes in the 40-150 mm range (Rubin et al. 2018). On the outer coast of Washington and Oregon, multiple efforts have shown a negative association with depth and Chinook salmon abundance for smolts in the 141-400 mm range, however these coastal surveys with sampling only in water deeper than 30 m likely aren't capturing the inshore areas where smolts may be more abundant (Bi et al. 2008; Peterson et al. 2010). One study that used downriggers to understand smolt distribution by depth found that longer and older sub-yearling Chinook salmon distribute deeper (Smith et al. 2024). Similarly, a study in Puget Sound, which collected abundances via tow netting, found a weak positive association between density and depth for smolts in the 60-225 mm range (Rice et al. 2011). Sub-yearling outmigrants, which are smaller than yearling outmigrants, are more often associated with shallower water than yearlings (Healey 1983; Miller et al. 1983; Fisher et al. 2007). Another study that explored realized function measured associations with juvenile Chinook salmon and a bacterial infection in the Salish Sea and found no difference in likelihood of infection at different depths (Rhodes et al. 2011). Shoreline armor that limits shallow water habitat is associated with reduced opportunity (Munsch et al. 2016, discussed below).

Substrate

Juvenile Chinook salmon are found in an array of nearshore habitat types, and do not appear to have different distributions or demographic variables at one substrate over another. With respect to distributions, smolts are known to be present over sand flats near the Fraser River outflow in British Columbia (BC) Canada (Levings 1982; Chalifour et al. 2019). Toft et al. (2007)

compared densities of Chinook smolts between subtidal habitats adjacent to beaches with sand and cobble substrate and found no differences using either enclosure nets or snorkel surveys. Similarly, another study in Puget Sound nearshore found no difference in smolt abundance between fines, sand, mixed sand, and large substrate (Brennan et al. 2004). In the Campbell River, BC transition zone, Chinook salmon smolt biomass at sites with gravel substrates is higher than other salmonid species (Korman et al. 1997). Some have suggested that there might be a concentrating effect on prey density, indicating increased capacity, on ebb tides over sand flats (Levings 1982; Chalifour et al. 2019). In Oregon, shallow sloped sandy beaches may serve as alternative nursery habitat for smaller smolts because fish observed there had similar growth rates and gut fullness, and as diverse a prey field as fish that occupied adjacent estuarine habitat, suggesting that estuaries and adjacent sandy beaches have similar realized function and capacity (Marin Jarrin and Miller 2013). There was no evidence for differences in opportunity between geomorphic substrate types.

There was also little evidence that the presence of other substrates mediates juvenile Chinook salmon habitat quality. In the present search, few studies examined juvenile Chinook salmon distributions in natural habitats with larger substrate, like boulders. This may be a function of the gear commonly used to assess nearshore fishes, surface trawls or beach seines, which can easily snag on large rocks and therefore are not typically used in those environments. However, Smith et al. (2024), who used microtrolling, explored whether probability of smolt detection varied when fish were captured over hard substrate, or near hard substrate, and found no support for including those variables in their models. There was also limited evidence that distribution, capacity, or realized function vary in response to oyster substrates. Semmens (2008) examined Chinook salmon associations with oyster beds in Willapa Bay, WA using acoustics to track smolts but did not detect any behaviors that suggested the presence of oysters was influencing movement. Similarly, Dumbauld et al. (2015) observed no difference in smolt density or their prey communities between sand/mudflats and oyster aquaculture, and no association between benthic habitat and diet (Dumbauld et al. 2015). I did not find any studies that asked whether measures of opportunity vary in response to substrate.

Habitat preference may have more to do with other biophysical conditions at a given shoreline. For example in Puget Sound, Chinook salmon exhibit the greatest holding behavior, associated with greater realized function, at protected shorelines with freshwater input, regardless of substrate type (Chamberlin et al. 2011). Although, in the nearshore adjacent to the Skeena River, BC there is no difference in smolt distribution, measured by abundance, at varying distances to the river (Sharpe et al. 2019).

3.4.2 *Submerged Aquatic Vegetation (SAV)*

Eelgrass

Chinook salmon do not preferentially distribute into areas where eelgrass is present, indicating that they do not strongly prefer eelgrass habitat for its high quality nor do they consistently use it to avoid habitats that are low quality. In the Salish Sea there is some evidence for positive associations between eelgrass (*Zostera spp.*) presence and Chinook smolt catch (Sharpe et al. 2019; Bishop et al. 2024). However, in the Skeena River estuary, BC some eelgrass beds were used by Chinook smolts and not others, suggesting that multiple factors combined to determine

habitat quality (Sharpe et al. 2019). This study also found no association between Chinook salmon abundance and eelgrass percent cover (Sharpe et al. 2019). More often, studies have found Chinook salmon using eelgrass habitat but not in greater quantities than in other habitats (Korman et al. 1997; Dumbauld et al. 2015; Woo et al. 2019; Francis et al. 2022). In the Fraser River delta, Rubin et al. (2018) found a significant interaction between eelgrass and time and location, so the effects of eelgrass were not consistent. In this case, spatial differences were hypothesized to be a result of differences in eelgrass morphology between areas, or fragmentation of the meadow close to the Fraser River mouth (Rubin et al. 2018). The authors also suggested that future work could explore whether the variable results related to early versus late migrants that were using the habitat differentially. Chalifour et al. (2019) found similar abundances of Chinook salmon in eelgrass and sand flats, and there were fewer individuals in both habitat types than were present in marsh habitats.

Eelgrass presence was associated positively with enhanced realized function or capacity in only one study identified by this review. Semmens et al. (2008) found a positive association between eelgrass presence and predator avoidance; however, this positive effect was limited to the native eelgrass species (*Z. marina*) and not non-native species. Otherwise, the effect of eelgrass presence is neutral or negative for metrics including survival, prey abundance, and stomach fullness (Kennedy et al. 2018; Hughes et al. 2021). Kennedy et al. (2018) also found that increased eelgrass density had no relationship with the composition of epifaunal prey, but the abundance of epifaunal prey species was higher when eelgrass was denser. Investigations into the composition of preferred prey of Chinook salmon in neuston samples also found no differences between areas with and without eelgrass (Dumbauld et al. 2015; Woo et al. 2019). Eelgrass presence actually had a negative association with smolt growth relative to an unvegetated control in one study using hatchery fish (Hughes et al. 2021). In the Nisqually Reach, in south Puget Sound, there was a weak negative association with energy consumption in eelgrass relative to an intertidal delta mudflat (Davis et al. 2018). There was no evidence to link eelgrass with opportunity.

Kelps

Fewer studies have been conducted on juvenile salmon associations with kelps, and other macroalgae, than with eelgrass. With respect to distribution in the Skeena River, Sharpe et al. (2019) observed a weak negative association between Chinook smolt abundance and macroalgae percent cover. In contrast, Shaffer et al. (2020) and (2023) found that Chinook smolts were more likely to be present and to be foraging inside floating beds of the kelp *Nereocystis luetkeana* than outside of the kelp beds. The authors suggest that juvenile salmon are taking advantage of edge effects at the boundaries of the kelp beds (Shaffer et al. 2023). Hughes et al. (2021) tested several varieties of associations between Chinook smolts and presence of the brown alga *Sargassum sp.* They observed no association with *Sargassum* and capacity, measured by epifaunal prey abundance (Hughes et al. 2021). *Sargassum*'s contribution to opportunity was equivocal, because the authors detected no effect on smolt growth or stomach fullness, but did detect a negative association with survival (Hughes et al. 2021). As with eelgrass, there were no studies that described measures of opportunity as they related to kelp presence or density.

Mixed SAV

The habitat quality of areas with mixed SAV is not conclusively higher than areas without. In the Puget Sound nearshore, Brennan et al. (2004) examined smolt distribution and found no association between smolt abundance and attached presence of SAV or presence of drift vegetation. Hughes et al. (2021) also tested for smolt associations with a combination of eelgrass and *Sargassum*, finding no differences in measures of distribution or realized function, including abundance, survival, growth, or stomach fullness, relative to the unvegetated control. The authors did find a positive effect on epifaunal prey abundance, which might be related to the findings discussed earlier that higher SAV density can augment salmon prey. In one instance, there was evidence for reduced realized function in SAV (Zeug et al. 2021). Zeug et al. (2021) found that SAV presence reduced survival in the presence of a predator, because juvenile Chinook salmon in a mark-recapture enclosure system had no affinity for SAV and did not display behaviors that would suggest using it for predator avoidance.

3.4.3 *Human Development*

Shoreline armor

There have been several efforts to examine the association between shoreline armor and habitat quality for Chinook salmon, particularly in the Puget Sound nearshore. In regards to distribution, one study found no associations between armor presence and Chinook smolt abundance (Francis et al. 2022) while Chapter 1 of this dissertation found a non-significant positive effect (Bishop et al. 2024). In contrast, Heerhartz and Toft (2015) found a negative effect of armor on Chinook smolt presence. Toft et al. (2007) found no difference in the density of Chinook salmon captured in enclosure nets in subtidal habitats adjacent to beaches with sand, cobble, or riprap, although, fork lengths of Chinook salmon at the riprap site were larger than at other shorelines, possibly because this site was deeper. In the same study, snorkel surveys revealed higher densities of Chinook smolts at the site with riprap that extended lower in the tidal frame, relative to other shoreline types, which all had comparable densities (Toft et al. 2007).

With respect to capacity, the diversity of the prey field is lower at riprap and seawall sites. More species of terrestrial insects and arthropods are found at enhanced shorelines relative to shorelines with riprap or seawalls and epibenthic invertebrate species richness is reduced adjacent to shorelines with armor comprised of riprap (Toft et al. 2013). With respect to opportunity, Munsch et al. (2016) observed that abundance of Chinook salmon was lower when the shoreline was truncated. In this case, smaller individuals were less likely to be present when armor reduced the availability of shallow water habitat (Munsch et al. 2016).

Evidence for the effect of armor on realized function is inconclusive. Munsch et al. (2014) found no effect of armor presence on feeding behaviors. Similarly, Heerhartz and Toft (2015) found no effect of armor on movement rate, feeding rate, or straightness index, which is a measure of movement tortuosity (Heerhartz and Toft 2015). In contrast, Toft et al. (2013) observed a decrease in feeding frequency in waters adjacent to armor. These studies found that Chinook smolt diet composition is no different at armored shorelines from diet composition at natural shorelines (Toft et al. 2013; Munsch et al. 2015). While diet composition may reflect feeding at a variety of shoreline types prior to sampling, Toft et al. (2007) found high proportions of undigested, i.e., recently consumed, prey in Chinook smolt stomachs. In contrast to the studies

that found no differences, these stomachs were comprised of more marine benthic-epibenthic taxa when fish were captured at armored sites versus more terrestrial and planktonic-neritic taxa when fish were captured at unarmored sites (Toft et al. 2007).

Overwater structures

Of any nearshore habitat feature, overwater structures appear to have the most direct effect on juvenile Chinook salmon habitat quality via changes to their behaviors and their interactions with prey. Lambert et al. (2024) provides a useful review of multiple salmonid species responses to overwater structures of all sizes. For Chinook salmon specifically, Toft et al. (2007) observed their distribution during snorkel surveys around overwater structures, and while sample size was low, they recorded no instances of smolts under the structure, with most observations occurring away rather than near the structure. Unlike other salmonids observed in this study, the density of Chinook salmon was no different adjacent to overwater structures relative to other shoreline types examined (Toft et al. 2007). However, piers, particularly those that reduce light penetration, have been associated with lower densities of Chinook smolts (Munsch et al. 2014) and altered migration behavior, possibly because of disorientation (Williams and Thom 2001).

Overwater structures may reduce habitat capacity because of changes in the prey field around structures. Cordell et al. (2017) observed that prey abundance and taxonomic richness were reduced under and within 10 m of piers. Altered migration, reflecting reduced opportunity, has also been seen in Chinook smolts migrating around ferry terminals in Puget Sound (Southard et al. 2006; Ono et al. 2010). However, there is evidence that the magnetic field from bridges does not influence opportunity by changing movement behavior (Klimley et al. 2017).

With respect to realized function, Chinook smolts are less likely to exhibit feeding behaviors near piers that restrict light penetration (Munsch et al. 2014). However, it is unclear if changes in behavior and feeding are ultimately associated with reduced survival. When tested directly in the San Francisco nearshore, docks were not found to influence survival of Chinook smolts (Zeug et al. 2021). In contrast, there is evidence that another large structure, a floating bridge that spans the north end of the Hood Canal in Puget Sound, directly impacts juvenile Chinook salmon survival (Hood Canal Bridge Assessment Team 2020). The Hood Canal Bridge is one of the longest floating bridges in the world, and its floats extend 4.6m under the surface across 80% of the width of the Canal. Telemetry tagging studies of steelhead smolts departing the Hood Canal have found that of the fish that make it to the Bridge, 49% don't survive past it (Moore and Berejikian 2022). No tagging studies have been performed on Chinook smolts, but observational studies have confirmed that Chinook salmon are experiencing similarly high mortality at the bridge (Hood Canal Bridge Assessment Team 2020). The concrete floats disrupt their migration, which is thought to lead to higher mortality because they are susceptible to predation as they attempt to navigate around the structure (Hood Canal Bridge Assessment Team 2020).

3.5 DATA GAPS

Many common features of marine coasts were not represented well in the literature from this search. Specifically, there was little or no information on Chinook salmon interactions with rocky shorelines or understory kelps. Rocky shores may host a different prey community than beaches, and they alter the hydrodynamics of the shoreline, adding potential areas feeding and

current relief. Understory kelps are understudied in general, but as habitats they may share some qualities with eelgrass and could be functionally redundant for migrating smolts. There are also types of shoreline development that receive less attention than ferry terminals and shoreline armor, for example marinas (Clynick 2006; Bouchoucha et al. 2016). Marinas provide shallow embayments with current relief that not only could promote feeding opportunities but also provide structure for bird and marine mammal predators to leverage for targeting salmon prey.

In addition to exploring more types of habitats that Chinook salmon use, there are opportunities to expand the types of data being collected. On the outer coasts of Oregon and Washington, Chinook smolts are migrating through the surf zone, which is not represented in data collected using offshore trawl surveys. Future work could use different sampling gear to target fish in shallow water. Most of the studies in this review evaluated distribution to judge impacts of habitat features. More studies that directly measure behavioral and physiological responses to habitat features, addressing capacity, opportunity, and realized function, will help us understand how salmon growth and survival varies between nearshore habitats better than simple distribution alone.

3.6 CONCLUSIONS

The current body of evidence does not suggest a strong direct association between most physical features of the marine nearshore and habitat quality for juvenile Chinook salmon. Rather, this review suggests that high quality habitat for Chinook salmon along exposed marine coastlines is characterized by the availability of multiple water depths and abundant prey resources.

Increased survival to adulthood has been conclusively linked to rapid growth for juvenile Chinook salmon in the early marine phase (Duffy and Beauchamp 2011). Subsequent work has hypothesized bottom-up drivers of growth, and found a strong association between primary productivity and zooplankton biomass, as well as a strong positive association between zooplankton biomass and positive growth metrics in subyearling Chinook salmon (Wells et al. 2016; Greene et al. 2020). Therefore, nearshore functions that promote productivity and increased zooplankton biomass are likely to improve survival. In contrast, habitat features like piers that decrease the abundance of small prey taxa may decrease survival if the cumulative impact of these features is enough that smolts are unable to compensate by increased feeding in other areas (Cordell et al. 2017).

Prey quality often matters as much as prey quantity, but this may not be the case for small Chinook salmon outmigrants. Juvenile Chinook salmon are opportunistic feeders and their diets vary by area and season (Beamish et al. 2003). Smaller individuals will eat insects, crustaceans, mysids, and euphausiids, which have variable energy density, but they will compensate for low energy density prey by consuming greater quantities (Woo et al. 2019). A comparative analysis of growth rates in the Salish Sea found that growth rates of smaller individuals does not differ based on prey composition (Davis et al. 2020). Prey composition only becomes important when smolts grow large enough to begin eating fish because piscivorous smolts grow much faster than smolts that eat other prey (Chamberlin et al. 2017a; Gamble et al. 2018; Davis et al. 2020; Duguid et al. 2021). Moreover, recent work indicates that Pacific herring (*Clupea pallasii*) exert both competitive and facilitative effects on Chinook salmon, depending on herring abundance. At

low abundances, herring compete for zooplankton prey, whereas abundant larval herring serve as a high-energy prey resource that enhances salmon growth (Chamberlin et al. 2017b). These findings suggest that access to abundant fish prey in Salish Sea neritic environments may be more important for Chinook salmon early marine growth than variation in habitat quality among nearshore microhabitats.

Conservation actions may therefore be more effective if they target landscape scale functions that increase survivorship, like supporting the availability of fish prey, rather than preserving or restoring one type of habitat over another except at known bottlenecks (e.g., the Hood Canal Bridge). This concept has been introduced for estuaries and may be equally relevant to the marine nearshore (Simenstad and Cordell 2000). To support forage fish prey resources, the solution might ultimately be habitat restoration, but it is helpful to know what nearshore functions need priority. For example, restoration might focus on providing substrate for herring spawn rather than removing intertidal armor that is altering insect prey abundance. Removal of armor that truncates the intertidal zone and reduces the availability of different water depths could be prioritized over armor that is high in the intertidal zone and does not change the bottom slope enough to alter the size-mediated distribution of smolts. Future work could ask whether the spatial extent of suitable spawning habitat is a bottleneck for intertidal spawning forage fish species or determine if there is another factor limiting their abundance, like contaminants, predation, or primary productivity. Also, other salmonids, like chum, may have more direct habitat preferences that should be considered for conservation efforts targeted at those species.

Although I did not find conclusive evidence of strong effects in this review, we cannot rule out the possibility that there is a habitat feature, or mosaics of habitat features, strongly associated with outmigrating Chinook salmon growth and survival. More work to address data gaps could reveal a particularly influential feature. This review did not comprehensively address secondary pathways by which habitat influences juvenile Chinook salmon, even though juvenile salmonid fitness is a product of multiple interacting pathways rather than individual drivers (Sobocinski et al. 2018). For instance, shoreline armor decreases terrestrial energy subsidies which in turn influence primary productivity and plankton prey abundance (Heerhartz 2013). These pathways likely have a significant impact. However, this review has effectively demonstrated that there are few habitat features that conclusively and consistently impact distributions or demography for juvenile Chinook in nearshore environments. Resource managers can use this information to prioritize actions that support high quality habitat for Chinook salmon, either directly by addressing known bottlenecks or indirectly by prioritizing actions that support prey resources. This work also informs the selection of metrics for monitoring Chinook salmon response to habitat change, by identifying which distributional or demographic variables are most sensitive to changing habitat features.

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Chapter 4. IDENTIFYING POPULATION DYNAMICS AND CATCH SCENARIOS TO SUPPORT SUSTAINABLE DUNGENESS CRAB FISHERIES IN PUGET SOUND, WA

4.1 ABSTRACT

Recent declines in Dungeness crab catch in some areas of Puget Sound have raised concerns about the sustainability of the fishery under the current management system. Like many fisheries, this management system is intended to be robust to uncertainty yet increasing stressors and expanding sources of uncertainty compromise robustness, warranting an evaluation of management under novel and intensifying threats. We conducted semi-structured interviews with staff of governments involved in Dungeness crab fishery management in Puget Sound to gather information about their objectives for fishery management and views on potential stressors threatening the recreational and commercial sectors. We then adapted an existing modeling framework to incorporate the threats identified by co-managers and simulated the fishery response. We examined model sensitivity to threats under the current management framework, then evaluated whether this sensitivity changed under overfished or low productivity conditions. Finally, we used a Monte Carlo simulation to compare fishery performance under alternative management strategies. We found that the current management system performs well, even when stressed by threats identified by interview respondents. The fishery was more sensitive to parameters that affected the mortality rate of legal-size males than parameters that controlled mortality of sublegal males and females. These relationships did not interact with fishing intensity or productivity in a meaningful way. Ultimately, the status quo management strategy is likely to meet objectives identified in interviews, but revisiting the system dynamics over time will help to ensure that model outcomes reflect the perspectives and goals of the many people that participate in this fishery.

4.2 INTRODUCTION

The cumulative impacts of global change are driving ecosystems worldwide into novel states (Hobbs et al. 2009). For example, human development is decreasing global biodiversity and limiting the area available for historically abundant species to carry out critical stages in their life histories (Bender et al. 1998; Pereira et al. 2012; Cooke et al. 2024). Increasing temperatures are causing species distribution shifts or, for species that have limited ability to relocate, physiological stress leading to increased susceptibility to disease and direct reductions in growth, reproduction, and survival (Perry et al. 2005; VanDerWal et al. 2013; Cohen et al. 2020). Exploited populations are the most vulnerable to ecosystem change and fisheries are some of the most susceptible to human activities (Brander 2007). While fisheries management aims to support sustainable harvest despite variable environmental states that influence available catch, new ranges of environmental states may exceed what current management structures can

accommodate (Perry et al. 2010). Thus, management strategies for fisheries that were effective under historical conditions may not be robust to new or increased stressors (Holsman et al. 2019).

In the culturally and economically significant Dungeness crab *(Metacarcinus magister)* fishery in the Puget Sound region of the Salish Sea, recent declines in historically productive fishing areas and perceived threats due to climate change are raising concerns about the continued success of the current management structure (Buckner et al. 2022). The current system consists of commercial Tribal and non-Tribal components, which are collectively co-managed by state and Tribal governments using a series of input and output controls. Input controls include regulations on the allowable fishing seasons within distinct management areas in Puget Sound. Output controls consist largely of size- and sex- limits on retained catch. These controls are collectively referred to as the 3-S system (referring to sex, size, and season). Fisheries take is additionally limited by a total allowable catch (TAC) that is established annually for each management area, and the state and Tribal fisheries can each retain up to 50% of the TAC. This existing management structure has supported robust populations of crab for over 30 years, but there have been few formal assessments of whether the current system is robust to projected future stressors within Puget Sound. The most recent assessment found that this system may fail to meet its objectives under increasing low oxygen conditions (Froelich et al. 2017). Co-managers have also cited changes in molt timing and multiple years of low recruitment (possibly related to ocean acidification or increasing temperatures) as likely threats to the fishery (Buckner et al. 2022). Evaluating fishery performance over a range of possible future threats through simulation enables testing of how robust the current management system is to the ecological impacts of environmental change and anthropogenic stressors, given uncertainties in the magnitude of these impacts on the ecosystem.

Here, we asked: to what extent is the current 3-S management strategy able to achieve co-management objectives given the manifestation of stressors viewed as threats by the co-managers? We addressed this question by undertaking a user-informed modeling process where model development was informed by interviews with staff of governments involved in Dungeness crab fishery co-management in Puget Sound. Through this process, we evaluated the robustness of the current management strategy to violation of assumptions, novel threats, and threats that may be increasing in severity. Then, we evaluated performance of the current management strategy relative to alternative strategies identified in interviews. We hypothesized that the 3-S management strategy, while robust to historical variability in Dungeness crab population dynamics, would result in a fishery that becomes less resilient in the face of unprecedented stressors than it has been historically.

4.3 METHODS

4.3.1 *Workflow overview*

The full modelling process was informed by input from staff of governments involved in management of the Puget Sound Dungeness crab fishery. An important first step was therefore to conduct semi-structured interviews with fishery co-managers, policy representatives, and

biologists that contribute to fishery management decisions. Details about interview methods and results are available in Appendix A. To summarize, we asked interview respondents about their perspective on *goals* for conducting this fishery, *threats* facing the fishery, and potential *alternative management strategies* that may enhance the ability for the fishery to meet goals given the manifestation of identified threats (interview questions are available in Appendix B). There are no formalized quantitative measurable criteria for this fishery, so goals determined the model outputs. Threats determined components that we incorporated into a base model and management alternatives determined the strategies we compared to the status quo. Interviews also provided invaluable context for the base model content and assumptions.

We heard several goals from the interviews, and we selected four common responses to assess model performance in this exercise. Respondents expressed that the primary goal for the Dungeness crab fishery was access to the resource, and successfully meeting this goal meant that catch is maintained for future generations. Secondly, respondents reported that a successfully managed fishery would not have big swings in catch between years. Thirdly, respondents said that opportunity to fish was a priority goal, particularly being able to successfully catch crab in both the summer and winter. The last goal we selected was abundance of legal-size males at the end of the season. We selected this goal based on feedback from respondents that a successful fishery leaves some large males in the water to support a healthy ecosystem.

In response to our questions about potential threats to the fisheries, respondents identified threats related to illegal harvest, handling mortality, and ghost fishing. Although illegal fishing is thought to be minimal in the Treaty and state commercial fisheries, many respondents expressed concern over illegal harvest from state recreational fishers. Handling mortality occurs when crab that are caught, but not retained as legal catch, die from injuries that result from being returned to the water. Recently molted, or “soft”, crab are particularly vulnerable to injury (Kruse et al. 1994). Ghost fishing refers to entrapment of crab in lost fishing gear, and has potential to significantly impact the fishery if mortality from entrapment affects enough of the crab population (Maselko et al. 2013). Between 2011 and 2021, increased fishing effort led to an 8.2% increase in the number of crab pots lost in Puget Sound, sparking concerns about the impact of this threat and leading to increased derelict gear removal efforts (Antonelis et al. 2011; NRC 2021; Dufault et al. 2026). In 2025 alone, Washington state invested $288,784 in shellfish gear removal to reduce the impacts of ghost fishing (Dufault et al. 2026).

Respondents additionally questioned whether these threats would become more severe under low productivity. Low productivity represents a scenario where various climate related factors (higher temperature, higher ocean acidification, lower oxygen) result in lower recruitment. Several respondents hypothesized that increased stress on a population that has lower recruitment potential may have compounding effects such that additional mortalities related to the identified threats would have greater fishery impacts.

Respondents identified three management alternatives to the status quo: no TAC, high catchability, and limiting seasons to avoid handling mortality. These alternatives do not necessarily represent viable options for the Puget Sound Dungeness crab fishery, but rather they represent alternatives that respondents were curious to explore. Respondents were curious whether the fishery could perform worse in a no TAC scenario because all the large males could

be removed from the system, which may limit the reproductive capacity of the population. Respondents also hypothesized that this alternative would result in higher handling mortality for sublegal males and females, because fishing would continue after most legal males were already caught. Similarly, respondents were curious about a high catchability alternative, where fishing is allowed to remove all of the legal-size males from the population every year. We consider this as a management alternative because it could represent a case where regulations allowed the efficiency of fishing gear to be maximized. Finally, respondents were curious about whether limiting seasons by closing the fishery when legal male catch rates are low would reduce handling mortality that might otherwise cause population level impacts.

The following sections detail how we integrated interview responses into the modeling process.

4.3.2 *Integration of goals*

We translated each of the four stated goals into quantitative model outputs to evaluate model performance. To evaluate catch, we averaged total legal catch. To evaluate interannual variation in catch, we evaluated the inverse catch coefficient of variation (1 / CV). To evaluate opportunity throughout the year, we averaged the catch rate (CPUE) of legal-size male crab in December. Finally, to assess population health, we averaged the abundance of legal-size males at the end of each model year, before recruitment occurs. Values for each metric were calculated over 100 model years.

4.3.3 *Base model overview*

We constructed the base population model by building on an existing deterministic age- and sex-structured Dungeness crab population model developed by Froehlich et al. (2017). This model was designed to explore how robust the fishery management system is to changes in catchability related to oxygen limitation, because Dungeness crab exhibit shoaling behavior when subjected to low oxygen conditions (Froehlich et al. 2014, 2017). It is not estimated statistically against data like a stock assessment, but it is parameterized based on empirical information to qualitatively explore which threats and management strategies affect performance metrics most.

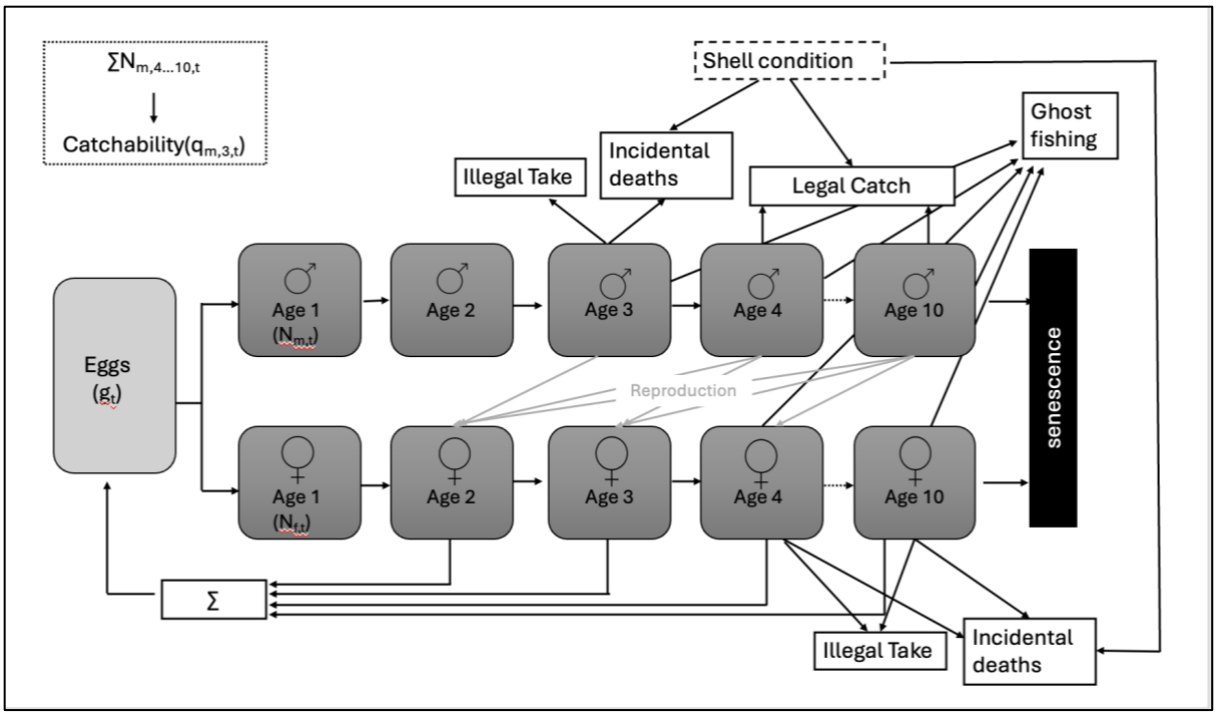

Figure 1. Conceptual framework of the population model, updated from Froehlich et al. (2017).

In the model, crab population abundance and catch were updated in monthly time steps, where the model year began in June and ended the following May. Males and females in the population were comprised of 10 discrete age classes in monthly time steps, with the following recursive equations:

$$N_{a,s,t} = \begin{cases} R_t(N_{t-12}), & \text{if t} \equiv 1 \text{ mod}(12) \text{ and a} = 1 \\ N_{a-1,s,t-1} \exp(-Z_{a-1,s}) & \text{otherwise} \end{cases}$$

$$Z_{a,s} = M_{s,a} + F_{s,r,a} + F_{s,i,a} + F_{s,g,a}$$

Where $N_{s,a,t}$ represents the sex and age (a) specific abundance of male ($s = m$) and female ($s = f$) crab in month t, and $\mathbf{N}_t$ is a vector of crab abundance in year t by age and sex, and $R(N_{t-12})$ is a function describing age-1 recruits based on the abundance and fecundity of adult crabs. Total mortality, $Z_{a,s}$, is the sum of the instantaneous rates $M_{s,a}$, $F_{s,r,a}$, $F_{s,i,a}$, and $F_{s,g,a}$, which respectively represent monthly natural mortality, retained fishing mortality, incidental fishing mortality, and mortality from derelict fishing gear. These rates will be described in later sections.

Recruitment occured annually on the first day of the model year and depended on egg production at the same time the year prior. It is calculated using a Beverton-Holt function (Beverton and Holt 1957) based on age-specific fecundity and sex ratio:
For $t \equiv 1$ mod(12) :

$$R_t = \frac{g_{t-12}}{a + b g_{t-12}} \exp(\varepsilon_t)$$

$$\varepsilon_t = \rho\varepsilon_{t-12} + \sqrt{1-\rho^2}\,\nu_t$$

$$\nu_t \sim \text{Normal}(-\frac{\sigma^2}{2}, \sigma^2)$$

Where R_t is total recruitment at time t, g_t is fertilized egg production at time t, a and b are Beverton-Holt parameters, and ε_t is a lognormal recruitment deviation with standard deviation ($\sigma = 0.7$) and autocorrelation ($\rho = 0.4$) between years. Total recruitment is then divided equally into male and female recruits. The Beverton-Holt parameters were calculated from the specified equilibrium unfished recruitment (R_0) and steepness (h) as follows:

$$b = \frac{5h-1}{4hR_0}, \qquad a = \frac{1-h}{4h}$$

Following Froehlich et al. (2017), we calculated the fertilized egg production rate based on age-specific fecundity and abundance of female crab, with corrections for the ratio of females to larger males, via a parameter termed the effective recruitment ratio ($\Phi_{a,t}$). This is based on local knowledge that females need larger males to effectively embrace them during molting. This mechanism uses age as a proxy for size, so females could only mate with males that are at least one year older:

$$g_t = \sum_{i=a}^{n} N_{f,a,t}\mathcal{F}_a\partial_a\Phi_{a,t}$$

$$\Phi_{a,t} = \frac{\xi_{a,t}}{\eta + \xi_{a,t}}$$

$$\xi_{a,t} = \min(1, \frac{\sum_{j=a+1}^{n} N_{m,j,t}}{N_{f,a,t}})$$

Where $N_{f,a,t}$ is the number of females at age a at time t, $\mathcal{F}_a$ is the age-specific fecundity of females, and ∂_a is the proportion of females at age a that are mature. The effective reproduction ratio ($\Phi_{a,t}$) is a function of $\xi_{a,t}$, the ratio of age $a + 1$ males to age a females at time t, and a half saturation constant ($\eta = 0.1$).

Monthly catch for each age- and sex-class was calculated with the Baranov catch equation, using age as a proxy for size to set vulnerability to capture, retention and mortality in fishing operations. This requires calculation of the following fishing mortality rates, which were based on shell condition, age- and sex-specific retention probability, and capture probability:

$$F_{s,r,a} = u_{s,a}\Omega_{s,a}$$

$$F_{s,i,a} = u_{s,a}(1-\Omega_{s,a})\delta_a$$

where $u_{s,a}$ is the probability that a crab of sex *s* and age *a* will be captured, $\Omega_{s,a}$ is the sex- and age- specific probability that an individual crab will be retained, and δ_a is the probability that a crab that is captured but not retained will experience incidental death due to injury from handling (described in section 2.4.2). Capture probability ($u_{s,a}$) was calculated as:

$$u_{s,a} = q_{s,a}E_t$$

where $q_{s,a}$ is the sex- and age- specific catchability of crab and E_t is the total fishing effort in month *t*. We sought to assess the model at fishing levels near F_{msy}, yet the effort and catchability levels that produce F_{msy} are not well known. We therefore defined plausible values of *E* and *q* by first calculating equilibrium catch and catch per unit effort (CPUE) for a range of values of total effort within the range described by Froehlich et al. (2017) for the Hood Canal basin of Puget Sound, using nominal values for all other parameters (Table 1). We then adjusted *q* so that (1) equilibrium CPUE was reasonable at all effort levels and (2) F_{msy} was produced within the effort range. The value $q = 2.5 \times 10^{-6}$ satisfied each of these conditions, so this value was used for model exploration. We defined reasonable CPUE as less than 32 crab per set, which is about half of the maximum capacity of a common style of commercial pot (per. comm. with fishery co-managers).

The base model includes several assumptions. Because we used a Beverton-Holt model, we assumed that recruitment is spawner-dependent, and that this is a closed system with no subsidies of larvae from any outside population. Recently molted, or soft, crab have greater susceptibility to injury and disease (Morado et al. 1999), but we used a constant natural mortality rate that we assumed represented average mortality for a given sex and age, regardless of molt condition. Finally, we assumed that catch rates were similar between commercial and recreational gear.

4.3.4 *Integration of threats*

Illegal harvest

Total catch was divided into crab that are retained legally and illegally. Retention probability depended on catch rate and shell hardness:

$$\Omega_{a,s,t} = \begin{cases} p_{illegal} \exp\left(-c\dfrac{C_t}{E_t}\right) & \text{if } s=m \text{ and } a<4 \\ H & \text{if } s=m \text{ and } a \geq 4 \\ p_{illegal}\gamma_f \exp\left(-c\dfrac{C_t}{E_t}\right) & \text{if } s=f \end{cases}$$

where $p_{illegal}$ is the maximum probability of illegal retention at low catch rate, *c* governs how the illegal retention declines with increasing legal retained catch rate, *H* is the proportion of the population with hard shells, and γ_f sets the maximum illegal take of females relative to that of sublegal males. In Puget Sound, the Dungeness crab fishery does not open each spring until >80% of legal-size male crab captured in test fisheries within a given management area have hard shells. In this model, we did not limit fishery openings based on shell hardness because we

were interested in exploring the effect of continuing to fish on a population that is vulnerable to handling injury.

We made several assumptions regarding illegal catch to limit complexity in the model. It is illegal to retain soft crab in Puget Sound, and this formulation assumes that all legal sized males with hard shells are retained. Soft crab are considered undesirable relative to hard crab due to their poor meat quality and because they are more likely to experience handling injury during shipment to live markets. We therefore assumed that there is no illegal take of legal-sized crab with soft shells in this model. Due to relatively robust enforcement in areas of Puget Sound where fishing occurs, we also assumed that there is no catch when the fishing season is closed. Finally, we assumed that recreational harvest was not limited by daily catch limits for license holders.

Handling mortality

We added two components to the model to describe the probability of incidental death due to fishing (δ_a). The first mechanism allows the probability of incidental death to decrease with increased shell hardness:

$$\delta_a = \delta_{max,a} + H\left(\delta_{min,a} - \delta_{max,a}\right)$$

Where δ_{min} and δ_{max} represents the minimum and maximum probability of incidental death, respectively. The second component augments the catchability of age 3 males as the abundance of age 4+ males decreases. This is based on respondent observations that smaller males will avoid pots that are full of larger males:

$$q_{min} = q * \gamma_m$$

$$q_{3,t} = q_{min} + (q - q_{min})e^{-\kappa \Sigma N_{m,4\ldots10,t}}$$

q_{min} represents the minimum catchability of age 3 males. This value is determined by γ_m, which represents the magnitude of change to q caused by the abundance of age 4+ males. The relationship between age 3 male catchability and age 4+ male abundance is log-linear with slope κ. When legal-size males are abundant, the catchability of age 3 males ($q_{3,t}$) is equal to q_{min}, and then as the abundance of large males decreases, catchability increases towards q. For the remainder of individuals, we accounted for size and sex specific differences in catchability. For males younger than age 3, and females younger than age 4, we assigned a catchability value of zero. For males older than age 3 and females age 4 and older, we assigned constant catchability (Table 1).

When incorporating this threat, we used age as a proxy for size and assumed smaller individuals could leave pots via escape rings. We also assumed the same incidental mortality rate for males as females.

Ghost fishing

Sex- and age- and gear-specific mortality from derelict gear was represented in the model as:

$$F_{s,g,a} = u_{s,a}G$$

where $u_{s,a}$ represents the vulnerability to capture based on the total number of derelict pots and age- and sex-specific catchability. *G* represents the estimated probability of mortality for crab that enter derelict pots. Derelict pots accumulate in the system based on fishing effort and gear decay:

$$D_{t+1} = D_t e^{-d-\psi\tau} + E_{t,f}\lambda_f$$

where D_t represents the total number of derelict pots present in the system in month t and *d* represents the decay of derelict pots over time. The parameter τ represents the proportion of pots removed per year relative to the current gear removal effort (ψ). λ is the rate of pot loss, and E_t and λ are also specific to the fishery type (*f*). NRC (2021) and Antonelis et al. (2011) both conservatively estimate that pots have a 2.2 year life span, though pots may continue to fish after 7 years. Based on this information, we calculated *d* as *d* = 1/(2.2*12) = 0.038. Starting in 2025, the WA state legislature requires that 11% of recreational crab endorsement fees be spent on derelict gear removal programs. WDFW does gear sweeps on days the recreational fishery is closed and contracts with the Northwest Straits Foundation to locate and remove derelict gear using remotely operated vehicles and divers (Dufault et al. 2026). ψ is currently set at 0.14 because these gear removal efforts resulted in recovery of 1,203 pots last year while the number of pots lost annually across all fisheries is estimated around 10,000 (Dufault et al., 2026; NRC 2021). NRC estimates that 4.7% of commercial pots are lost in Puget Sound (NRC 2021). There is no data on recreational effort to estimate an equivalent recreational pot loss rates. However, derelict gear recovery efforts show that more than 86% of recovered pots come from the recreational fishery (Dufault et al., 2026; NRC 2021). For simplicity, we assumed that catchability was the same for both gear types.

Table 1. Fixed model parameters and parameters added to explore via simulations using a uniform distribution within the range of values listed.

Parameter	Value	Nominal value	Source
M_a = natural mortality at age a	Age 1-2 = 0.067 month^{-1} Age ≥ 3 = 0.025 month^{-1}	-	Froehlich et al. (2017)
$\mathcal{F}_a$ = fecundity at age a	Age 1 = 0 Age 2 = 1 million Age 3-5 = 2 million	-	Froehlich et al. (2017)
∂_a = proportion of females at age a that are mature	Age 1 = 0 Age 2 = 0.2 Age ≥ 3 = 1	-	Froehlich et al. (2017)
h = steepness	0.65	-	Moderate steepness value from Froehlich et al. (2017)
R_0 = unfished number of age 1 recruits	7,000,000 crab	-	Froehlich et al. (2017)

$p_{illegal}$ = probability of retention at age a, sex s.	Males Age 1-2 = 0 Age 3 = 0 - 1 Age ≥ 4 = 1 Females Age 1-3 = 0 Age ≥ 4 = 0 - 1	0.2	Range informed by Froehlich et al. (2017)
γ_f = probability of capture retention modifier for females	0 -1	0.8	
$\delta_{max,a}$ = maximum probability of incidental death at age a	Age 1-2 = 0 Age 3-10 = 0 - 1	0.2	
$\delta_{min,a}$ = minimum probability of incidental death at age a	Age 1-2 = 0 Age 3-10 = 0.05	-	Aulthouse et al. (2023)
q = catchability	2.5×10^{-6}	-	
γ_m = catchability modifier for smaller males	0 - 1	0.8	
κ = slope of the relationship between the abundance of larger males and the catchability of age 3 males	1.0×10^{-11} - 1.0×10^{-10}	5.0×10^{-10}	
E_{rec} = state recreational effort	F_{msy} = 12,000 pots per month $1.5F_{msy}$ = 26,000 pots per month	-	Informed by Froehlich et al. (2017)
E_{com} = commercial effort (combined state and Tribal)	16,000 pots per month	-	Informed by Froehlich et al. (2017)
H = proportion of the population with hard shell condition	0.1 - 1	0.8	
λ_{rec} = proportion of pots lost in the recreational fishery	0 – 0.5	0.3	Range informed by NRC (2021)
λ_{com} = proportion of pots lost in the commercial fishery	0 – 0.1	0.05	Range informed by NRC (2021)
G = probability that crab that die in derelict pots	0.3 – 0.8	0.5	Range informed by Antonelis et al. 2011
d = rate of derelict pot decay	0.038 per month	-	NRC (2021)
ψ = rate of current derelict gear removal	0.14 per month	-	Dufault et al. (2026), NRC (2021)
τ = fraction of derelict gear removed relative to current removal efforts	0 - 2	1	

$CPUE_{min}$ = minimum CPUE of legal size males to close the fishery under the Limit Handle Mort management scenario	0.1 - 1	-	

4.3.5 *Management inputs*

In addition to the sex- and size- specific harvest controls detailed above, we included other control rules to model status quo fishery management. Fishing occurred in June and September – March for the commercial sector, which encompassed both the state and Tribal fisheries. We modeled the state and Tribal commercial fisheries together because interview participants indicated that they operate very similarly and therefore are likely to have similar impacts. For the recreational sector, summer fishing occurred in July and August and winter fishing occurred October – December. We calculated the total allowable catch (TAC) using a three-year running average of legal catch. At the start of each month, cumulative catch for the year was compared to the TAC, and if the TAC was met or exceeded commercial fishing stopped for the year. Cumulative recreational catch at the end of the summer fishery was assessed relative to its allocated 50% share of the TAC. If cumulative catch from the recreational sector was less than 50% of the total TAC, the winter recreational fishery opened. If catch was greater than 50% of the TAC and the abundance of legal-size males was high, indicated by high legal male catch per unit effort, then the TAC increased by 5%. If the summer recreational catch was less than the updated TAC, the winter recreational fishery opened, otherwise the recreational fishery remained closed for the remainder of the year. We did not include a subsistence or ceremonial sector in the model due to feedback that catch from this sector is so low that its impacts are likely negligible.

4.3.6 *Model behavior*

We first explored the sensitivity of the population model to key parameters by exploring how the model performed when individual parameters related to the three threats were perturbed over a range of values (n = 20) while all other parameters were held at nominal values (Table 1), taking the average over 50 replicates for each set of parameter values. This analysis used status quo management measures, as described above. We evaluated model performance metrics over the range of parameter values at baseline effort (28,000 pot sets per month) and high effort (42,000 pot sets per month) representing F_{msy} and a 50% effort increase over F_{msy} (overfished) scenarios. We then compared the relationship between parameter values at F_{msy} and model performance with low productivity. We adjusted productivity by multiplying R_0 by a factor of 0.5 to simulate scenarios with lower productivity.

We also explored two other model parameters, which were related to density dependent catchability, to determine the potential importance of lower sublegal male catchability when legal size males are abundant. These parameters controlled the amount that the catchability of sublegal males was reduced relative to the catchability of legal-size males (γ_m), and the slope of

the relationship between the abundance of larger males and the catchability of age 3 males (κ). The model was not sensitive to either parameter, nor did sensitivity change under overfished and low productivity conditions (Appendix C).

4.3.7 *Integration of management alternatives*

Next, we aimed to explore the performance of management alternatives: status quo, no TAC, high catchability, and limiting seasons to avoid handling mortality. The status quo scenario represents current management practices in Puget Sound. Under the no TAC scenario, catch is not limited and therefore recreational and commercial fisheries open based solely on season regardless of annual catch. For the high catchability scenario, where all legal size males (LSMs) are caught, we set the catchability of Age 4+ males = 1. Finally, under the limit handle mortality scenario, there is an additional parameter $CPUE_{min}$ that determines the minimum encounter rate of legal-size males for the fishery to remain open. Once the CPUE of legal-size males drops below $CPUE_{min}$, the fisheries close for the year.

We could have repeated a similar sensitivity for every management alternative, but that would have resulted in an unreasonably large number of comparisons. One way to achieve many comparisons in one step is via a Monte Carlo simulation, where parameters all change simultaneously over enough replicates to evaluate general trends. We conducted a Monte Carlo simulation for 100 parameter combinations and 50 replicates per combination at F_{msy} effort. This allowed us to examine a range of outcomes over both stochastic recruitment and parameter uncertainty. We sampled each parameter from a uniform distribution with specified min and max values (Table 1). We evaluated the distribution of model performance metrics among these alternatives and the proportion of replicates where model performance metrics exceeded a threshold, set as the 50th percentile of values across all alternatives. We also repeated the Monte Carlo simulation under low productivity conditions. All analyses were conducted in R version 4.5.3.

4.4 RESULTS

4.4.1 *Model behavior: illegal harvest*

We explored the threat of illegal harvest by perturbing the illegal retention probability ($p_{illegal}$) and the modifier for females (γ_f). At F_{msy}, increased retention of sublegal male and female crab reduced legal size males available to the fishery. This is apparent in the negative linear relationship between the probability of retention and legal catch, the CPUE of legal size males in December, and the abundance of legal size males at the end of the fishing season (Figure 3a). The relationship between illegal retention of crab and model performance appears to be driven by the abundance of sublegal males, because the model is not sensitive to reductions in the probability of retaining females relative to sublegal males (Figure 3b). Under conditions with higher fishing effort and lower productivity, as expected, the fishery performed worse (Figures 4 & 5). However, the direction and scale of the relationships between either parameter related to

illegal take and model performance did not change under these scenarios relative to fishing at F_{msy} and baseline productivity (Figures 4 & 5).

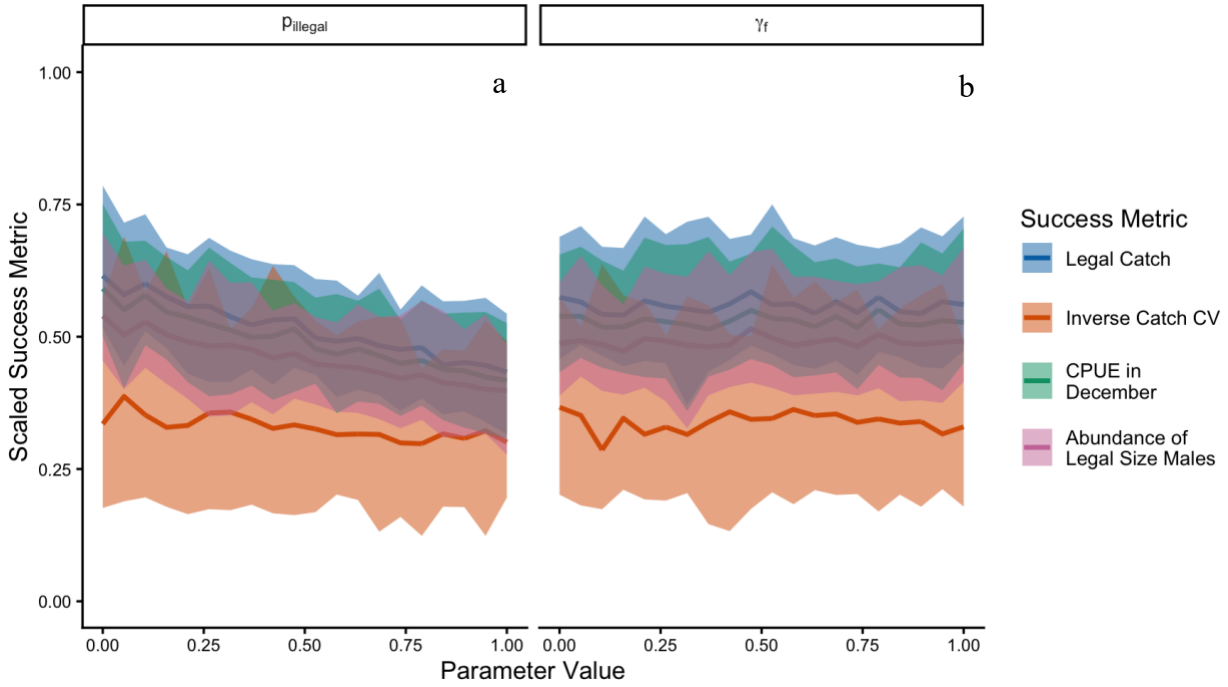

Figure 3. Performance of the model assessed with four success metrics when individual parameters related to illegal take are perturbed and all other parameters are set at nominal values and effort = F_{MSY}. Illegal take parameters include the probability of retention ($p_{illegal}$) and probability of capture retention modifier for females (γ_f). Success metrics are average values over 100 model years, with 50 replicates per parameter value. The values for each success metric are scaled relative to the maximum value observed for each metric. The dark line shows the median value across all replicates and the shaded area represents the 95% prediction interval. Parameter descriptions are given in Table 1.

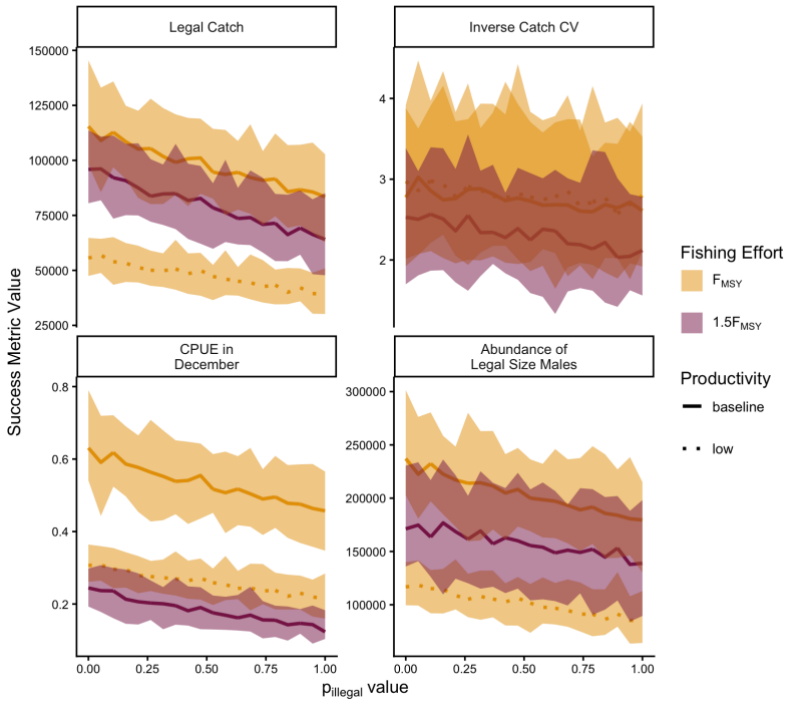

Figure 4. Performance metrics vs. illegal retention probability ($p_{illegal}$), for different fishing effort levels and productivity levels. Success metrics are average values over 100 model years, with 50 replicates per parameter value. The shaded area represents the 95% prediction interval.

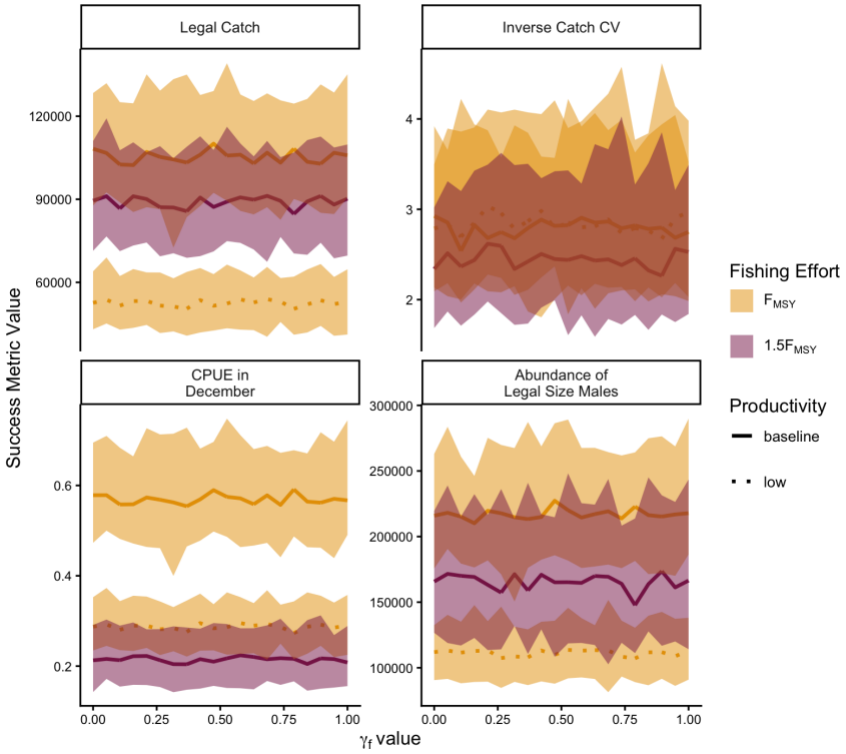

Figure 5. Performance of the model vs the probability of capture retention modifier for females (γ_Ω) for different fishing and productivity levels. Success metrics are average values over 100

model years, with 50 replicates per parameter value. The shaded area represents the 95% prediction interval.

4.4.2 *Model behavior: handling mortality*

To explore potential impacts of threats related to incidental deaths resulting from handling injury, we perturbed the proportion of the population with hard shells (H) and the maximum incidental mortality rate ($\delta_{\max}$). The model was very sensitive to hardness (Figure 6a), which affects the fishery by controlling the proportion of legal size males that can legally be retained and the incidental mortality for discarded catch (δ_a). Catch and CPUE of legal-size males in December increase linearly with hardness, while the abundance of legal-size males decreases, because a higher number of crab can be legally retained when more crab are hard. In contrast, the model was not sensitive to the maximum incidental mortality rate ($\delta_{\max}$, Figure 6b). Therefore, the predominant effect of hardness on performance metrics is related to the ability of the fishery to retain crab, rather than through its effect on incidental mortality.

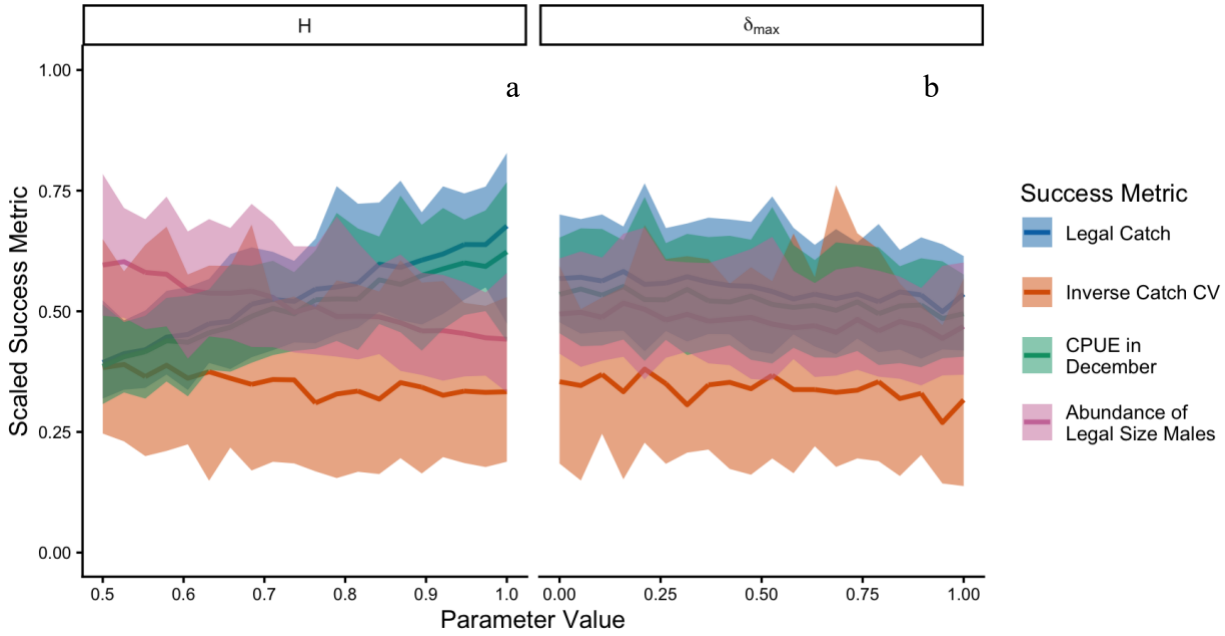

Figure 6. Performance of the model when individual parameters related to incidental mortality are perturbed and all other parameters are set at nominal values and effort = F_{MSY}. These parameters included population with hard shell condition (H) and the incidental mortality rate ($\delta_{\max}$). Success metrics are average values over 100 model years, with 50 replicates per parameter value. The values for each success metric are scaled relative to the maximum value observed for each metric. The dark line shows the median value across all replicates and the shaded area represents the 95% prediction interval. Parameter descriptions are given in Table 1.

Overfishing suppressed the effect of hardness on CPUE in December but did not impact other measures of model success (Figure 7). This is because high fishing rates lead to earlier fishery closures, so there is less opportunity to catch crab even when remaining crab in the system have hard shells. Similarly, the model is slightly less sensitive to hardness when productivity is low;

fewer fishery openers in the fall and winter buffer the effects of fishing on the overall crab population. The model's sensitivity to incidental handling did not increase in either the increased fishing effort or reduced productivity scenarios (Figure 8).

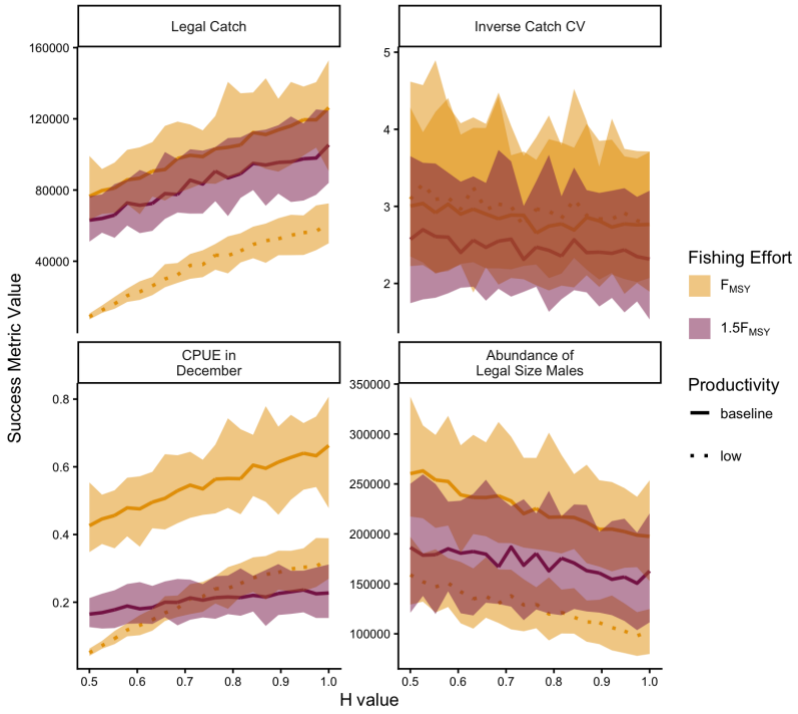

Figure 7. Performance of the model assessed vs the proportion of crab that are hard (*H*) for different fishing and productivity levels. Success metrics are average values over 100 model years, with 50 replicates per parameter value. The shaded area represents the 95% prediction interval.

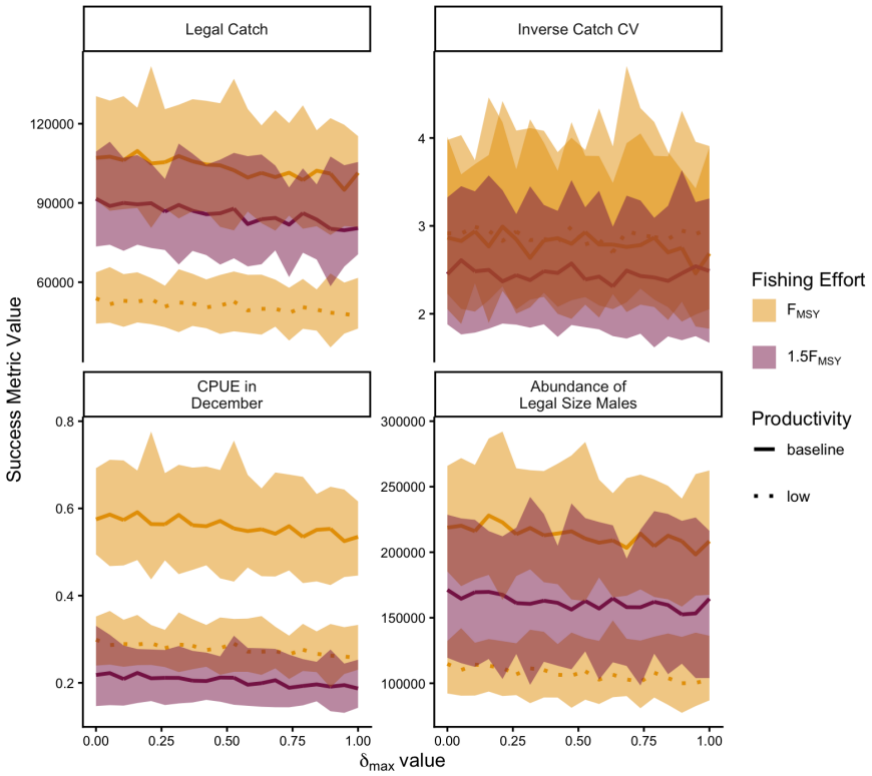

Figure 8. Performance of the model assessed vs the maximum incidental mortality rate ($\delta_{\max}$) for different fishing and productivity levels. Success metrics are average values over 100 model years, with 50 replicates per parameter value. The shaded area represents the 95% prediction interval.

4.4.3 *Model behavior: ghost fishing*

We explored the effects of ghost fishing by perturbing parameters that accounted for accumulation of derelict gear and crab mortality in that gear. Accumulation of derelict gear was more influential in the model than crab mortality in the derelict gear. Variability in catch was not sensitive to parameters related to ghost fishing, but other measures of model performance (legal catch, CPUE in December, and abundance of legal size males) had strong relationships with these parameters (Figure 9).

High gear loss rates in the recreational fishery (λ_{rec}) resulted in substantial linear decreases in legal catch, CPUE in December, and in the abundance of legal-size males (Figure 9a). The impact of derelict commercial gear loss (λ_{com}) was less pronounced (Figure 9b), likely because we explored a smaller range of loss rates for this parameter, based on information available to us about real world gear loss rates (Figure 9b). In this model the loss of derelict gear from the commercial fishery could double from current estimates (4.6%) with negligible impact to model performance. Rate of mortality in derelict gear had a sizable effect on modeled performance measures (Figure 9c). Removal of derelict gear offset these effects, as evidenced by fishery performance increases as the removal rate of derelict gear (τ) increases, until reaching an asymptote around 1.5 times the removal rate of gear relative to the present (Figure 9d).

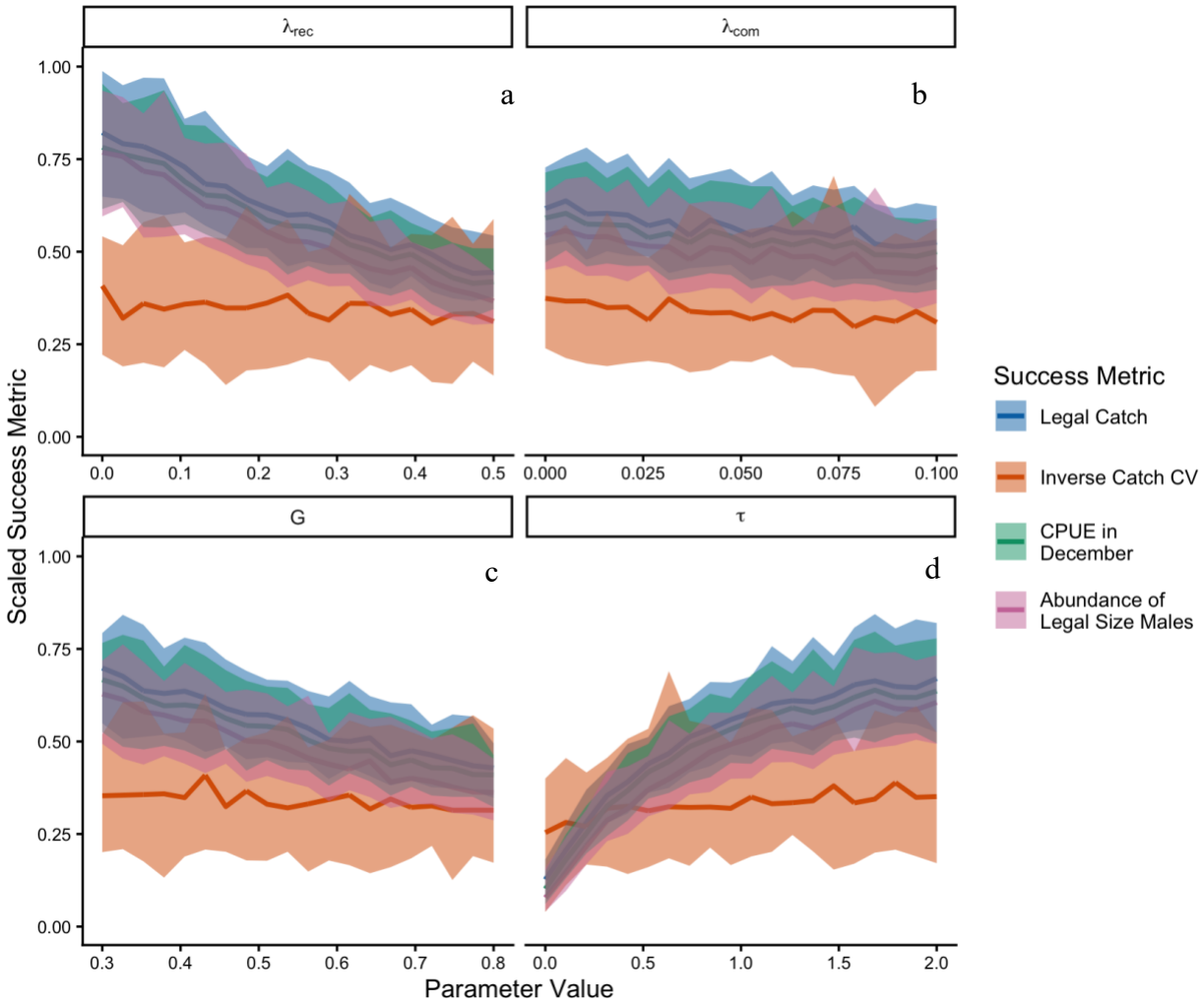

Figure 9. Performance of the model when individual parameters related to ghost fishing are perturbed and all other parameters are set at nominal values and effort = F_{MSY}. Ghost fishing parameters include the rate of pot loss in the recreational (λ_{rec}) and commercial (λ_{com}) fisheries, the probability that crab die in derelict pots (G), and the rate of derelict gear removal relative to present (τ). Success metrics are average values over 100 model years, with 50 replicates per parameter value. The values for each success metric are scaled relative to the maximum value observed for each metric. The dark line shows the median value across all replicates and the shaded area represents the 95% prediction interval. Parameter descriptions are given in Table 1.

Increased fishing pressure with the same range of pot loss rates resulted in a higher absolute number of pots lost annually, leading to greater fishery impacts. In overfished conditions, the model was therefore more sensitive to the rate of pot loss in the recreational fishery (Figure 10). This was particularly evident in the legal catch and CPUE in December performance metrics, where catch and CPUE were high at low pot loss values, but decreased as loss values increased. In contrast, the model was slightly less sensitive to the rate of recreational pot loss when productivity was low (Figure 10). This is because under the status quo management scenario, low catch over time reduces the TAC and fishing closes for the year once TAC has been met.

Fishery closures earlier in the year reduce the potential for pot loss, while the existing number of derelict pots in the system is continually reduced via removal programs. For the commercial fishery, changes in the rate of pot loss did not affect model performance differently under overfished or low productivity conditions (Figure 11).

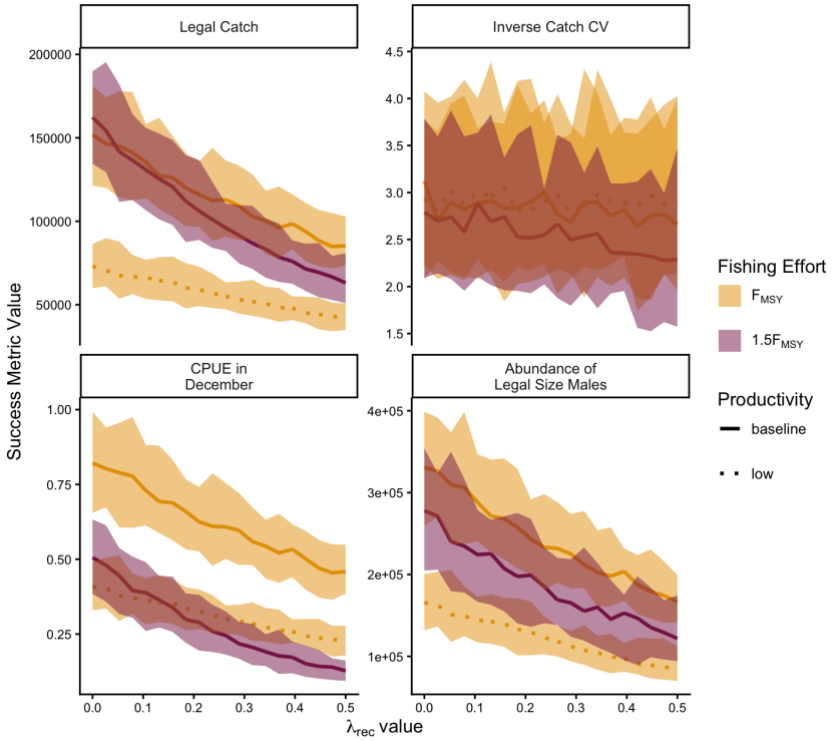

Figure 10. Performance of the model vs the rate of pot loss in the recreational fishery (λ_{rec}) for different fishing and productivity levels. Success metrics are average values over 100 model years, with 50 replicates per parameter value. The shaded area represents the 95% prediction interval.

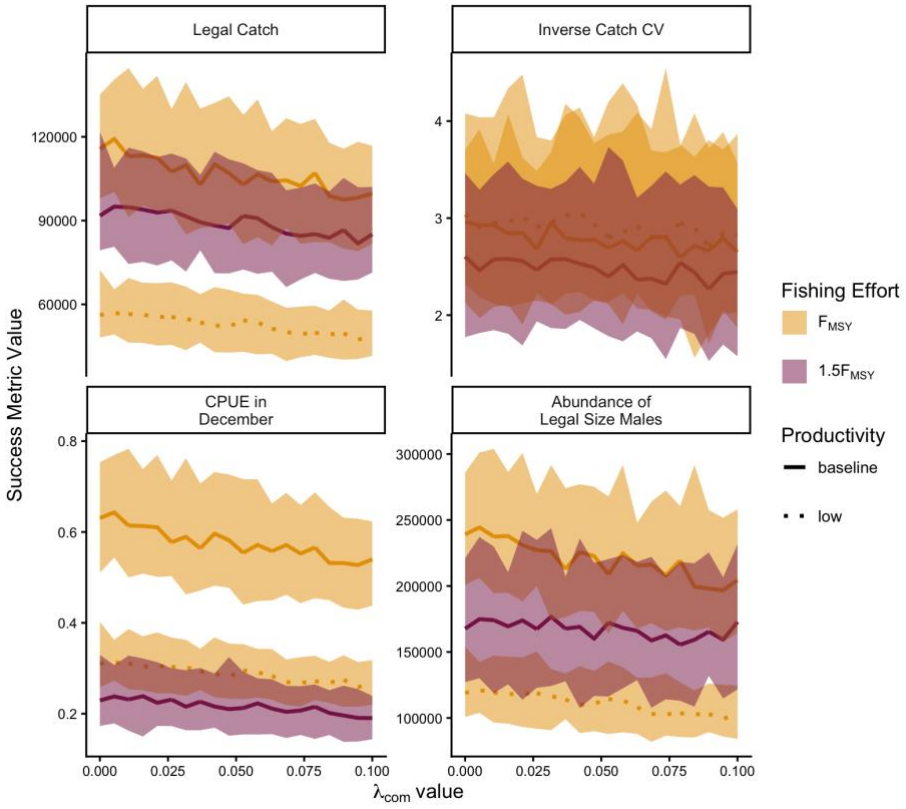

Figure 11. Performance of the model assessed vs the rate of pot loss in the commercial fishery (λ_{com}) for different fishing and productivity levels. Success metrics are average values over 100 model years, with 50 replicates per parameter value. The shaded area represents the 95% prediction interval.

The mortality rate of crab in derelict gear had a strong influence on success metrics. However, model sensitivity to the mortality rate of crab in derelict gear was similar across effort and productivity conditions (Figure 12). The effect of high mortality was buffered in low productivity conditions by fishery closures that limit the number of pots lost, as discussed above. The sensitivity of the model to derelict gear removal was slightly suppressed under low productivity conditions (Figure 13). This is also likely because fishing occurs during fewer months of the year when less crab are available to catch, resulting in less pot loss and therefore a proportionally smaller benefit from cleaning up lost pots.

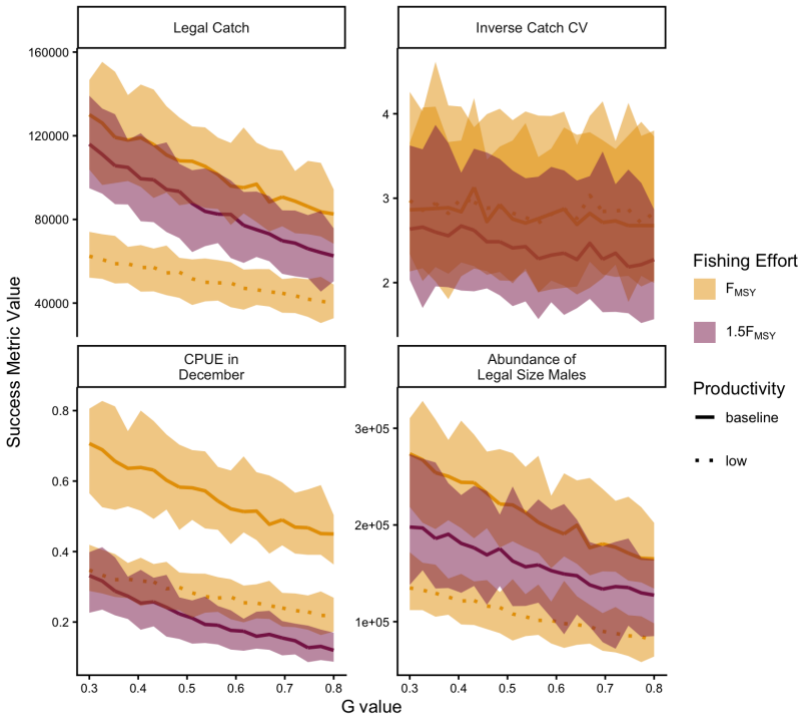

Figure 12. Performance of the model assessed vs the proportion of crab that die in derelict gear (*G*) for different fishing and productivity levels. Success metrics are average values over 100 model years, with 50 replicates per parameter value. The shaded area represents the 95% prediction interval.

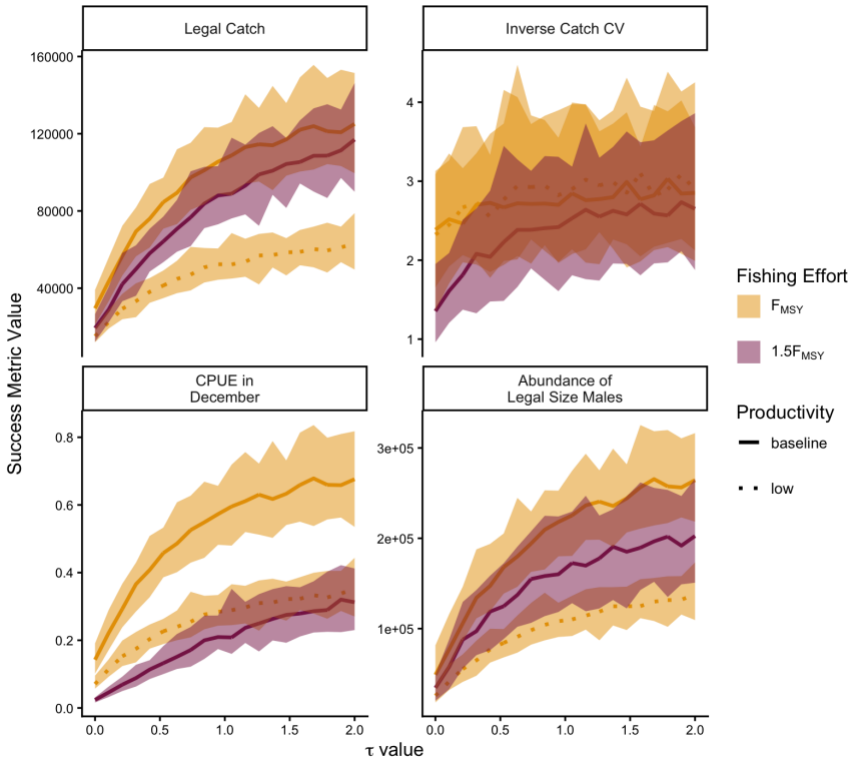

Figure 13. Performance of the model assessed vs the rate of derelict gear removal relative to present (τ) for different fishing and productivity levels. Success metrics are average values over 100 model years, with 50 replicates per parameter value. The shaded area represents the 95% prediction interval.

4.4.4 *Management alternative performance*

No single management strategy outperformed others for all outcome measures, and no single strategy was outperformed by another across all outcome measures. Instead, different management scenarios reflect potential tradeoffs among objectives. The status quo management strategy resulted in the lowest variability in catch, with a moderate performance among other metrics (Figure 14). In the scenario with no TAC, the proportion of times that the catch and CPUE in December was high was similar to the status quo, but performance was reduced for other metrics. In contrast, the management scenario where the fishery is allowed to catch all legal sized males results in more potential opportunities for high catch has poor performance across all other metrics (Figure 14, Appendix D). Conversely, limiting handling mortality results in the highest abundance of legal-size males at the end of the fishing season but the tradeoff is a loss of opportunity to fish, so legal catch and CPUE in December are reduced. We observed the same outcomes when productivity was low (Appendix E).

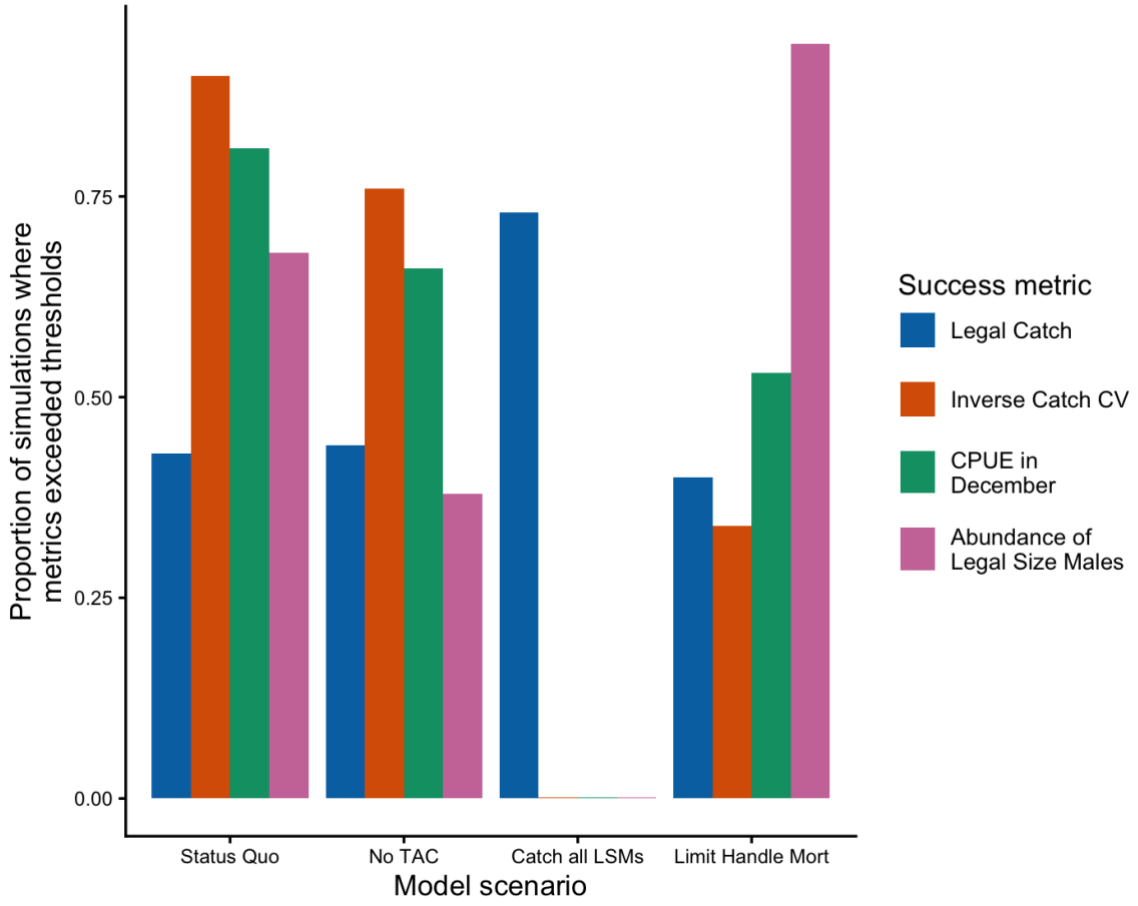

Figure 14. Proportion of successful simulations under multiple success criteria across three management scenarios and one scenario where under the Status Quo management strategy, the catchability of legal sized males = 1. Thresholds for each metric were calculated as the 50th percentile metric value among all scenarios.

4.5 Discussion

Resource managers worldwide are facing increasing challenges to establish management strategies that sustain fisheries in the face of interacting anthropogenic pressures and climate change impacts. This is, in part, because management structures that perform well given dynamics of a particular stable state may no longer hold if the system undergoes a perturbation into a new stable state where dynamics are changed (MacNeil et al. 2010). Given uncertainties in future conditions, it is useful to understand how management strategies perform under a plausible range of conditions (Punt et al. 2014). Here, we developed a model that enables exploration of multiple threats that are specific to the Puget Sound Dungeness crab fishery and proved its ability to detect differences in performance among model scenarios. We also demonstrated that the model can show how different management scenarios may be successful depending on management goals.

Multiple modeling efforts have projected decreases in Dungeness crab abundance in response to climate change scenarios (Toft et al. 2014; Froehlich et al. 2017; Berger et al. 2021). Yet, empirical evidence from California fishery has shown increasing abundances in response to changing oceanographic conditions (Richerson et al. 2020). Given this range in potential futures, we expected respondents to identify climate related threats, and potential management strategies to respond to these threats, as high priority elements to include in the statistical model. Instead, we found that respondents assigned higher priority to exploring the impacts of threats that can be addressed within local management and policy frameworks. Respondents noted that given the geography and accessibility of crabbing grounds in Puget Sound, especially to recreational fishers, these threats may be uniquely stressful to this fishery. By allowing this feedback to drive model development, we incorporated ghost fishing, a threat to Dungeness crab that had previously not been included in Salish Sea Dungeness crab population models (Zhang and Dunham 2013; Toft et al. 2014; Froehlich et al. 2017; Aulthouse 2023) and revealed that this threat has a high potential to impact fishery performance under moderate productivity scenarios.

We found that model performance was most influenced by threats that removed legal-sized males. Specifically, influential parameters were related to the number of derelict pots in the system, the proportion of hard crab regulating the number of crab that fishers can legally retain, and, to a lesser extent, the probability of illegal take and the mortality rate of crab in derelict gear. Both illegal take and incidental mortality were surprisingly unimportant relative to the impacts of ghost fishing. This indicates that reduced performance was generally not due to population level impacts that altered stock productivity, but rather the removal of legal-size males that consequently rendered them unavailable to be caught in the fishery. Therefore, conservation actions that reduce mortality of large males (e.g., derelict gear removal) are likely to increase fishery performance.

In the current study, other impacts of human stressors associated with increased coastal development were all secondary to the biggest driver of fishery success: productivity. Froehlich et al. (2017) found that increased hypoxia led to increased sensitivity to other pressures (illegal harvest and incidental mortality), and interview respondents expressed concern that low productivity would similarly increase sensitivity. Instead, we found that productivity did not interact with other unknown parameters in a meaningful way. Low productivity reduced the number of crab available to catch but did not erode management effectiveness. This result is valuable for anticipating where to allocate resources and whether to limit fishery openers in cases when low productivity is observed. Co-managers have expressed concerns about the impacts of multiple years of low recruitment in the system, and here we showed that the fishery management system has controls that buffer impacts of other threats when legal catch is low. However, low productivity in the ecosystem might also affect crab growth, adult survival, or cannibalism rates, which were not explored here and could be in future work.

There were several limitations in this study, driven by necessary tradeoffs between model breadth and depth (Walters 1986). This model does not explicitly represent the molting process, which has been a primary goal of other Dungeness crab modeling efforts (e.g., Zhang and Dunham 2012, Aulthouse et al. 2023). For example, respondents described observing waves of soft crab throughout the year. However, by accounting for hardness as a constant proportion of the entire population, we addressed the core concern that there was some average latent proportion of the population that was soft during the fishing season. Besides functional illegal take, there are other elements of fisher behavior that were not accounted for, and fisher behavior is a key uncertainty in fishery management (Fulton et al. 2011). For example, many respondents noted that commercial fishers will curtail fishing if CPUE is low. Therefore, it could be that that real-world behavior results in outcomes closer to the limit handle mortality management scenario, even when status quo rules are in place, particularly if fishers can switch to a more lucrative resource when crab catch is low. That tradeoff is more challenging to predict for recreational fishers, who are not motivated by profit. Finally, as noted earlier, we only talked to staff – managers, scientists, and policy representatives - not harvesters or other groups concerned with Dungeness crab (NGOs) who are likely to have different perspectives, although managers may represent an intersection of knowledge groups in some cases (Gray et al. 2012).

Several assumptions in this model warrant further investigation. Given that reproduction in this model depends on the availability for larger males to mate with smaller females, removal of large males via ghost fishing is likely to substantially impact recruitment potential. However, the strength of this relationship may be reduced if we removed the effective reproduction ratio component of the model, which limits the reproductive capacity of females when males with larger body sizes are sparse. This may be valuable to explore given evidence from California that large female reproductive rates remain high even if abundance of large males is low (Hankin et al. 1997). Conversely, the relationship between illegal harvest and fishery performance may have been stronger had we not included functional illegal take, where the probability of illegal retention is reduced when catch rates are high, which is known to suppress the impacts of illegal take on model performance (Froehlich et al. 2017).

Using semi-structured interviews to inform an operating model can be an effective alternative to a traditional Management Strategy Evaluation (Damiano et al. 2022). We employed this method

to demonstrate that performance of the Puget Sound Dungeness crab management system is robust to threats identified by staff of governments involved in fisheries management even under different fishing and productivity conditions. In the future, this model can serve as a tool to compare additional management scenarios, in collaboration with regional fishery managers. Incorporating feedback from managers and other local knowledge holders resulted in meaningful model additions both in Froehlich et al. (2017) and in the current study. Both studies highlight the importance of incorporating multiple perspectives on ecosystem dynamics and priority threats in the context of a complex social ecological system (Hollowed et al. 2025). Continuing to engage those involved in management of this fishery may provide opportunities to include more threats, and interactions between threats, that reflect evolving perspectives as we learn more about the impacts of ecosystem change.

4.6 ACKNOWLEDGEMENTS

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SYNTHESIS

Coastal ecosystems are increasingly modified by human activities, yet understanding and responding to the consequences of these changes remains challenging. For instance, multiple anthropogenic pressures compound and affect ecosystem structure and function, which in turn impact decisions about resource management (Fu et al., 2013; Levin & Möllmann, 2015). Understanding how human-caused ecosystem changes play out is therefore extremely valuable for managers to effectively conserve and protect natural resources (Bennett et al., 2009; Cuddington et al., 2013; Kremen, 2005). This dissertation furthers that understanding by moving from species-specific responses, to community ecological impacts, to evidence synthesis, and finally to evaluating management performance under multiple anthropogenic threats. Addressing these topics enhances the potential for restoration and fisheries management to remain effective when ecological responses to coastal changes are complex and uncertain.

Decision making for natural resource management involves multiple questions, such as where to direct conservation and restoration efforts, and which ecological functions are a priority to maintain. We are currently in the United Nations "Decade on Ecosystem Restoration," which was initiated as a response to rapid coastal change that occurred over the course of the last century (United Nations General Assembly, 2019). After witnessing the consequences of increased pressures on coastal ecosystems, communities around the globe have demonstrated significant interest and investment in determining where restoration will be most effective and developing solutions for ongoing development that also maintain or recreate desired ecosystem functions. Modern restoration best practices seek to restore processes that support ecological function (Higgs et al., 2014), rather than focusing restoration on individual species, because re-establishing the ability for natural systems to maintain functions in the face of future change or disturbance builds resilience (Campbell et al., 2009). Resilient coastlines have more capacity to maintain important ecosystem services that people rely on, such as sustainable fisheries and recreational opportunities.

Yet maintaining or restoring ecosystem services looks different depending on the goals of management. Priority services are determined by the values and knowledge systems within social-ecological systems, and can vary between different knowledge systems, economic classes, and age groups (Das et al., 2022; Volpe et al., 2024). Sometimes these values also include supporting the persistence of culturally significant species, known as "cultural keystone species" (Garibaldi & Turner, 2004). In the Salish Sea, for instance, management priorities include improving the status of endangered wild populations of Chinook salmon—a prime example of a cultural keystone species—and supporting healthy food webs (PSP, 2022). Uncovering the extent to which species' success in the marine nearshore is due to habitat condition can inform when and where habitat conservation or restoration actions may be most effective at supporting these goals.

This dissertation suggests that for subtidal fishes like salmon, habitat condition alone is an incomplete predictor of ecological response. In Chapter 1, I found that associations between shoreline armor and fish abundance in the nearshore were weak, inconsistent in direction, and scale-dependent. Other factors, for example life history and mobility, are more likely to govern

where fish are found. In Chapter 2, despite marked differences in species among sites, multiple measures of functional diversity were largely insensitive to shoreline condition. In Chapter 3, I discuss evidence suggesting that most direct associations between nearshore habitat features and Chinook salmon survival are weak or absent. Where effects are detectable, they may operate through secondary or indirect pathways (e.g., prey availability, thermal regime, predator exposure) rather than a direct habitat-quality-to-survival link. The variable strength in associations between nearshore fishes and shoreline habitat condition that I uncovered in this work suggests several potential pathways for improving resource management decision making in the Salish Sea.

One approach is to prioritize armor removal at shorelines based on maximizing restoration of geomorphic processes and intertidal invertebrate communities, rather than basing decisions on impacts to nearshore fishes. The equivocal results from Chapters 1-3, and personal observations in the field and from reviewing literature, make this process-based approach to restoration appealing. In taking this approach, restoration practitioners would not need to explicitly consider which, or if any, fish species may specifically benefit from a given restoration action. Instead, decisions about where to prioritize restoration may focus on where armor removal will have the greatest effect on physical changes to the beach, or the greatest likelihood to promote habitat for invertebrates through accumulating logs and wrack (Toft et al., 2023; Toft et al., 2025). This contrasts with a hypothetical alternative scenario where armor removal is prioritized in areas where a certain species was absent or had low abundance. Benefits to fish in subtidal water adjacent to armor may still manifest through secondary pathways if beach function is restored throughout the region.

Another approach for improving restoration in the Puget Sound is to promote habitat heterogeneity whenever possible. Diverse habitats offer opportunities for subtidal fishes to fill a variety of ecological niches; supporting this variety will preserve any underlying processes that we have yet to uncover. This approach acknowledges that armor is likely to continue being a part of coastal infrastructure in the future, especially as increased frequency of storms and rate of sea level rise associated with climate change necessitates more shoreline protection (Beasley & Dundas, 2021). Results from this dissertation (Chapters 1-3) suggest that short segments of armored shoreline are unlikely to affect the distribution of nearshore fishes. A heterogeneous shoreline that includes armor is therefore unlikely to have a direct and significant adverse effect on fishes' abundance in adjacent subtidal waters. However, how shoreline armor impacts the growth and survival of nearshore fishes is less studied and more challenging from a practical perspective (e.g., scaling of mark-recapture studies). Continued research on how armor impacts these vital rates and overall demography is particularly important for increasing survival of species like endangered wild Puget Sound Chinook salmon.

Stewardship of Salish Sea resources should also consider the spatial context of habitat restoration within a broader landscape mosaic. Comparing fish response to armor across multiple spatial scales proved to be a robust way of testing multiple hypotheses about the spatial scale at which drivers are operating (Chapter 1), and I recommend restoration efforts consider the spatial scale most necessary for species' restoration. For example, in Chapter 3, I discuss how the evidence for Chinook salmon response to shoreline condition is weak. This is in part because smolts are moving through habitats during their outmigration, and some metrics that directly associate

habitat quality with fish growth and survival (e.g. stomach fullness) cannot be easily attributable to the habitat where they are observed. Connectivity between habitats should be a priority so that fish can access resources they require at different points in their life history. The challenge in this approach, however, is the increased resources required to conduct and monitor broad scale restoration when such a scale is needed.

These approaches are also applicable to other regions beyond the Salish Sea region. While restoration actions in the Puget Sound focus on reinstating natural erosion processes, other areas of the U.S. that are subject to storm activity that is accelerating coastline erosion are actively installing erosion control structures (Bilkovic et al., 2016). Evaluating the effect of these structures should account for spatial scale and measure multiple complementary evidence streams. As this dissertation demonstrates, using multiple lines of evidence increases the chances of detecting when and where nearshore fishes respond to shoreline habitats. Different measures of biodiversity and ecological processes at multiple scales and levels of biological organization can provide complementary perspectives on fish–habitat relationships beyond single habitat or community metrics. Assessments of coastal infrastructure should consider focusing on function alongside composition, by complementing traditional species-based monitoring with evaluations of functional diversity (Chapter 2). Future work to establish which fish species play important functional roles (e.g., nutrient cycling or ecosystem engineering) will be valuable for monitoring whether functions are lost or altered during ecosystem change. Specifically, as sea levels continue to rise and flooding increases over the next century, it will also be important to look for novel or changing interactions between coastal fishes and infrastructure.

The Salish Sea region could also learn from stewardship practices in other regions. In the Puget Sound, shoreline erosion is a natural process that we are seeking to maintain or reactivate with armor removal. Yet on the East Coast of the U.S., increased storm activity and sea level rise are depleting shorelines and adding an erosion control structure to minimize loss is a step towards conservation or restoration (Bilkovic et al., 2016). In engineering solutions for erosion reduction along the Southeast and Gulf Coasts, there has been innovation in designing structures that support ecological function in multiple ways, such as by providing water filtration and nursery habitat for fishes (Smith et al., 2020). While there are some examples of similar nature-based solutions in Puget Sound (e.g., at the Seattle seawall), there are likely more opportunities to think expansively about how armor could be re-designed to serve more functions and what role fishes play, if any, in supporting those functions. Changes to the slope of structures or adding planter boxes for vegetation would mitigate some of the negative impacts for intertidal species, such as reduced shade and habitat for insects (Chapman & Underwood, 2011). Such updates to armor form might gain traction in the Salish Sea if they are implemented to be as aesthetically pleasing as possible, motivating landowners to invest in design upgrades.

In addition to habitat restoration, sustainable fisheries management will also be a pillar of conservation in the Salish Sea. Chapter 4 of this dissertation demonstrated that improved ecological understanding supports more informed evaluation of alternatives for sustainable resource management. By exploring the impacts of different threats on the Dungeness crab fishery in Chapter 4, I found that some threats were more influential on fishery outcomes than others, and that the impacts of multiple threats were less significant (i.e., there was a smaller absolute change in performance measures) under low productivity scenarios. Under the baseline

productivity scenario, threats related to take of legal-size males were more influential than threats related to higher mortality of females and smaller males. By comparing the performance of multiple management alternatives, I highlighted the tradeoffs between management decisions that emerged across a range of threats, which can help inform decision-making processes. For this model, and future similar work, it will be valuable to continue connecting with respondents, incorporate additional stressors as they develop, and iterate updated population models that can stay relevant as ecosystems change and new anthropogenic threats emerge.

Future work to support decision making will be strengthened by continuing to evolve how researchers focus their efforts. Chapters 1-3 of this dissertation focused on links between nearshore fishes and shoreline habitat features because habitat is thought to be a key ecological driver, yet this relationship was weak and difficult to detect. In contrast, in Chapter 4 of this dissertation I asked resource managers directly what ecosystem dynamics they think likely to have the strongest impact on fishery outcomes. By allowing interview results to drive the simulation modeling exercise in this chapter, I was able to ensure that the simulation study addressed the mechanisms that were the priority concerns of interview respondents. This approach was valuable to co-produce knowledge that addresses the needs of management, and it revealed priority threats to consider that contributed to a much richer population model than would have been possible with insights from published papers alone. By further engaging with managers to guide future research directions, researchers can avoid the "loading dock approach", where science is conducted and published while assuming that resource managers will benefit from knowledge that has been packaged for them without their input (Francis et al., 2018), and build on practical and actionable advice.

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CHAPTER 1 APPENDIX

Table S1. Descriptions of sample sites. A single lat/long was created for each shoreline segment (representing different shoreline types) within each site by snapping subtidal station coordinates within each site to nearest shoreline feature then using then generating centroid points. Basin codes are derived from the Puget Sound nearshore and Estuarine Research Program (PSNERP) designations: San Juan Islands (SJ), WH (Whidbey Basin), South Central (SC), and South Puget Sound (SP). Core sites were sampled monthly during the field season over 4 years and supplemental sites (supp) were sampled only in June 2021 and 2022. Armor type at armored shorelines within sites is represented as either bulkhead (bulk) or riprap revetment (rev). Restoration year corresponds with the restored shorelines within sites. Distances between depth stations represents the range of Euclidean distances between paired shallow and deep sampling stations, in meters. The final four rows contain survey coverage details where C designates complete sampling (i.e. a lampara net set at each depth station at each shoreline type).

	Family Tides	**Turn Island**	**Cornet Bay**	**Maylor Point**	**Waterman Preserve**	**Howarth Park**	**Seahurst Park**	**Dockton Park**	**Lost Lake**	**Titlow Park**	**Penrose Point**	**Edgewater Beach**
Site code	FAM	TUR	COR	MA	WA	HO	SHR	DOK	LL	TL	PR	EDG
centroid Lat/Long	48.6114, -122.979	48.5309, -122.975	48.4043, -122.627	48.2739, -122.625	47.9987, -122.371	47.9606, -122.246	47.4815, -122.361	47.3710, -122.453	47.3598, 122.488	47.2517, -122.552	47.2624, -122.751	47.1539, -122.929
basin	SJ	SJ	WH	WH	WH	WH	SC	SC	SC	SP	SP	SP
Core/Supp	core	core	core	supp	supp	supp	core	core	supp	supp	supp	core
Eelgrass?	no	yes	yes	no	yes	yes	yes	no	no	yes	yes	no
Land Ownership	Private/ Summer camp	State Park / Private	State Park / Private	Private/ Naval base	Private	State Park	State Park	County Park	Private	County Park	County Park	Private
Dock?	yes	no	yes	no	no	no	no	yes	no	no	no	no
Armor type	rev	bulk	bulk	rev	bulk	rev	bulk	bulk	bulk	bulk	bulk	bulk
Restoration year	2015	N/A	2012	2018	2016	2016	2014	2013	2018	2017	2013	2016
Distances between depth stations (m)	72.3 - 85.1	47.4 - 51.1	75.4 – 82.5	99.6 - 224.4	70.9 - 84.3	70.1 – 89.5	91.6 – 121.4	87.4 – 92.7	51.4 – 57.9	47.7 – 85.0	84.2 – 102.4	73.0 – 117.2
2018 (Jun-Aug)	C	C	C	-	-	-	C	C	-	-	-	C
2019 (Apr-Sept)	C	C	C	-	-	-	C	C	-	-	-	C
2021 (Apr-Aug)	C	C	June	Armored	C	C	Armored, Aug	C	C	C	C	July
2022 (Apr-Sept)	C	C	C	C	C	C	C	C	C	C	C	C

Table S2. Equations for the 8 models used in model selection for each species. The subscript *i* denotes sampling events and j denotes variable intercepts by site.

Model Name (if applicable)	Model Equation
base	$log(\mu_i) = site_{j[i]} + \beta_1 year_i + \beta_2 log(day\ of\ year)_i + \beta_3 log(day\ of\ year)_i^2 + \beta_4 veg_i$ $site_j \sim Normal(0, \sigma^2)$
	$log(\mu_i) = site_{j[i]} + \beta_1 year_i + \beta_2 \log(day\ of\ year)_i + \beta_3 \log(day\ of\ year)_i^2 + \beta_4 veg_i + \beta_5 shore\ type_i$ $site_j \sim Normal(0, \sigma^2)$
	$log(\mu_i) = site_{j[i]} + \beta_1 year_i + \beta_2 \log(day\ of\ year)_i + \beta_3 \log(day\ of\ year)_i^2 + \beta_4 veg_i + \beta_5 \%\ shoreline\ armor\ in\ 500m_i$ $site_j \sim Normal(0, \sigma^2)$
	$log(\mu_i) = site_{j[i]} + \beta_1 year_i + \beta_2 \log(day\ of\ year)_i + \beta_3 \log(day\ of\ year)_i^2 + \beta_4 veg_i + \beta_5 \%\ shoreline\ armor\ in\ 1.2km_i$ $site_j \sim Normal(0, \sigma^2)$
	$log(\mu_i) = site_{j[i]} + \beta_1 year_i + \beta_2 log(day\ of\ year)_i + \beta_3 log(day\ of\ year)_i^2 + \beta_4 veg_i + \beta_5 \%\ shoreline\ armor\ in\ 10km_i$ $site_j \sim Normal(0, \sigma^2)$
	$log(\mu_i) = site_{j[i]} + \beta_1 year_i + \beta_2 log(day\ of\ year)_i + \beta_3 log(day\ of\ year)_i^2 + \beta_4 veg_i + \beta_5 shore\ type_i + \beta_6 \%\ shoreline\ armor\ in\ 500m_i$ $site_j \sim Normal(0, \sigma^2)$
	$log(\mu_i) = site_{j[i]} + \beta_1 year_i + \beta_2 log(day\ of\ year)_i + \beta_3 log(day\ of\ year)_i^2 + \beta_4 veg_i + \beta_5 shore\ type_i + \beta_6 \%\ shoreline\ armor\ in\ 1.2km_i$ $site_j \sim Normal(0, \sigma^2)$
	$log(\mu_i) = site_{j[i]} + \beta_1 year_i + \beta_2 log(day\ of\ year)_i + \beta_3 log(day\ of\ year)_i^2 + \beta_4 veg_i + \beta_5 shore\ type_i + \beta_6 \%\ shoreline\ armor\ in\ 10km_i$ $site_j \sim Normal(0, \sigma^2)$

Sampling Summary

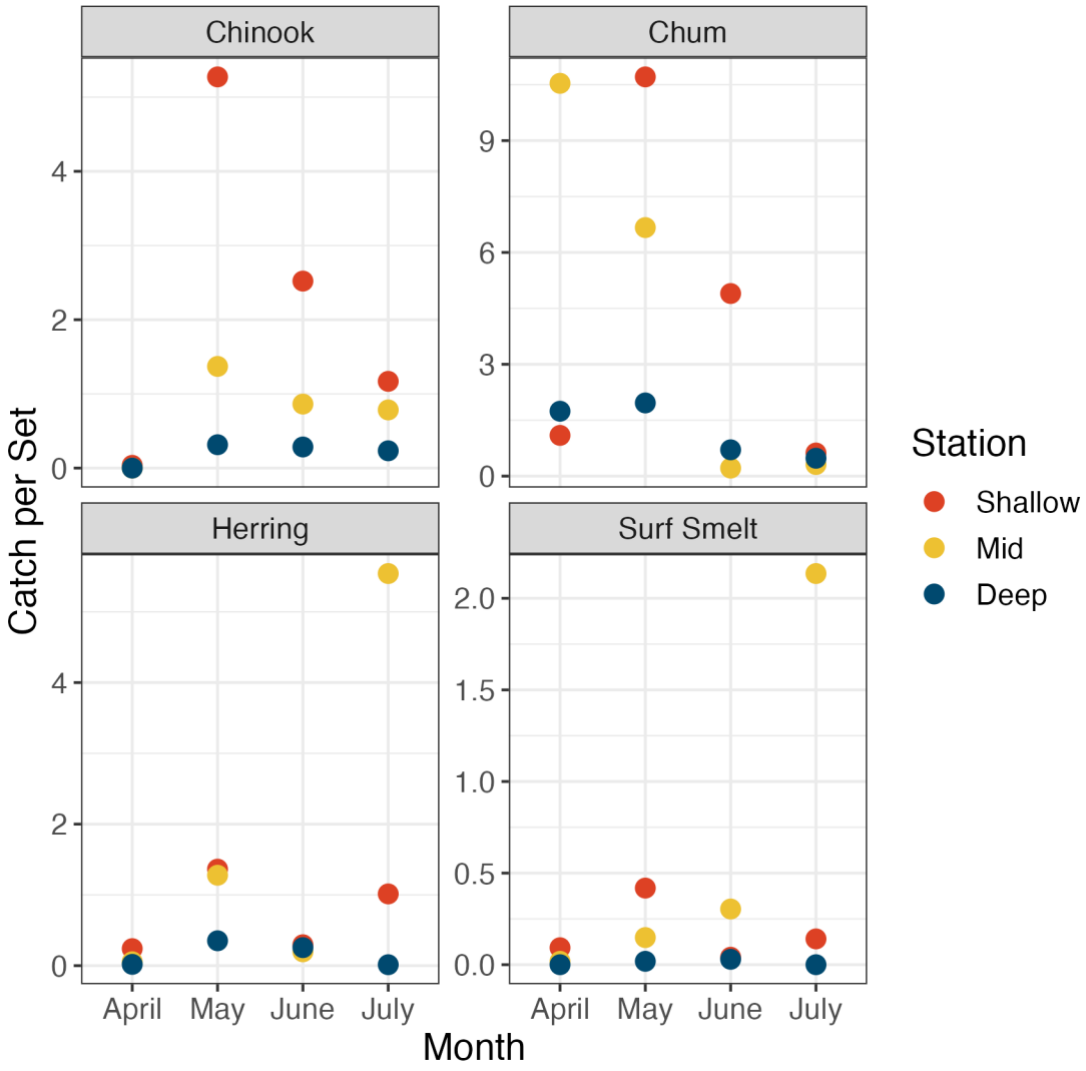

Fig S1. Average catch per set of target species at three depth stations. Months with peak abundances are displayed, for clarity. The shallow depth station at each site was in 1 meter water depth, the mid station was in about 5 meter water depth, and the deep station was approximately 50 meters offshore of the mid station.

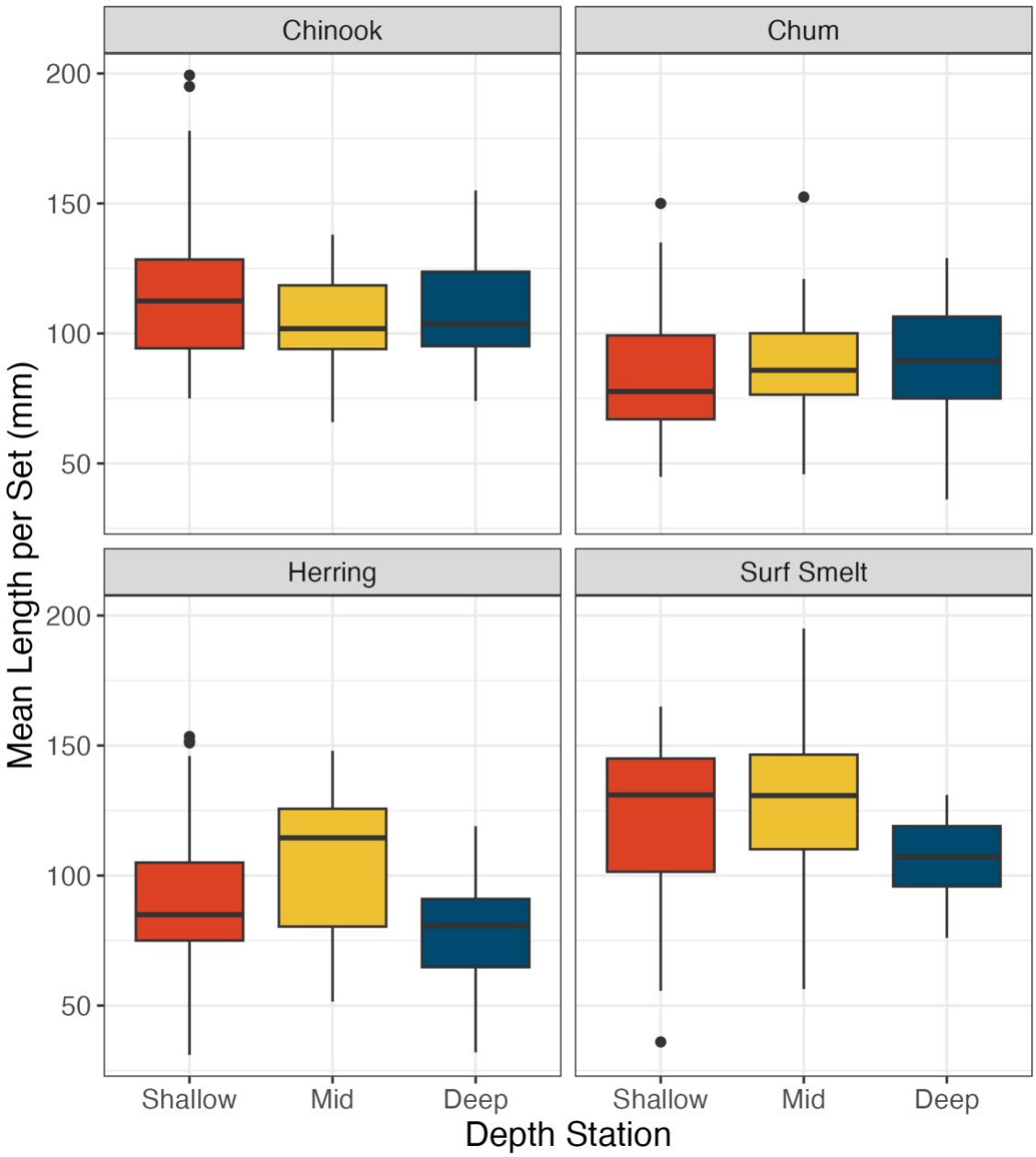

Fig S2. Mean lengths of target species measured at three depth stations. We measured the fork length of the first 20 individuals of each fish species captured in each net set. The shallow depth station at each site was in 1 meter water depth, the mid station was in about 5 meter water depth, and the deep station was approximately 50 meters offshore of the mid station.

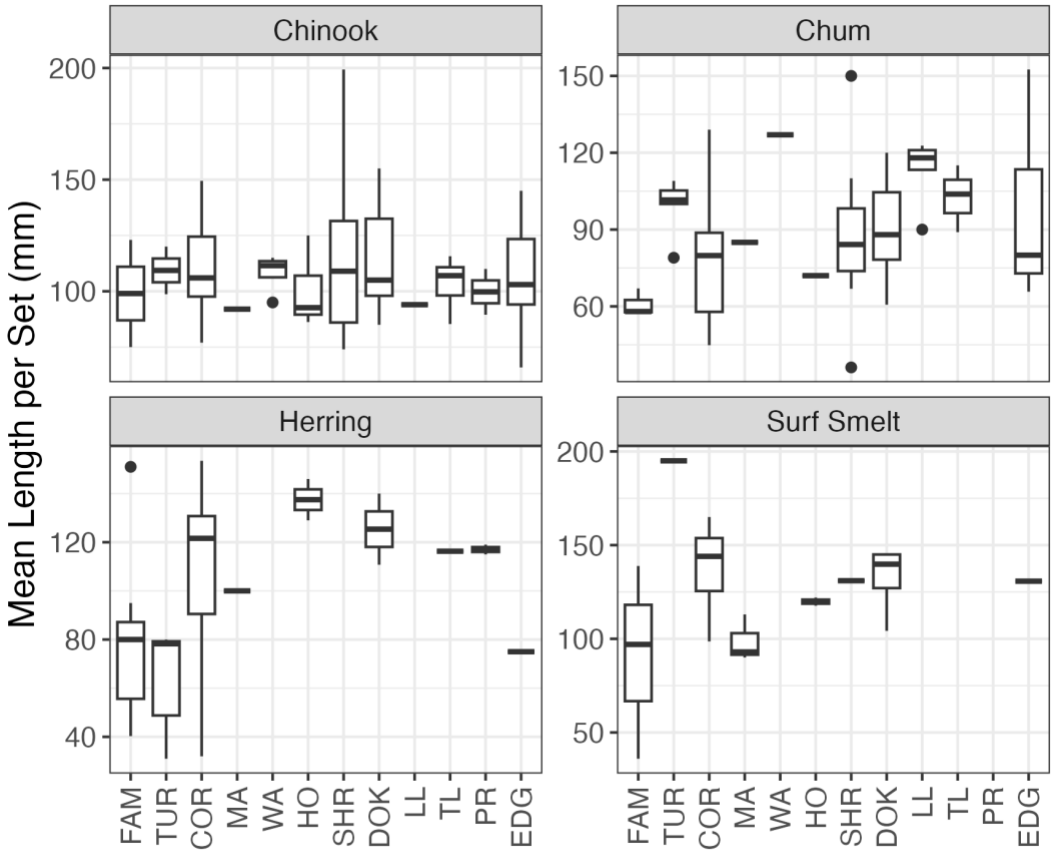

Fig S3. Mean lengths of target species measured at each site. Site codes are associated with sites described in table S1. Three letter site codes correspond to core sites, sampled spring-summer over 4 years, while two letter site codes correspond with supplemental sites that were sampled only in June over 2 years. We measured the fork length of the first 20 individuals of each fish species captured in each net set.

Model Diagnostics

We conducted diagnostic checks for the model with the lowest AIC_c value for each species, as follows:

Chinook (armor extent within a 500m radius) and Herring (within a 10km radius)

$$\lambda_i = \alpha + \beta_1 year_i + \beta_2 logyday_i + \beta_3 logyday_i^2 + \beta_4 veg_i + \beta_5 armor.extent_i + site_{j[i]}$$

Chum

$$\lambda_i = \alpha + \beta_1 year_i + \beta_2 logyday_i + \beta_3 logyday_i^2 + \beta_4 veg_i + \beta_5 shoreline_i + site_{j[i]}$$

Smelt

$$\lambda_i = \alpha + \beta_1 year_i + \beta_2 logyday_i + \beta_3 logyday_i^2 + \beta_4 veg_i + site_{j[i]}$$

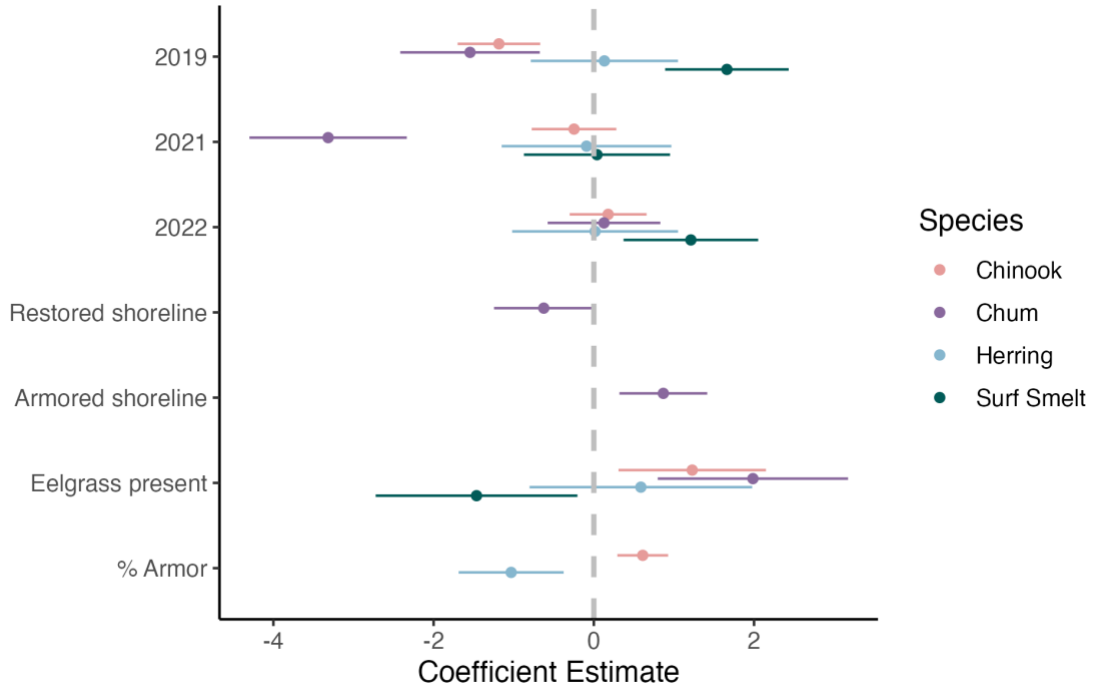

Fig S4. Coefficient estimates for models with the lowest AIC_c value for each species

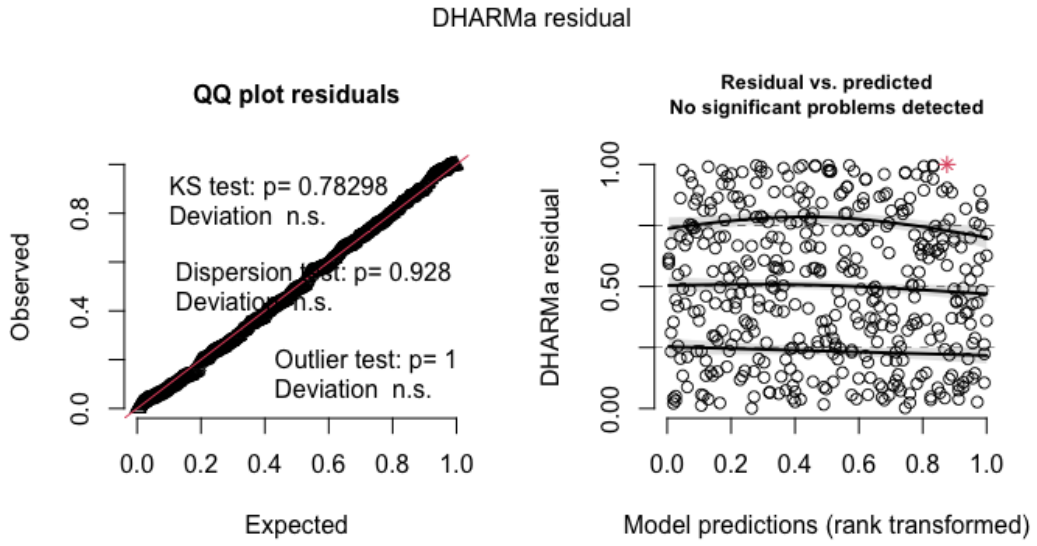

Fig S5. Chinook salmon model diagnostic plots from the R package DHARMa

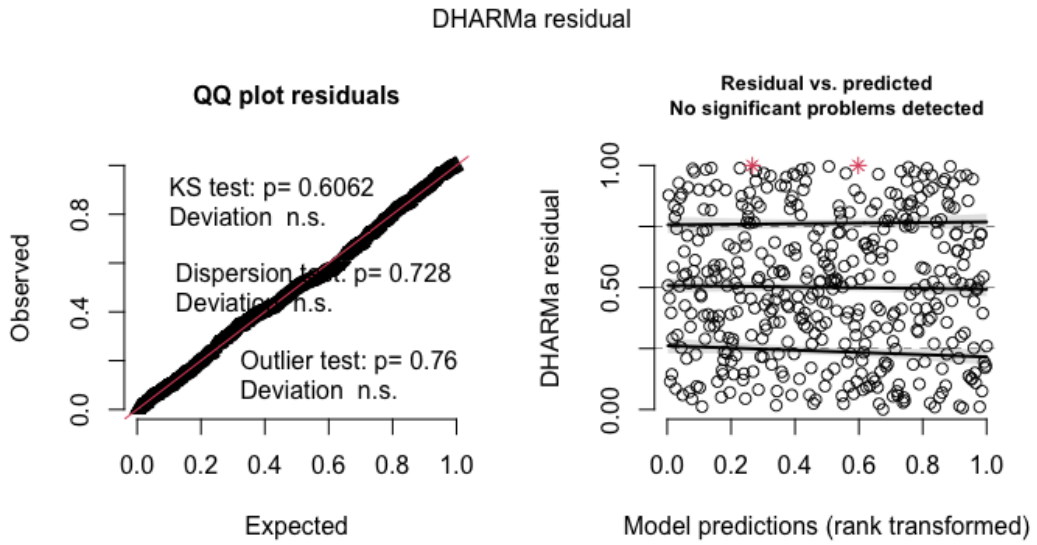

Fig S6. Chum salmon model diagnostic plots from the R package DHARMa

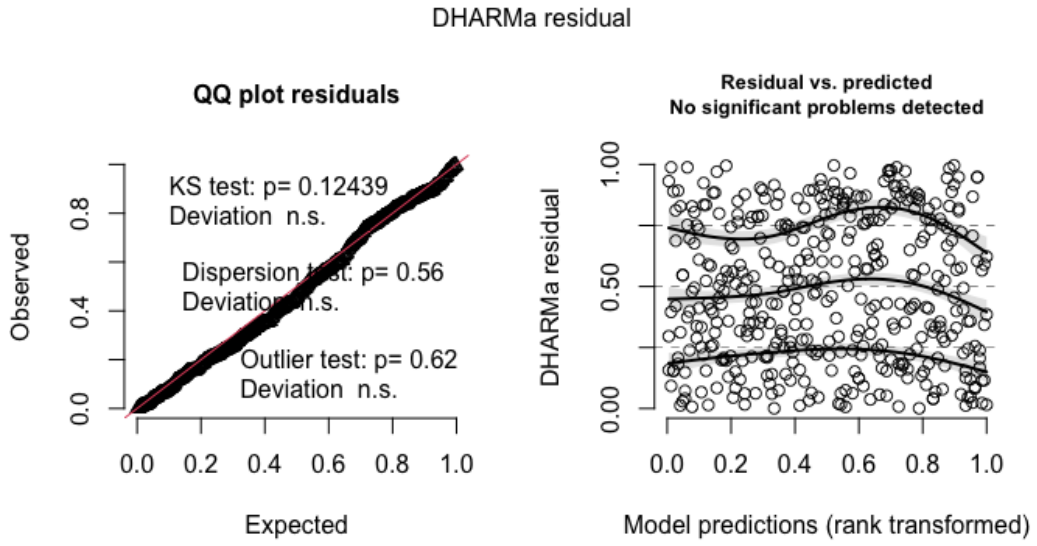

Fig S7. Pacific Herring model diagnostic plots from the R package DHARMa

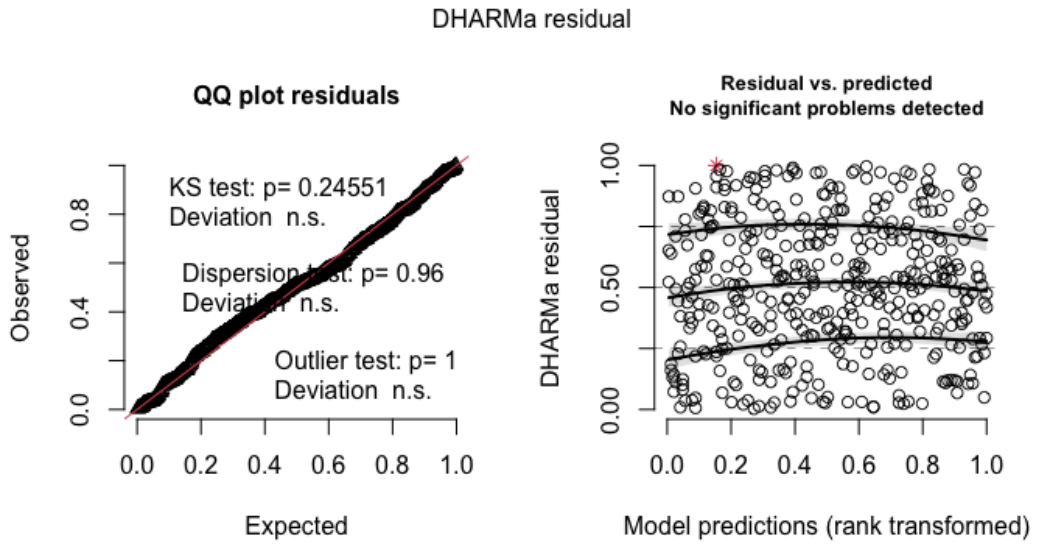

Fig S8. Surf Smelt model diagnostic plots from the R package DHARMa

CHAPTER 2 APPENDIX

Table S1 Descriptions of sampling locations. Armor type at armored shorelines within sites is represented as either bulkhead (bulk) or riprap revetment (rev). Restoration year corresponds with the restored shorelines within sites. The depth of the deepest station is relative to Mean Lower Low Water.

	Site code	Eelgrass?	Relative Exposure	Shoreline condition	Lat	Long	Land Ownership	Nearby Dock?	Armor type	Restoration year	Depth of deepest station (m)
Family Tides	FAM	No	Sheltered	Armored	48.61626	-122.98079	Private	Yes	rev		-10.2
				Natural	48.60786	-122.97894	Private	Yes			-8
				Restored	48.61088	-122.9809	Private	Yes		2015	-6.76
Turn Island	TUR	Yes	Sheltered / High current	Armored	48.53035	-122.98018	Private	No	bulk		-8.78
				Natural	48.53147	-122.97154	State park	No			-6.54
				Natural	48.53119	-122.97409	State park	No		N/A	-10.81
Cornet Bay	COR	Yes	Sheltered	Armored	48.41538	-122.62817	Private	No	bulk		-8.57
				Natural	48.40192	-122.6215	State park	Yes			-5.57
				Restored	48.40078	-122.62306	State park	Yes		2012	-3.75
Seahurst	SHR	Yes	Exposed	Armored	47.48251	-122.36122	City park	No	bulk		-14.48
				Natural	47.48348	-122.36105	City park	No			-10.84
				Restored	47.48006	-122.36187	City park	No		2014	-12.17

Dockton	DOK	No	Sheltered	Armored	47.37055	-122.45391	Private	No	bulk		-6.86
				Natural	47.37245	-122.45165	County park	Yes			-6.61
				Restored	47.37073	-122.45658	County park	Yes		2013	-7.18
Edgewater	EDG	No	Exposed	Armored	47.15205	-122.93036	Private	No	bulk		-8.95
				Natural	47.15622	-122.92663	Private	No			-12.28
				Restored	47.15502	-122.92818	Private	No		2016	-13.77

Trait Assignment Details

Feeding guild: We classified diet based on dominant prey items listed for each species in FishBase. We considered life stage and locality when assessing main food in the Food Items and Diet Composition tables and consulted the biological description to confirm findings when clarification was necessary. If a species had multiple main food types listed that fit under different feeding guilds, we classified it as omnivorous.

Vertical position: We aggregated pelagic-neritic into the pelagic category, because there were few species representing these groups. We assigned juvenile salmonids to the epipelagic group, based on Quinn (2005) and Munsch et al. (2017).

Migrations: Species were coded as migratory if any type of migration was listed. Those without any information were assumed to be resident.

Table S2 Trait data assigned to each species in the dataset. Mean length was calculated from individuals sampled in the field and is displayed here with standard deviation, but only the mean value was used in the functional diversity analysis. All categorical traits were extracted from FishBase (FishBase code in parentheses).

Species	**Common Name**	**Mean length** (mm, ± SD)	**Transverse Shape** (BodyShapeI)	**Vertical distribution** (DemersPelag)	**Migrations** (AnaCat)	**Feeding Guild** (FoodI)
Syngnathus leptorhynchus	Bay pipefish	135.54 (46.96)	eel-like	demersal	resident	zoobenthivorous
Enophrys bison	Buffalo Sculpin	81.24 (78.44)	fusiform / normal	demersal	resident	omnivorous
Pleuronichthys coenosus	C-O Sole	70.00 (0)	short and / or deep	demersal	resident	zoobenthivorous
Oncorhynchus tshawytscha	Chinook salmon	107.48 (29.29)	fusiform / normal	epipelagic	migratory	omnivorous[1]
Oncorhynchus keta	Chum salmon	70.26 (35.90)	fusiform / normal	epipelagic	migratory	planktivorous[2]
Oncorhynchus kisutch	Coho salmon	123.99 (33.26)	fusiform / normal	epipelagic	migratory	omnivorous[3]
Pholis laeta	Crescent Gunnel	99.63 (30.10)	eel-like	demersal	resident	zoobenthivorous
Oncorhynchus clarkii	Cutthroat trout	206.50 (47.38)	fusiform / normal	epipelagic	migratory	omnivorous
Parophrys vetulus	English sole	58.78 (53.21)	short and / or deep	demersal	migratory	zoobenthivorous
Myoxocephalus polyacanthocephalus	Great Sculpin	200.00 (0)	fusiform / normal	demersal	migratory	omnivorous
Hexagrammos decagrammus	Kelp Greenling	60.05 (36.75)	fusiform / normal	demersal	resident	zoobenthivorous

[1] Chinook salmon juvenile diet (Beamish et al., 2004; Duffy et al., 2010; Kennedy et al., 2018)
[2] Chum salmon juvenile diet is primarily plankton (Kennedy et al., 2018)
[3] Coho salmon juvenile diet (Beamish et al., 2004)

Ophiodon elongatus	Lingcod	83.75 (19.45)	elongated	demersal	migratory	zoobenthivorous[4]
Engraulis mordax	Northern Anchovy	98.13 (67.06)	elongated	pelagic	resident	planktivorous
Gadus macrocephalus	Pacific Cod	62.54 (36.52)	fusiform / normal	demersal	migratory	planktivorous
Clupea pallasii	Pacific herring	79.99 (0)	fusiform / normal	pelagic	resident	planktivorous
Ammodytes hexapterus	Pacific sand lance	76.27 (33.39)	elongated	benthopelagic	migratory	planktivorous
Psettichthys melanostictus	Pacific sand sole	117.25 (79.58)	short and / or deep	demersal	resident	omnivorous
Trichodon trichodon	Pacific sandfish	83.00 (0)	elongated	demersal	resident	omnivorous
Lumpenus sagitta	Pacific snake prickleback	130.66 (39.76)	eel-like	benthopelagic	resident	zoobenthivorous
Leptocottus armatus	Pacific staghorn sculpin	118.31 (75.19)	elongated	demersal	migratory	omnivorous
Microgadus proximus	Pacific tomcod	39.30 (26.73)	fusiform / normal	demersal	migratory	zoobenthivorous[5]
Artedius fenestralis	Padded Sculpin	80.00 (0)	elongated	demersal	resident	omnivorous
Apodichthys flavidus	Penpoint Gunnel	122.61 (62.97)	eel-like	demersal	resident	zoobenthivorous
Phanerodon vacca	Pile Perch	148.19 (87.59)	short and / or deep	demersal	resident	zoobenthivorous
Oncorhynchus gorbuscha	Pink salmon	55.39 (32.91)	fusiform / normal	epipelagic	migratory	planktivorous
Porichthys notatus	Plainfin midshipman	57.50 (0)	elongated	demersal	resident	omnivorous
Lepidopsetta bilineata	Rock Sole	215.00 (0)	short and / or deep	demersal	resident	omnivorous
Pholis ornata	Saddleback Gunnel	97.58 (33.22)	eel-like	demersal	resident	zoobenthivorous
Limanda limanda	Sand Dab	61.90 (11.46)	short and / or deep	demersal	migratory	zoobenthivorous
Cymatogaster aggregata	Shiner Perch	69.76 (29)	short and / or deep	demersal	resident	zoobenthivorous
Blepsias cirrhosus	Silverspotted sculpin	54.99 (26)	elongated	demersal	resident	zoobenthivorous[6]
Citharichthys stigmaeus	Speckled sanddab	110.00 (44.79)	short and / or deep	demersal	resident	zoobenthivorous
Platichthys stellatus	Starry Flounder	220.25 (55.25)	short and / or deep	demersal	migratory	omnivorous
Oncorhynchus mykiss	Steelhead trout	209.00 (11.53)	fusiform / normal	epipelagic[7]	migratory	omnivorous
Embiotoca lateralis	Striped Seaperch	136.34 (57.85)	short and / or deep	demersal	resident	zoobenthivorous

[4] Juvenile diet in FishBase
[5] Juvenile diet in FishBase
[6] There was no diet information for Silverspotted sculpin in rfishbase, but there was diet information under the species description on the FishBase website.
[7] Juvenile steelhead are surface oriented (Daly et al., 2014)8/19/2026 12:02:00 AM

Hypomesus pretiosus	Surf Smelt	116.16 (41.66)	elongated	benthopelagic	resident	omnivorous
Psychrolutes paradoxus	Tadpole Sculpin	32.38 (11.15)	elongated	demersal	resident	omnivorous
Gasterosteus aculeatus	Three-spined stickleback	44.89 (21.94)	fusiform / normal	benthopelagic	migratory	omnivorous
Oligocottus maculosus	Tidepool Sculpin[8]	89.00	elongated	demersal	resident	zoobenthivorous
Liparis florae	Tidepool Snailfish	117.00 (0)	elongated	demersal	resident	zoobenthivorous[9]
Aulorhynchus flavidus	Tube-snout	134.32 (48.01)	elongated	benthopelagic	resident	omnivorous
Hexagrammos stelleri	Whitespotted greenling	93.50 (64.09)	fusiform / normal	demersal	resident	omnivorous

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Quinn, T.P., 2005. The Behavior and Ecology of Pacific Salmon and Trout. UBC Press.

[8] We did not record the length of Tidepool sculpin in our field dataset, so we used the maximum length recorded in Fish Base.

[9] There was no diet information for the Tidepool Snailfish so we substituted information for another snailfish species in the same genus (*Liparis pulchellus)*

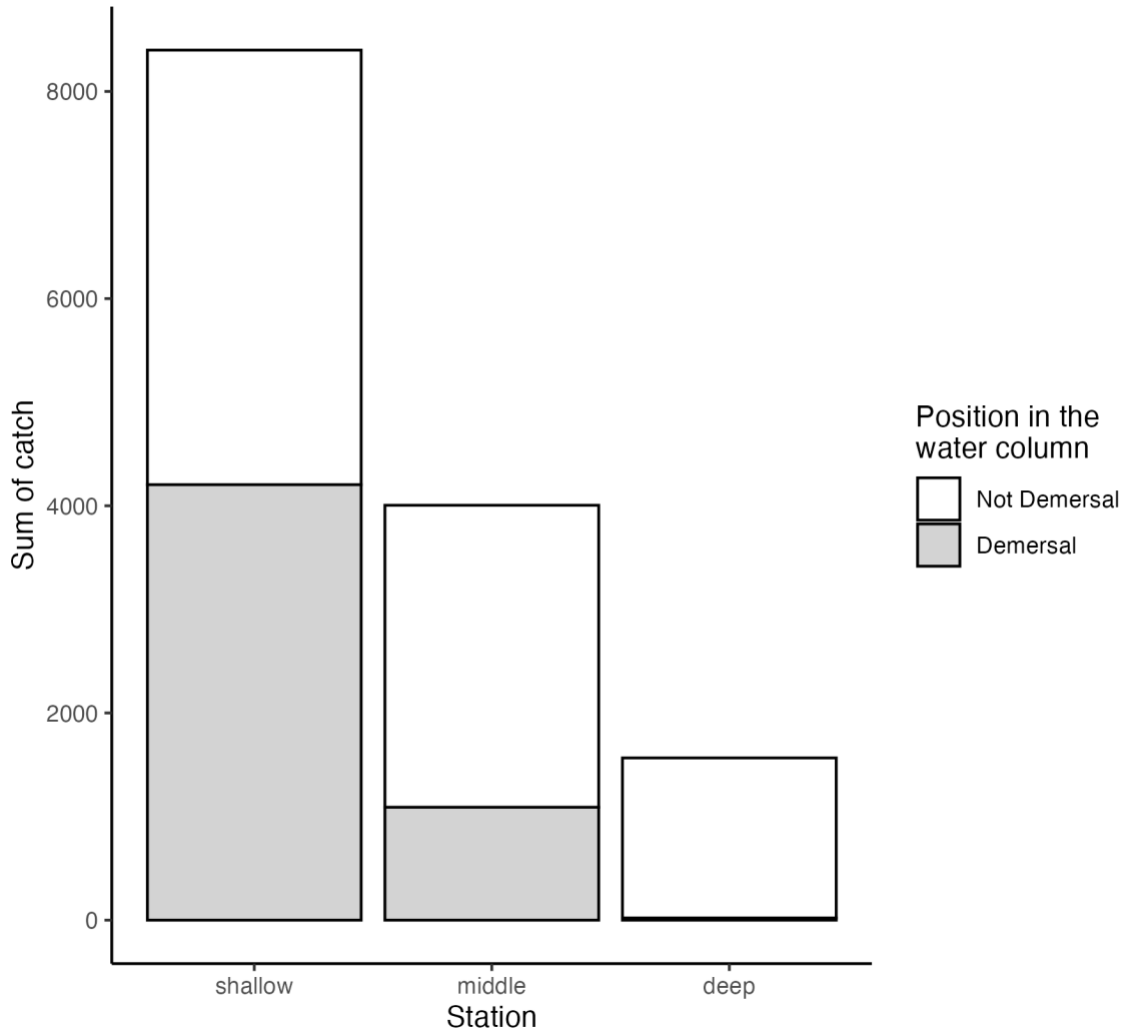

Fig S1 Total catch of nearshore fishes captured using a lampara net at shorelines in the Salish Sea, by depth station. The stacked bar chart displays species' functional traits split into two groups: demersal fishes and all others. Trait assignments can be found in Table S1.

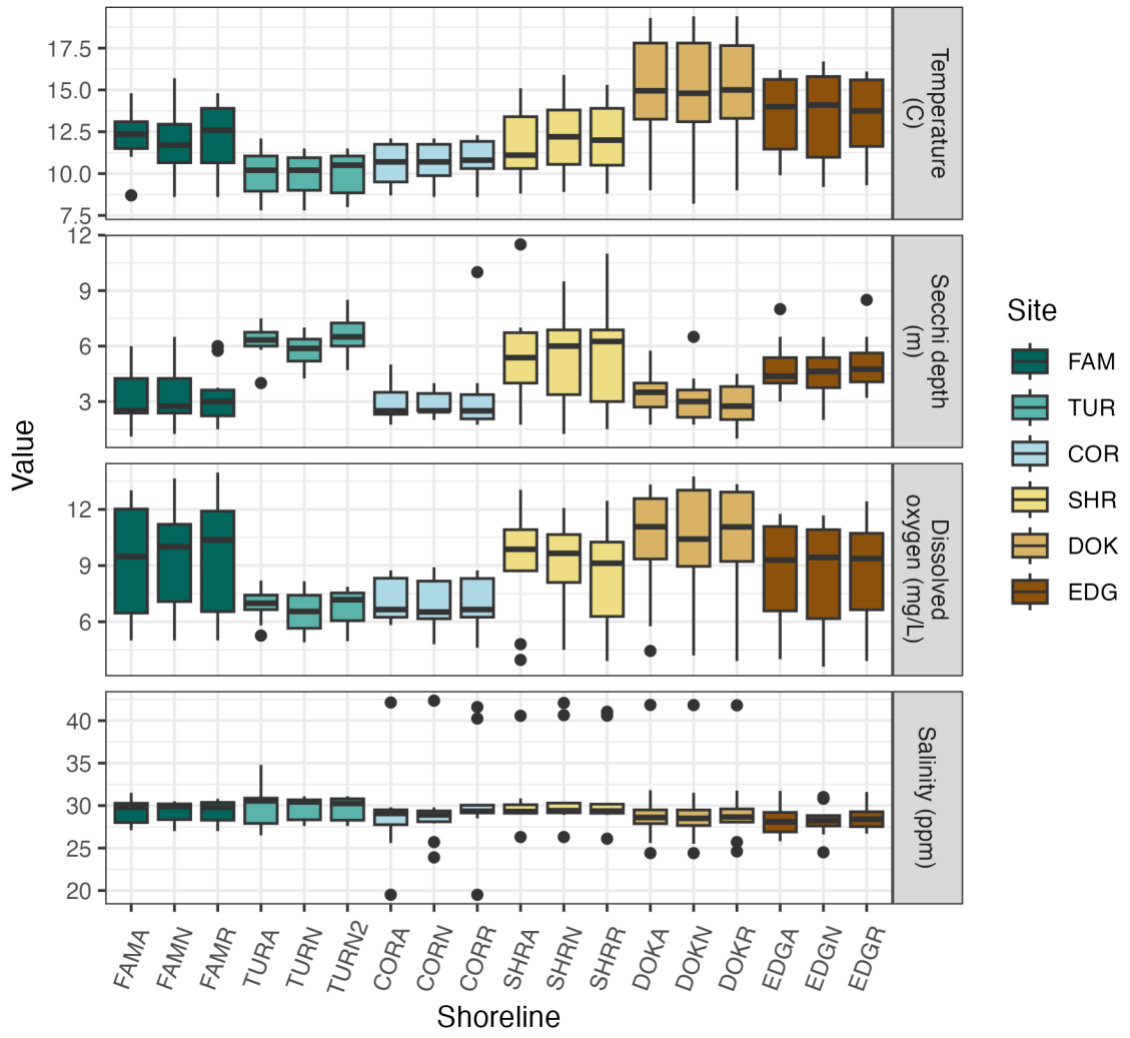

Fig S2 Water quality measurements by shoreline for a given metric. Points represented measurements collected monthly between April and September in 2021 and 2022 at each shoreline. Shorelines are identified by their site (codes in main text Figure 1) and shoreline condition category (A = Armored, N = Natural, R = Restored). Boxplots show the median value and the interquartile range.

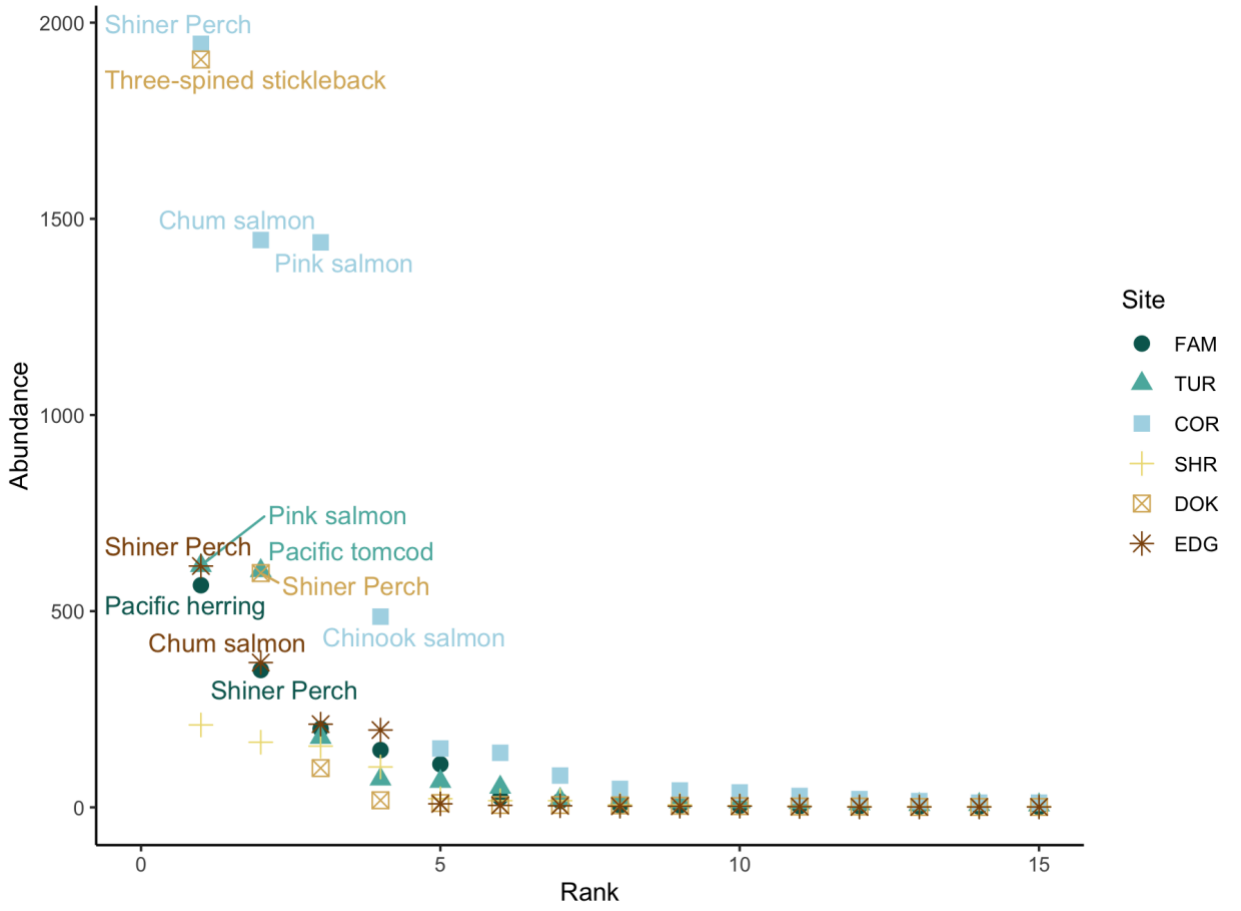

Fig S3 Rank abundance curve of raw species abundances grouped by site. Rank values above 15 have been excluded to ease interpretation of lower rank values.

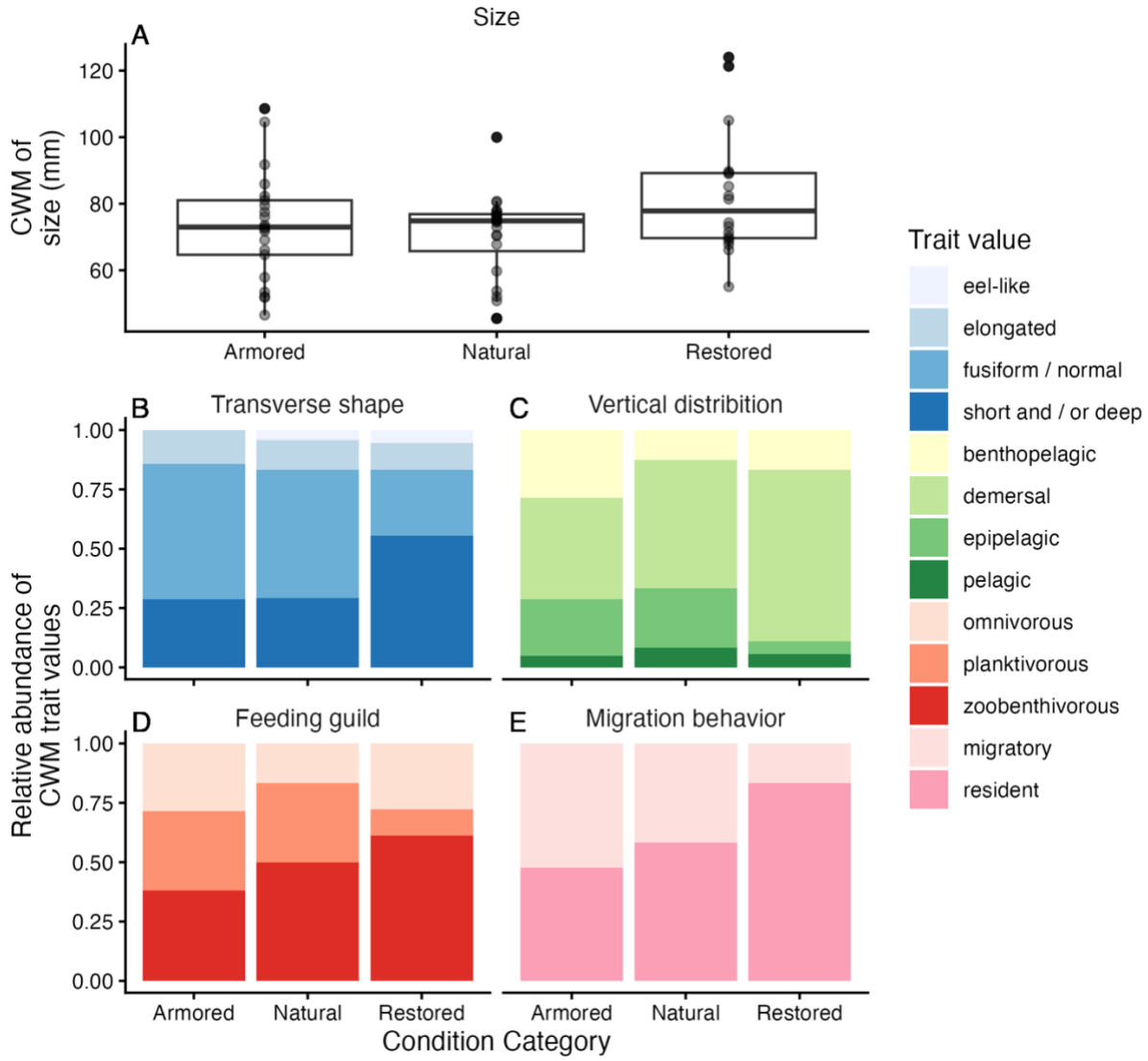

Fig S4 Community-level weighted mean (CWM) trait values associated with nearshore fishes in the Salish Sea. Catch data for fish is summarized in samples, where each sample represents the summed catch at each shoreline segment for a given year (n = 84 Armored, 96 Natural, and 72 Restored). This figure displays samples grouped by shoreline condition category, which describes the history of anthropogenic impact at each shoreline segment. The CWM for size (A), the only continuous trait, is a weighted average of the mean length values for fishes in a given sample. CWM for the categorical traits (B-E) is the trait value with the highest abundance in each sample and is displayed here as the proportion of samples when the CWM was a given trait value.

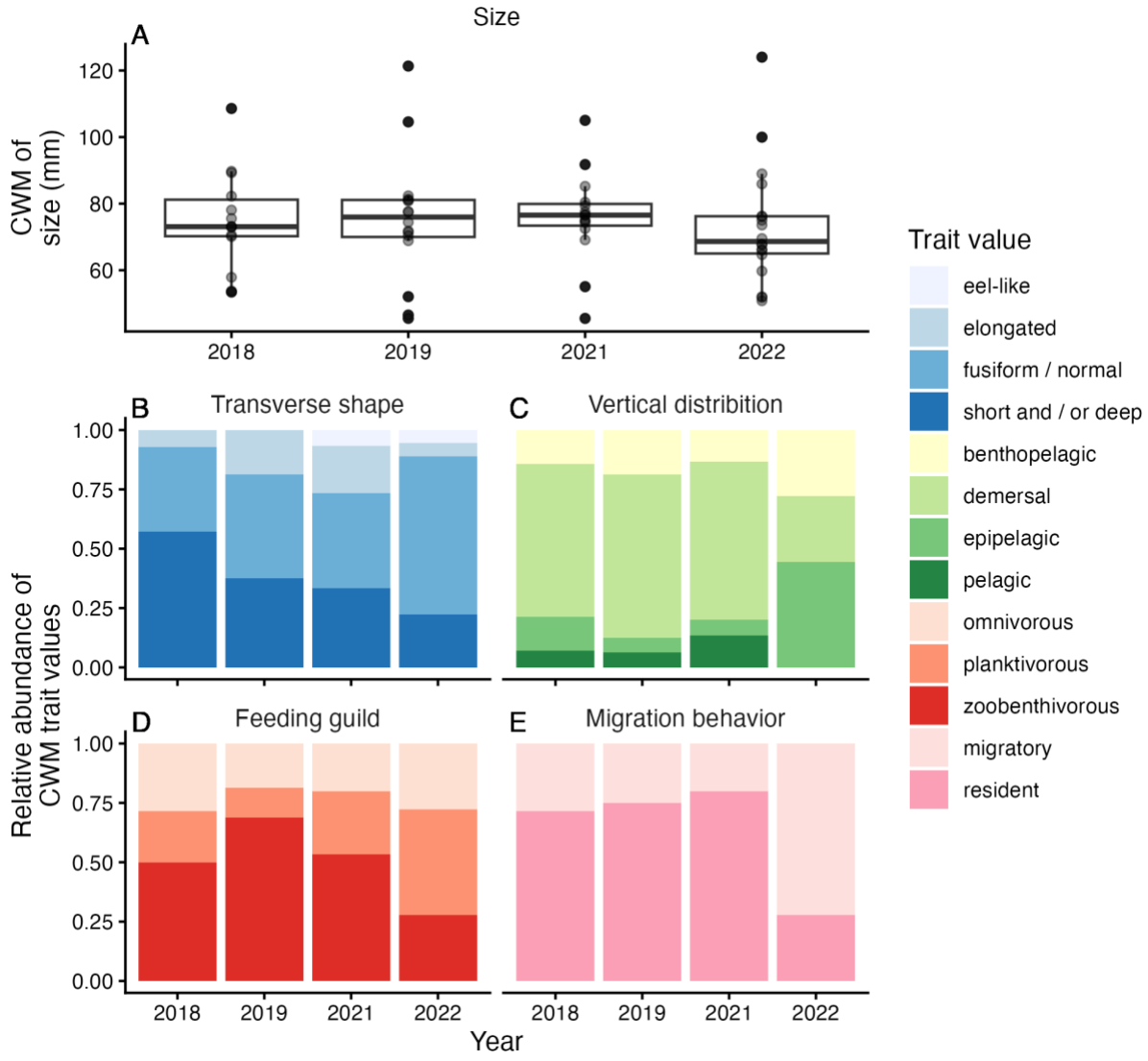

Fig S5 Community-level weighted mean (CWM) trait values associated with nearshore fishes in the Salish Sea. Catch data for fish is summarized in samples, where each sample represents the summed catch at each shoreline segment for a given year (n = 56 in 2018, 64 in 2019, 60 in 2021, and 72 in 2022). This figure displays samples grouped by year. The CWM for size (A), the only continuous trait, is a weighted average of the mean length values for fishes in a given sample. CWM for the categorical traits (B-E) is the trait value with the highest abundance in each sample and is displayed here as the proportion of samples when the CWM was a given trait value.

CHAPTER 3 APPENDIX

See attached excel file.

CHAPTER 4 APPENDIX

Appendix A. Interview methods and responses

Interview methods

We conducted semi-structured interviews with staff of governments involved in co-management of the Puget Sound Dungeness crab fisheries. We consulted the Pacific Northwest Crab Research Group and the Northwest Indian Fisheries Commission to identify staff at different governments who would be able to speak to the current fishery management structure and potential future threats to the fisheries. We used the list of contacts they provided to reach out via email to individuals at the Washington State Department of Fish and Wildlife, 14 Puget Sound Treaty Tribes, and one Tribal consortium called Point No Point Treaty council, which provides natural resources management services to two member Tribes. We received responses from the state and 13 Tribes, and the Tribal consortium, and successfully conducted 15 interviews with 18 staff members: the two from the state, and 15 from 12 different Tribal governments, and one from Point No Point Treaty Council. Respondents were comprised of fishery managers, biologists, and policy representatives, depending on who at each government participates in work related to Dungeness crab research and fishery management.

One important caveat to the results of these interviews is that all the staff interviewed in this study are operating within a management framework where goals are set at a higher policy level. At the state level, the governor-appointed Fish and Wildlife Commission sets policy for the Washington Department of Fish and Wildlife. This includes, for example, decisions about how much of the state's allocation to reserve for recreational or commercial fishing. The state also has an advisory panel made up of members of the public that meets annually to weigh in on management of the recreational fishery. For Tribes, policy is set by Tribal Council and Fish Committees. When fishery management decisions require policy level input, policy representatives are invited into discussions between co-managers and technical staff. Therefore, it's important to note that feedback on goals of the fisheries described by staff interviewed for this project represent a subsample of the perspectives that ultimately shape fisheries management in this region. Here, they serve as a representation of the potential range of viewpoints that participants in this management system hold.

We developed a set of questions aimed at understanding the Puget Sound Dungeness crab fisheries under three themes: goals, threats, and system structure (Appendix B). These themes encompassed the goals of respondents when participating in co-manager negotiations, their perceived future threats to the fishery given uncertainty in future environmental conditions, potential weaknesses in the current system structure, and opportunities to improve it. We conducted pilot interviews with three people knowledgeable about the fisheries, then conducted formal interviews between June and August 2025. Each interview lasted between 1 and 2.5 hours. With permission from all respondents, we used voice recording and transcription software to record all conversations then reviewed transcripts for relevant quotes and summarized main themes. This project was deemed Exempt by the University of Washington Institutional Review Board.

Interview responses

Many interview respondents identified high level potential future threats related to climate change, such as increasing water temperatures, increased ocean acidification, and lower oxygen conditions impacting Dungeness crab population health. However, the ultimate impacts of these threats are unknown, because so little is understood about how the compounding and likely nonlinear interactions among multiple threats will manifest. Because of this uncertainty, respondents commonly assigned higher priority to understanding the ability for 3-S management system to support sustainable populations of Dungeness crab under scenarios of current threats that have known impacts. Respondents cited several threats that have the potential to cause fishery performance decline, including threats that may violate key assumptions of the 3-S management system, even when harvest is successfully controlled by rules related to size, sex, and season. We developed a conceptual diagram (Figure 2) to visualize these mechanisms. Threats that may lead to a decline in fishery performance are displayed as two categories that specify whether the 3-S system is being followed. Boxes with dashed outlines are more hypothetical than the boxes with solid outlines, which are tied to mechanisms that represent a commonly held opinion (e.g., recruitment limitation) or have been empirically tested (e.g., handling mortality is higher on soft crab).

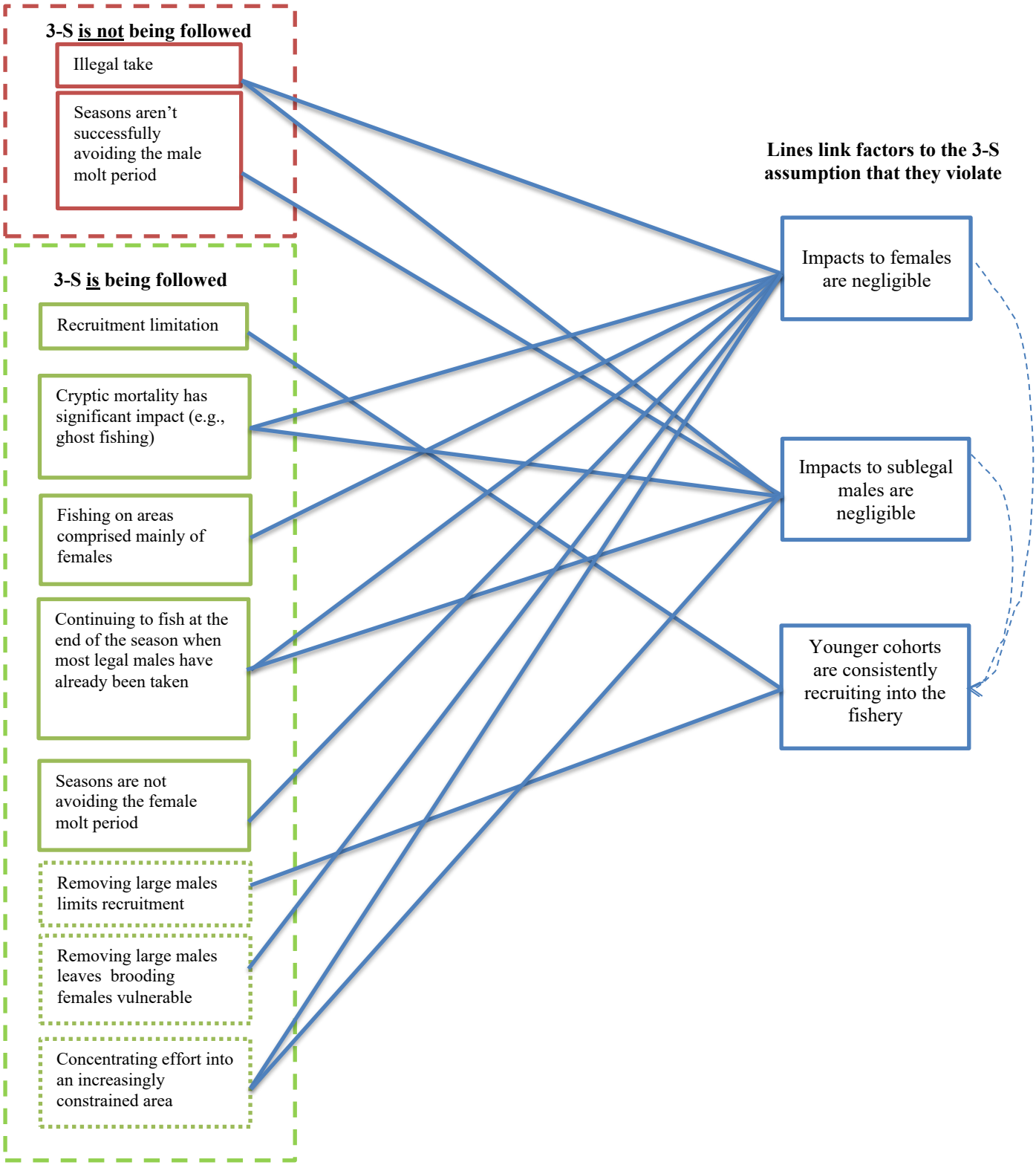
3-S is not being followed
Illegal take
Seasons aren't successfully avoiding the male molt period
3-S is being followed
Recruitment limitation
Cryptic mortality has significant impact (e.g., ghost fishing)
Fishing on areas comprised mainly of females
Continuing to fish at the end of the season when most legal males have already been taken
Seasons are not avoiding the female molt period
Removing large males limits recruitment
Removing large males leaves brooding females vulnerable
Concentrating effort into an increasingly constrained area
Lines link factors to the 3-S assumption that they violate
Impacts to females are negligible
Impacts to sublegal males are negligible
Younger cohorts are consistently recruiting into the fishery

Figure A1. Conceptual diagram representing mechanisms by which the performance of the Puget Sound Dungeness crab fisheries may decline under the current management system. Boxes on the left side with solid lines are mechanisms that represent a commonly held opinion (e.g., recruitment limitation) or have been empirically tested (e.g., handling mortality is higher on soft crab). Boxes on the left that have a dotted outline were identified as respondents as being more hypothetical. Lines link mechanisms to the assumption of the current management system (3-S) that is violated by these mechanisms. Dashed lines on the right signify that impacts to the population spawning biomass could reduce the abundance of younger cohorts recruiting into the fishery.

We included cases when 3-S is not being followed to capture threats described by respondents that may be currently impacting the resource, essentially due to imperfect implementation of the 3-S system. Although illegal fishing is thought to be minimal in the Treaty and state commercial fisheries, many respondents expressed concern over illegal harvest from state recreational fishers. The other threat in this category was related to the male molt period because while the current process for setting fishing seasons was designed to avoid the peak male molt period, there are a few cases when it may not achieve that goal. For instance, test fisheries are conducted by the state and Tribes to ensure a majority of crab have hard shells when fisheries are open, but most test fishing occurs before the annual fishing season opens, not during. There is evidence that some proportion of crab molt throughout the year, so there may be cases when the fishery remains open even with high proportions of soft male crab. Prolonged co-manager negotiations may also lead to fishing at less ideal times when the proportion of soft males is higher, even if it is still within the acceptable limit.

There are several ways that key assumptions of the 3-S management system may be violated, even when harvest is successfully being limited by size, sex, and season. With respect to recruitment limitation, respondents were primarily concerned about areas that may have limited input from the coastal larval supply that is known to supplement some of the most productive areas in the Sound. Low productivity in a local population over multiple years may result in too few recruits surviving to maturity to sustain the population, particularly if fisheries are removing larger males. Other threats concern impacts to the population spawning biomass for the same reason. The 3-S management system is designed to avoid impacts to females and sublegal males, which are then available to reproduce and maintain sufficient recruitment to sustain fisheries. However, respondents identified multiple potential pathways that the spawning biomass may be impacted.

One of these pathways includes cryptic sources of mortality, the primary example being ghost fishing. Ghost fishing occurs when lost fishing gear becomes derelict and causes mortality, which has well known and large impacts in this system. Mortality can result from individuals becoming entrained and starving or experiencing cannibalism. Fishing gear can be lost in strong currents, deep water, or areas of high boating traffic particularly if fishers are inexperienced in finding suitable areas to set pots. Respondents identified this threat because not only could ghost fishing reduce the number of legal-size males available to the fisheries, but it may also reduce the population spawning biomass, and associated recruitment potential, if a high enough proportion of females and sublegal males are experiencing mortality.

In some areas, like Dabob Bay and Saratoga Passage, unpublished data from test fisheries indicate that the sex ratio has shifted over time to being almost entirely females. One of the threats identified by respondents was fishing on areas comprised mainly of females, because allowing fishing in these areas could be perpetuating high incidental mortality from handling injury if females are repeatedly caught and returned to the water. Aggregations of females may not be an issue on the coast where the primary fishery is commercial, and commercial fishermen have the expertise to avoid areas with females, but it could be a much larger issue in Puget Sound where there is a strong recreational fleet. Recreational fishers might not have the local knowledge to avoid females, and respondents from the state suggested that recreational fishers are often motivated by spending time on the water more than having abundant catches to bring home. Recreational fishers are also likely to have strong geographic affinity based on water access.

Sublegal males and females may be impacted when the fishery remains open even after most legal males have been taken. Interview respondents identified continuing to fish when most legal males have been removed from the system as a threat and referred to it as "scratch fishing" or "scratching for the last legal males." Commercial fishers may continue to fish even when catch rates are low if the price per pound is high. Recreational fishers may continue to fish when catch rates are low because they value the experience of being on the water more than catching many crab. In either case, continually deploying pots exposes females and sublegal males to incidental mortality from handling. Anecdotally, respondents also referenced that sublegal males are more likely to enter a pot if it does not contain large males, so catchability for sublegals may be increased when legal males have been fished out.

Similarly, females may be subject to high handling mortality if fishing occurs during periods when higher proportions of females are soft. For this reason, respondents identified fishing seasons that do not avoid the female molt period as a threat. As noted, the management system in Puget Sound was designed to avoid the male molt period, but it does not necessarily avoid the female molt period. Respondents commonly noted that females molt at different times from males, based on observations and an understanding that for the mating embrace, females need to be recently molted and males need to have hard shells.

The hypothetical threats to the fishery involved largely similar mechanisms as have already been discussed. Respondents hypothesized that removing large males limits recruitment because females are thought to require males with a larger body size than themselves for spawning. Selecting for large males in the fishery may therefore reduce the spawning potential of females, even if the abundance of females should be enough to support recruitment to sustain fishing. Respondents also hypothesized that removing large males may leave females remaining in the system vulnerable because males are thought to exhibit brooding behavior and protect females post-spawning. Without this protection, females may experience higher natural mortality. Finally, respondents hypothesized that if cumulative threats to the fishery are resulting in a lower abundance of legal-sized males, fishing effort may concentrate where legal-size males are available. This could result in localized depletions and situations where females and sublegal males in a given area are repeatedly captured and therefore experience higher incidental mortality.

Appendix B. Semi-structured interview questions

Goals

- Fishery management often aims to achieve multiple outcomes. What are the values of your constituents for Dungeness crab fisheries?
- What are the broader set of goals [e.g., financial or related to access] that you have when it comes to the Dungeness crab fisheries that you represent when you go to the negotiating table?
- What are some outcomes that, if present, would make the Dungeness crab fishery management system successful?
- What are some outcomes that, if present, would represent a failure of the management system?
- Are some outcomes more important than others?

Threats

- As a manager of the Dungeness crab fisheries, you are responsible for working with other co-managers to operate a system intended to ensure that fisheries are sustainable. Currently, Dungeness crab fisheries are managed under the 3-S management system, where catch is limited based on rules related to size, sex, and season. We do not know if this system will be robust to environmental changes in Puget Sound and continue to provide desired outcomes of the management system. This project aims to gain information on the threats that environmental change poses to Dungeness crab populations and fisheries, and how those threats might impact the performance of the 3-S management system. When we say threats, we mean plausible future changes to a fishery that might impair the ability to provide desired outcomes. What comes to mind when you think about potential threats to the Dungeness crab population in Puget Sound, given unprecedented environmental conditions?
- Are there any scenarios under which you question the efficacy of the 3-S system?
- We are unable to address every threat to the fishery management system in our study, so we will have to choose a subset to focus on. The choice of this subset will be made based on the likelihood that a threat happens, and the size of its impact.
- Which threats would you like to see in this subset?
- Through what pathways do you think that this threat will impact the crab population? For example, do you expect low recruitment to result in increased mortality for juveniles that prey on smaller crabs?
- Do you think this threat will occur as an extreme event? Or would it manifest more like a “new normal”? Or both?

- How would you expect fishers to respond?

System Structure

- Part of this work is to explore not only plausible threats, but potential solutions. What amendments to the current management plan do you see as potential options to increase the likelihood of meeting management goals?

Appendix C. Model sensitivity to density dependent catch parameters

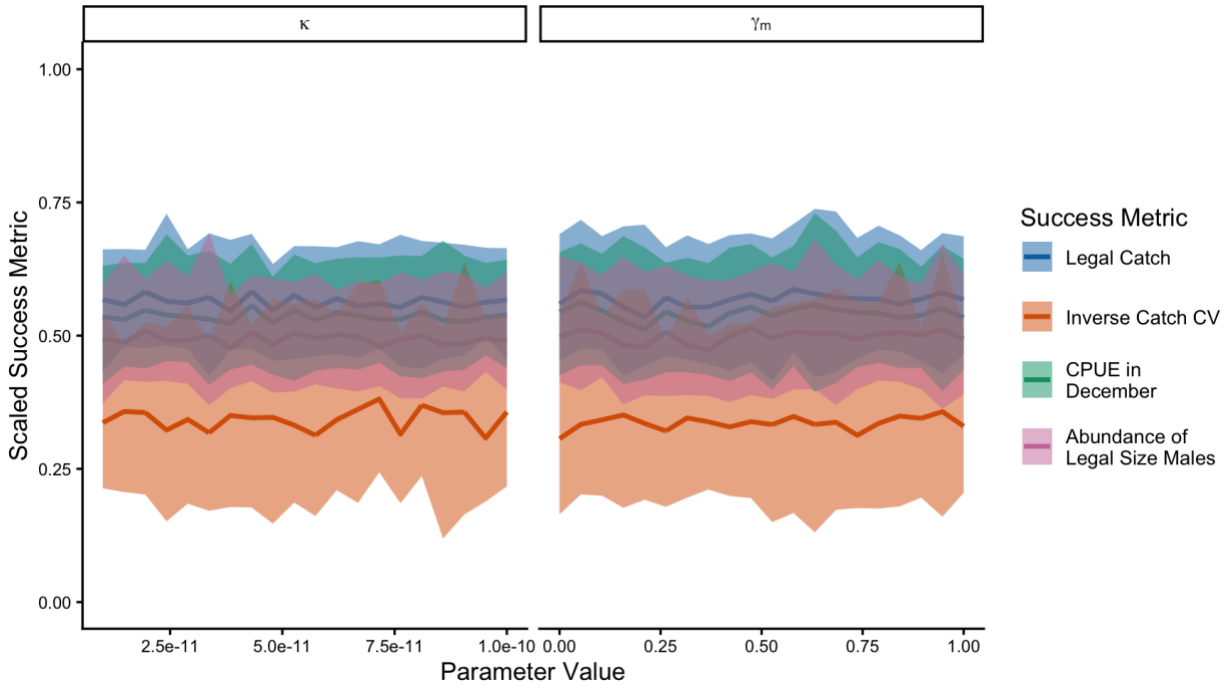

Figure C1. Performance of the model when individual parameters related to density-dependent catch are perturbed and all other parameters are set at nominal values, effort = F_{MSY}, and p = 1. These parameters included the amount that the catchability of sublegal males was reduced relative to the catchability of legal size males (γ_q), and the slope of the relationship between the abundance of larger males and the catchability of age 3 males (κ). Success metrics are average values over 100 model years, with 50 replicates per parameter value. The values for each success metric are scaled relative to the maximum value observed for each metric. The dark line shows the median value across all replicates and the shaded area represents the 95% prediction interval. Parameter descriptions are given in Table 1.

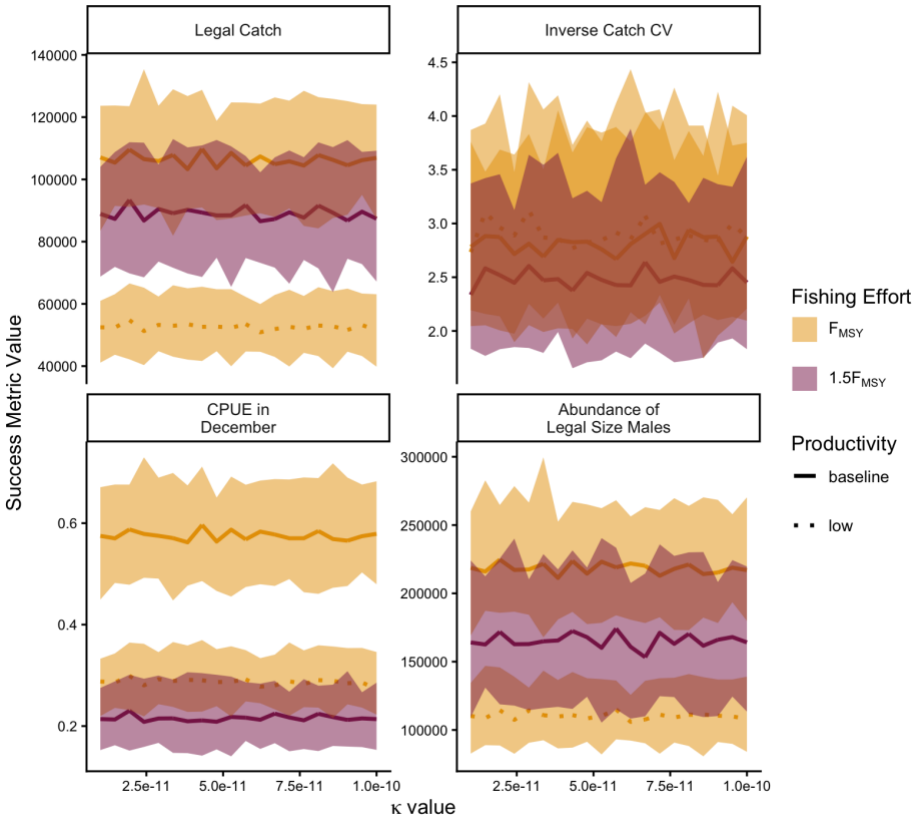

Figure C2. Performance of the model assessed vs the slope of the relationship between the abundance of larger males and the catchability of age 3 males (κ) for different fishing and productivity levels. Success metrics are average values over 100 model years, with 50 replicates per parameter value. The shaded area represents the 95% prediction interval.

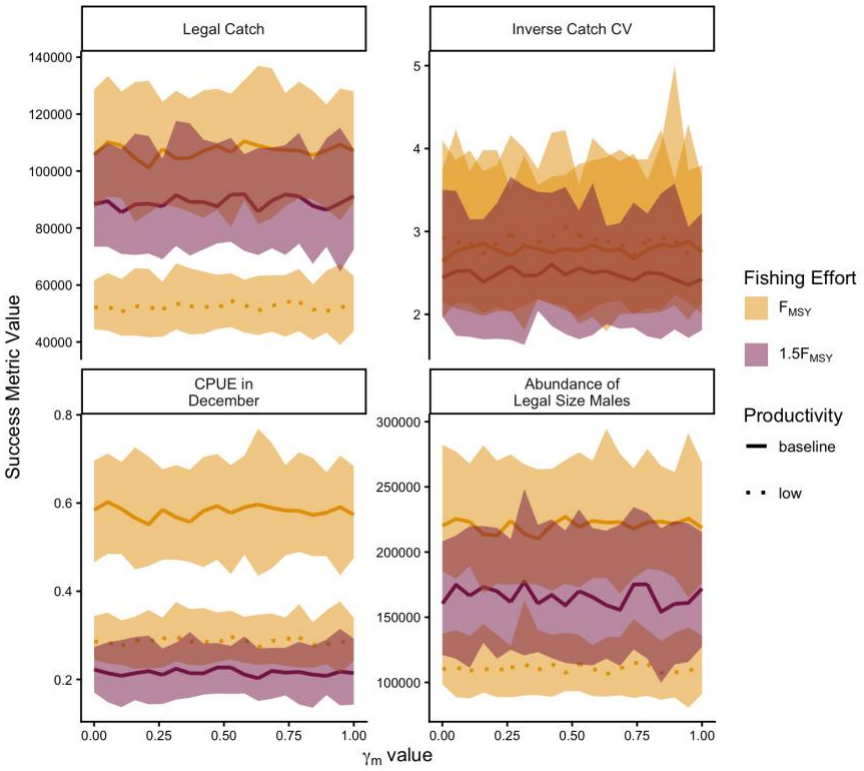

Figure C3. Performance of the model assessed vs the amount that the catchability of sublegal males was reduced relative to the catchability of legal size males (γ_m) for different fishing and productivity levels. Success metrics are average values over 100 model years, with 50 replicates per parameter value. The shaded area represents the 95% prediction interval.

Appendix D. Management strategy performance at baseline productivity

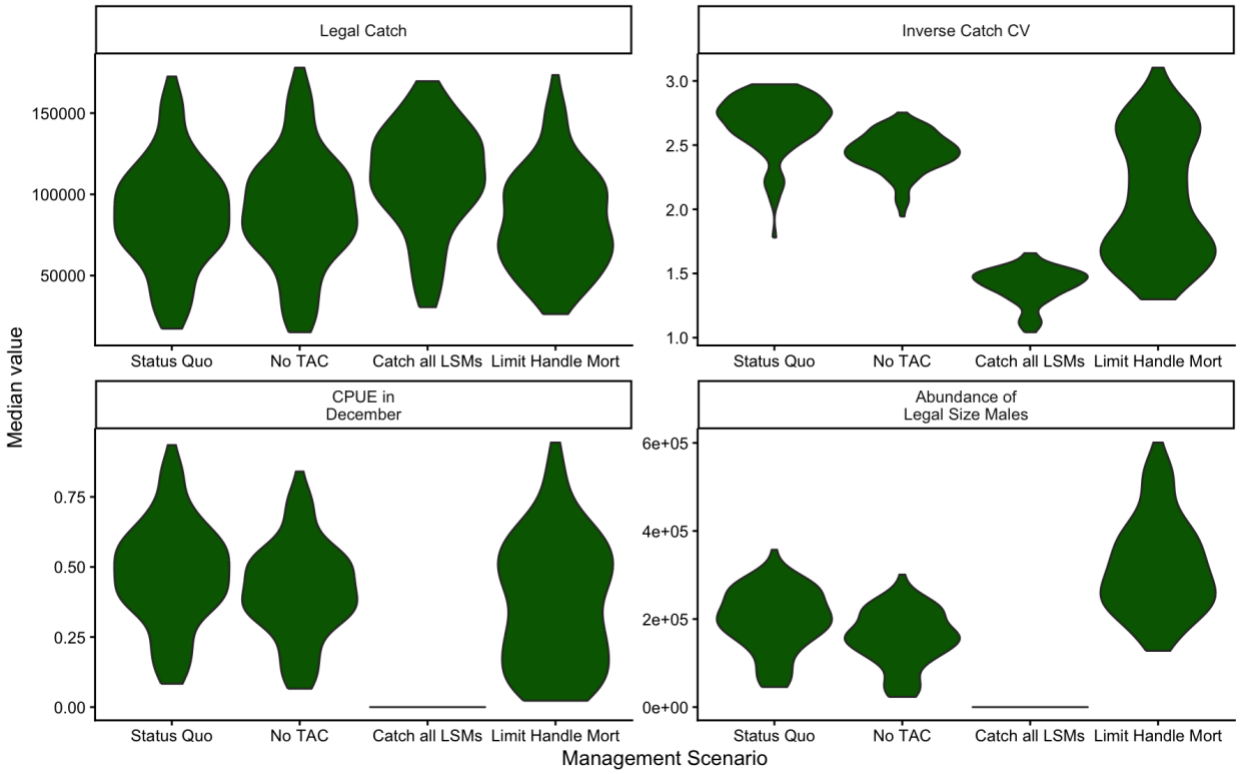

Figure D1. Violin plots showing the distribution of median success metric values from 100 combinations of randomly simulated parameter values. Success metric values were averages from 50 replicates of each parameter combination.

Appendix E. Monte carlo under low productivity conditions

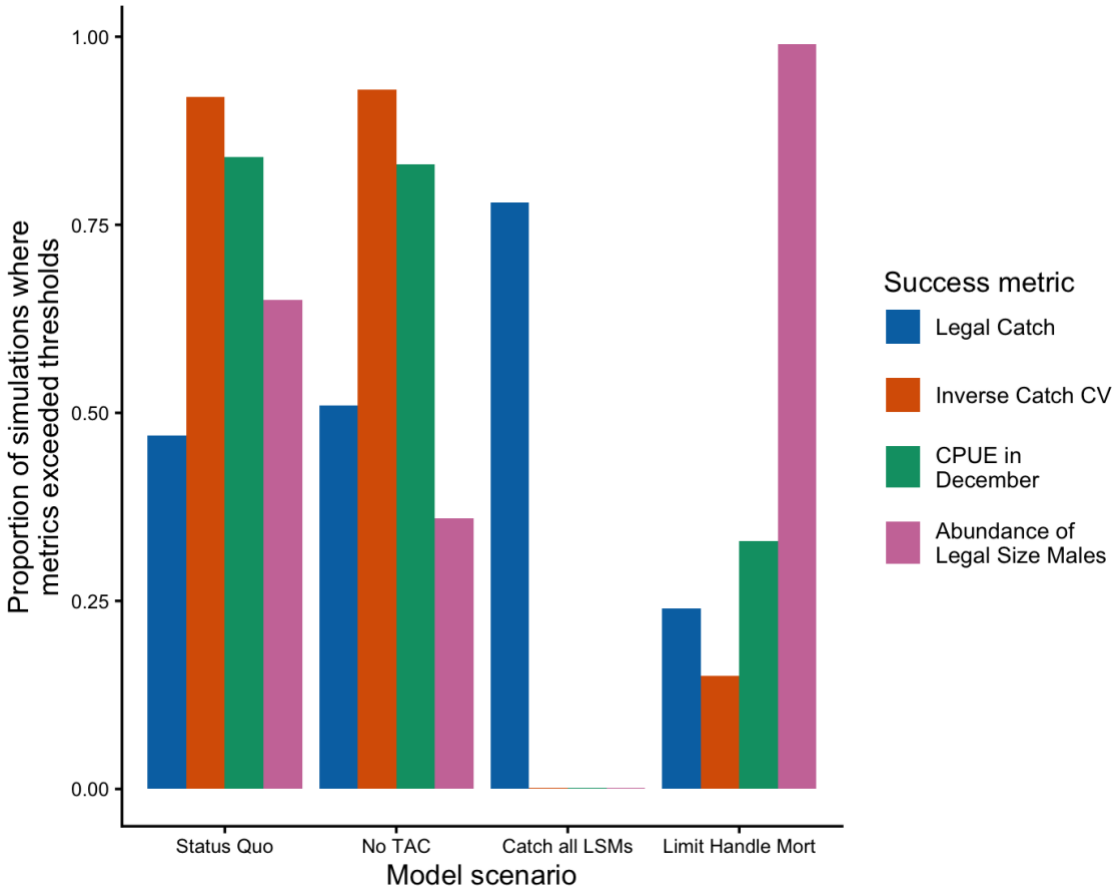

Figure E1. Proportion of successful simulations under multiple success criteria across three management scenarios and one scenario where under the Status Quo management strategy, the catchability of legal sized males = 1. Thresholds for each metric were calculated the 50th percentile metric value among all scenarios.