

THE ROLE OF APEX PREDATORS, HABITAT, AND SEASCAPE COMPLEXITY ON
NEARSHORE FISH ASSEMBLAGES IN SOUTHEAST, ALASKA

By

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Abstract

Nearshore marine ecosystems contain dynamic and complex submerged vegetated habitats that offer shelter and prey for juvenile, migratory, and residential species, including many commercial, subsistence, and recreationally important species. The efficacy of the nursery role, shelter, and source of prey of the nearshore is influenced by various abiotic and biotic forces and in this dissertation, we examine the influence of submerged vegetation type, presence of apex predators, and the seascape context on patterns of nearshore fish assemblages in southern Southeast Alaska. We found species-specific responses by juvenile salmon in the nearshore, with seasonality overwhelmingly driving juvenile salmon abundance in eelgrass meadows and Chum Salmon present in greater abundance in understory kelp beds compared to eelgrass meadows, whereas Pink Salmon exhibited no difference. As a known apex predator, the reintroduction of sea otters likewise altered the nearshore fish assemblage with increased richness in eelgrass meadows and assemblage-wide shifts in understory kelps. Finally, in addition to habitat type and apex predators, spatial patterning and presence of adjacent vegetation can affect the nursery role of nearshore habitats. We observed differences in the fish assemblage in eelgrass meadows sampled in homogeneous seascapes with continuous eelgrass meadows and heterogeneous seascapes that included adjacent habitats, including more abundant commercial and forage species in heterogeneous seascapes. This research reinforces the importance of nearshore ecosystems in supporting robust fisheries and highlights the structuring role that submerged vegetation, apex predators, and complex seascapes have in sustaining diverse fish populations. Considering the greater ecological dynamics in the nearshore is vital for decision making in habitat conservation and management and for evaluating its role for fisheries, particularly in the context of increased threats to nearshore ecosystems.

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Chapter 1: General introduction

Nearshore shallow-water (< 6 m) marine ecosystems are some of the most diverse and productive ecosystems in the world. High primary production along the coast supports a variety of organisms including invertebrates, fishes, and submerged vegetation and confer auxiliary benefits to humans. Nearshore habitats serve as nurseries for marine species, promoting recruitment, predator avoidance, foraging opportunities, and enhancing survival (Heck Jr. et al. 2003, Beck et al. 2006, Semmens 2008, Lefcheck et al. 2019). Various abiotic and biotic forces influence the productivity and nursery role of the nearshore including the type and quality of nearshore submerged vegetation, wave exposure, species dispersal and connectivity, presence of apex predators, spatial patterning of habitat patches, and seascape attributes. This dissertation explores several of these factors including comparisons of nearshore submerged vegetation, presence and abundance of apex predators, and the nearshore seascape attributes and habitat heterogeneity, and examines their synergistic impact on nearshore fish assemblages.

Temperate nearshore waters contain structurally complex vegetation including seagrasses, algae-forming beds, and canopy kelps as well as unvegetated patches such as high-relief rocky shorelines, gravel and/or sandy substrate. In addition to supporting robust and diverse organisms, submerged vegetation provides ecosystem services. Seagrasses are marine flowering plants with rhizomes that anchor it in soft-sediment areas (Arber 1920, Short et al. 2007) and can play roles in carbon sequestration (Fourqurean et al. 2012, Duarte et al. 2013), sediment stabilization, water clarity improvement (Orth et al. 2006), and wave attenuation and larval settlement (Eckman 1983, Orth et al. 2006). Kelps, brown macroalgae (order Laminariales), similarly are important foundation species with roles in primary and secondary

production, energy subsidies to nearby ecosystems, and habitat formation for juvenile and adult fishes as well as other organisms (Mann 1973, Anderson and Millar 2004, Olson et al. 2019).

Due to their structural complexity and productivity, nearshore regions form coastal habitats for fishes. While unvegetated patches can be important predator refuge for certain species (Pinto et al. 1984), submerged vegetation is more often lauded as nursery grounds for invertebrates and fishes (Dean et al. 2000, Beck et al. 2001, Heck Jr. et al. 2003, Lefcheck et al. 2019). In Alaska, eelgrass (*Zostera marina*) is the dominant seagrass in soft-sediment habitats and in Southeast Alaska often occurs as narrow fringing beds along the coastline (McRoy 1968). The other two dominant structured habitats include understory kelps that grow in dense mats, and canopy kelp forests that generally occur along more exposed and rockier substrates than eelgrass.

Ecologically, commercially, and culturally important species such as herring, rockfish, and salmon use nearshore habitats for protection, the enhanced food availability they confer, or as spawning grounds. Herring will often use submerged vegetation, like kelps, as spawning habitat during late spring (Haegele 1985). Juvenile rockfish in Southeast Alaska use shallow nearshore vegetated habitat, both understory kelps and eelgrass, for habitat during the summer and early fall (Murphy et al. 2000). Rockfish recruit to nearshore shallow habitats before moving out into deeper waters (Love et al. 1991, Murphy et al. 2000). For salmon (*Oncorhynchus* spp.), nearshore habitats such as estuaries and eelgrass meadows are commonly highlighted as important habitats for juveniles during the physiologically difficult and life-threatening transition from freshwater to marine waters (Levings 1994, Thorpe 1994). Therefore, juvenile salmon are often present in estuaries and nearshore habitats, including eelgrass meadows (Shaffer 2004, Dumbauld et al. 2015, Kennedy et al. 2018, Lundstrom et al., 2022). In Washington and British

Columbia eelgrass can provide ample prey and protection from predation during outmigration from rivers (Simenstad et al. 1982, Semmens 2008, Kennedy et al. 2018). Additionally, the algal abundance and species diversity can structure and influence fish communities (Efird and Konar 2014). Finally in addition to fishes, mammals, such as harbor seals, sea otters, and humans all frequent these nearshore ecosystems to find prey (Estes and Duggins 1995, Hughes et al. 2013, Luxa and Acevedo-Gutierrez 2013). Overall, submerged underwater vegetation is used by different fishes for protection, spawning, recruitment, and for foraging.

Despite seagrasses and kelps being found on almost every continent and their ecological importance, they are vulnerable to disturbance. Seagrasses have been declining worldwide due to decreased water clarity, grazing, nutrient and sediment loading, pollution, fishing practices, and disease (Short and Wyllie-Echeverria 1996, Hall et al. 1999, Duarte 2002). Kelps have experienced declines globally (Krumhansl et al. 2016) and specifically along the Eastern Pacific west coast connected with increased temperatures and food web alterations (Estes et al. 2004, Starko et al. 2019).

Apex predators and keystone species, like sea stars (*Pisaster ochraceus* or *Pycnopodia helianthoides*) and sea otters (*Enhydra lutris*), alter food webs and, through changes in their populations, have a disproportionately large ecological role in kelp and seagrass ecosystems (Estes and Palmisano 1974, Paine 1980, Estes et al. 2011, Hughes et al. 2013). Through strong linkages between ecosystem community members, changes in abundance of apex predators that serve as keystone species can cause phase shifts. Sea otters are one such apex predator and play a role in kelp forest ecology through their ability to reduce sea urchins resulting in prolific increases of canopy forming kelp forests extent (Estes and Duggins 1995). In California, Hughes et al. (2013) found that in seagrass meadows, sea otters, through their consumption of crabs,

released herbivores from depredation allowing increased consumption of seagrass epiphytes that have previously been inhibiting growth of seagrass meadows. This resulted in healthier seagrass meadows. In Southeast Alaska Raymond et al. (2021) found an increase in eelgrass biomass where sea otters were more abundant but did not find all the hypothesized relationships for a trophic cascade. Indirectly through physical disturbance while digging for clams in eelgrass meadows, sea otters have increased the eelgrass genetic diversity through boosting sexual rather than asexual reproduction of the plants (Foster et al. 2021) and increased plant growth potentially tied to removing below-ground competitors (Saavedra 2021).

In the Pacific, sea otter recovery and subsequent population growth is a successful conservation example. Historically, sea otters were present from Japan along the Aleutian chain down through southern California until commercial hunting during the maritime fur trade extirpated the population in many places, including Southeast Alaska (Kenyon 1969). In the 1960's, 412 sea otters were reintroduced in Southeast Alaska and have expanded to a population of approximately 22,000, still well below the proposed carrying capacity of 74,650 (CI = 36,778 - 136,506) sea otters (Tinker et al. 2019, Schuette et al. 2023). Legal hunting of sea otters continues to be practiced by the Indigenous people of coastal Alaska and can keep sea otters out of traditional harvest areas, but has a low-level impact on sea otters at the stock (i.e. Southeast Alaska-wide) scale (Raymond et al. 2019). The combination of the re-introduction, subsequent recolonization of new coastlines, and legal harvest of sea otters created a gradient of sea otter density as well as areas with and without sea otters. This spatial heterogeneity in sea otter occupation allows us to investigate the indirect influence of sea otters on nearshore fish assemblages. In Chapter 2, we explore the nursery role of nearshore habitats and the impact of apex predators on juvenile salmon (*Oncorhynchus* spp.), a culturally and commercially important

species as well as an iconic feature of Alaska’s waters. Chapter 3 disentangles the effect of time and sea otters on fish assemblage composition in eelgrass and understory kelp beds by employing historical and contemporary data in areas where sea otters have and have not recolonized over time.

While apex predators may impact nearshore fish assemblages, these habitats (eelgrass and understory kelps) are situated in a matrix of adjacent habitats. This mosaic of interconnected habitats can alter species survival and drive species distribution and nearshore biodiversity depending on the spatial composition and heterogeneity of the nearshore. Seascape ecology uses a conceptual framework to interpret ecological patterns in the context of complex spatial patterning of marine environments (Pittman et al. 2011, Pittman 2017). While employing a seascape approach to better understand temperate nearshore ecology is becoming more common (Staveley et al. 2017, Perry et al. 2018, Olson et al. 2019, Proudfoot et al. 2023), no studies to our knowledge have applied it to contextualize and understand Alaskan nearshore fish assemblages. Chapter 4 investigates habitat heterogeneity surrounding eelgrass meadows and its influence on eelgrass-associated fish assemblages.

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Chapter 2: Juvenile Chum and Pink Salmon use of submerged vegetative habitats in Southeast Alaska¹

2.1 Abstract

Apex predator initiated trophic cascades occur in many nearshore marine habitats including eelgrass meadows and kelp forests and simultaneously serve as critical refuge, habitat, and food source for commercially and ecologically important juvenile and adult fish species, including salmon (*Oncorhynchus* spp.). Yet the potential relationships among apex predators such as sea otters (*Enhydra lutris*), submerged vegetated habitats, and juvenile salmon are not well understood. We investigated 1) juvenile salmon abundance in eelgrass meadows and understory kelp beds in Southeast Alaska using data from historical NOAA surveys (sampled 1998- 2007) and 2) potential drivers of juvenile Chum (*Oncorhynchus keta*) and Pink Salmon (*O. gorbuscha*) abundance in Southeast Alaska eelgrass meadows, including seasonality, sea otter density, eelgrass biomass, and distance from anadromous stream outlets. We found greater abundance of juvenile Chum Salmon in understory kelp compared to eelgrass, whereas Pink Salmon abundance did not differ between habitats. Pink Salmon abundance in eelgrass meadows showed strong seasonality and was positively associated with sea otter density, distance from anadromous stream, and negatively associated with eelgrass biomass, while seasonality and sea otter density were most important for explaining Chum Salmon abundance. Growth and survival while juvenile salmon are out-migrating from streams and relying on nearshore vegetated habitats can determine if salmon recruit to fisheries as adults, thus understanding driving forces,

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like apex predators and vegetated habitats in the nearshore is critical for informing adaptive coastal and fisheries management.

2.2 Introduction

Nearshore marine ecosystems have high primary productivity, support a diverse community of organisms, and in particular submerged vegetated habitats are considered critical nursery habitats for various species. As such, coastal regions are an important yet convenient location to examine the role of biotic and abiotic forces on ecologically and commercially key species. Juvenile salmon, are one such group of species that migrate through the nearshore marine environment, including eelgrass beds and kelp forests, as they transition from freshwater to marine life stages (Murphy et al. 2000; Beck et al. 2001; Shaffer 2004; Kennedy et al. 2018). These salmon are ephemeral yet abundant features of springtime nearshore fish communities in Southeast Alaska. The early marine juvenile phase is a critical time-period for growth and can influence survival to adulthood (Beamish et al. 2004). Juvenile salmon use of nearshore habitats varies by species. Juvenile Coho (*Oncorhynchus kisutch*), Chinook (*Oncorhynchus tshawytscha*), and Sockeye Salmon (*Oncorhynchus nerka*) are caught more frequently in nearshore vegetated habitats compared to open-water, rocky or sandy habitats in British Columbia (Sharpe et al. 2019). Chum Salmon may be less discriminatory in southern Southeast Alaska, as they are present in similar frequencies in understory kelp (53%), eelgrass (46%), sand/gravel (53%), and bedrock (33%) (Johnson et al. 2012). Juvenile Pink Salmon have the highest frequency of occurrence in bedrock (78%) compared with the other three habitats (31% in eelgrass, 38% in understory kelp, and 53% in sand/gravel). The relationship between juvenile salmon and nearshore habitats can be altered through external forces including apex predators that exert

strong driving forces in ecosystems, and their presence should be evaluated as a potential factor in fisheries management.

Trophic cascades, resulting from changes in the abundance of top predators, can cause structural changes and phase shifts in entire food webs through strong linkages (Paine 1980). Sea otters (*Enhydra lutris*) are an example of an apex predator that induces trophic cascades with resulting increases in kelp and eelgrass (*Zostera marina*) through reduction of grazers, control of mesopredators, reduction in competitors, and disturbance (Estes and Duggins 1995; Hughes et al. 2013; Raymond et al. 2021b; Saavedra 2021; Foster et al. 2021). Sea otters were reintroduced in Southeast Alaska in the 1960s and have expanded from a handful of release sites to a population of around 22,000 in 2022 (Schuette et al. 2023). Legal hunting by coastal Alaska Native peoples reduces sea otters in certain areas and creates a gradient of sea otter density (Burriss and McKnight 1973; Raymond et al. 2019). Consequences of sea otter induced trophic cascades on fish assemblages have infrequently been studied (except Reisewitz et al. 2006, Markel and Shurin 2015, Silberg 2015); therefore, we use this gradient in sea otter occupation as a natural experiment to investigate sea otter driven changes to nearshore habitats and potential consequences for nearshore juvenile salmon.

We investigate if juvenile salmon preferentially occupy eelgrass meadows or understory kelp in Southeast Alaska using historical (1998-2007) NOAA beach seine surveys (Johnson et al. 2012) and then use contemporary seines in eelgrass meadows (2017, 2019) to explore a range of environmental and biological drivers of juvenile Chum (*O. keta*) and Pink (*O. gorbuscha*) Salmon abundance, including sea otter density, distance from anadromous stream, date, sediment classification, and eelgrass biomass. Due to juvenile salmon dependence on the nearshore during a critical timeframe for growth and survival, the success of commercial harvest and longevity of

salmon populations may be tied to the availability of suitable nearshore nursery habitats. Understanding juvenile salmon use of the nearshore and how apex predators may impact the nearshore may contribute to our ability to sustainably manage fisheries and coastal resources.

2.3 Methods

2.3.1 Study area

Our sampling areas and analysis of historical NOAA data encompassed southern Southeast Alaska (57°N, 131°W to 54°N, 134°W) along the western coast of Prince of Wales Island, in the vicinity of Revillagigedo Island, and surrounding smaller islands (Figures 1a and 1b). These two regions, western Prince of Wales Island and Revillagigedo Island, have similar oceanographic conditions and species distribution to one another, as described in Johnson et al. (2012). Prince of Wales Island, the largest island in the Alexander Archipelago, and is exposed to the Gulf of Alaska along its west coast and to Dixon Entrance at the south. Revillagigedo Island, located east of Prince of Wales Island and closer to the mainland, and is exposed in the south to Nichols and Revillagigedo channels that connects to Dixon Entrance. The sampling region includes a diversity of habitats, ranging from highly exposed rocky habitats to low-energy soft-sediment estuaries and protected bays. In high-energy areas, understory kelps (*Laminaria* and *Saacharina* among others) and canopy kelps (*Nereocystis luetkeana* and *Macrocystis pyrifera*) occupy rocky shores (Harper and Morris 2014). Protected shorelines have both expansive and narrow, fringing seagrasses meadows (*Zostera marina* and *Phyllospadix sp.*) in the low intertidal to subtidal zones.

2.3.2 Habitat comparison use by juvenile salmon

We analyzed historical (1998 - 2007) National Oceanic and Atmospheric Administration (NOAA) beach seine data from eelgrass and understory kelp habitats (Johnson et al. 2012) to evaluate juvenile salmon use of these habitats. We subset the data to include sites ($n = 42$) in the southern Southeast Alaska outside region, which included the west and southeastern coasts of Prince of Wales Island, southern Revillagigedo island, Gravina Island, Annette Island, Duke Island, and the southern tip of the mainland of the southeast panhandle (Figure 2.1a, Supplementary Table 2.1). Most sites were seined once; however, at a subset of sites ($n = 12$), the fish assemblage was resampled across multiple months for a total number of 72 seine events across all 42 sites sampled during the 10-year NOAA effort. To contextualize juvenile salmon use of eelgrass and understory kelp beds, we used ShoreZone habitat classifications (<https://www.fisheries.noaa.gov/alaska/habitat-conservation/alaska-shorezone>) to calculate linear coastline (km) of continuous eelgrass and soft brown kelp (representing the understory kelp bed habitat) and the resulting percentage that each coastal habitat occupied in outer southern Southeast Alaska. ShoreZone data were generated from aerial imagery from daylight low tides with GIS classification of coastal habitats (Harper and Morris 2014).

In order to compare juvenile Chum and Pink Salmon use of understory kelp and eelgrass meadows we used historical NOAA data in southern Southeast Alaska (Johnson et al. 2012). We analyzed the number of Chum and Pink Salmon per seine using a generalized linear mixed model framework implemented using the R package 'glmmTMB, which specified a negative binomial error distribution to account for the overdispersion in these count data (Brooks et al. 2017). Each species was analyzed separately using the same suite of candidate models each containing a random effect of site, as some sites were resampled across months (April - July).

We compared random effect structure including a random intercept of month and site or a random intercept of site fit with Restricted Maximum Likelihood (REML). After determining the best random effect structure, we fit the model using Maximum Likelihood (ML) and included categorical fixed effects of habitat type and month, if month was not included as a random effect. We incorporated sampling date as categorical months since sampling time was clustered during negative low-tide cycles. We evaluated goodness of fit for both the random effect structure and fixed effects using second order Akaike Information Criterion (AICc; (Burnham and Anderson 2002), suited for small sample size, and Bayesian Information Criterion (BIC). The best model was refit using Restricted Maximum Likelihood (REML) to better estimate model parameters.

2.3.3 Drivers of juvenile salmon in eelgrass meadows

In addition to the historical data, we conducted beach seines in eelgrass meadows to quantify juvenile salmon and drivers of their abundance in the nearshore. We sampled eelgrass fish assemblages using the same methods used by the historical surveys, including a 37 m beach seine with variable mesh that tapered in width from 10 m in the center to 5 m in the sides with mesh size 32 mm along sides, decreasing to 6 mm towards the center with a 3.2 mm square mesh (Murphy et al. 2000; Johnson et al. 2012; Raymond et al. 2021b) along the western coast of Prince of Wales Island in 2017 (sites = 21) and 2019 (sites = 20) (Figure 2.1b, Supplementary Table 2.1) (Raymond et al. 2021a). We identified all fish to lowest possible taxonomic level, counted, and measured individual fish (fork length or total length depending on the species) to the nearest mm. All seines occurred around the negative low tides of the month (-0.1 to -3.0 ft below mean lower low water, MLLW) as the tide dropped. We selected sites based on presence of eelgrass (*Zostera marina*) across a gradient of sea otter density (Raymond et al. 2021b). We

conducted fish sampling with permits from Alaska Department of Fish and Game (#CF-17-50 and CF-19-067) and with approval from the Institutional Animal Use and Care Committee at the University of Alaska Fairbanks (project #892147).

At each beach seine location in 2017 and 2019, we focused on understanding potential drivers of salmon abundance in the nearshore. This approach investigates the influence of sea otters using a gradient of sea otter density (no. km⁻²), seine site distance from anadromous stream (km), date, qualitative sediment categorization, and eelgrass biomass (g m⁻²). At each site, we measured the habitat structure by counting eelgrass density (including flowering shoots) for five to eight 0.5 x 0.5 m quadrats adjacent to where the beach seine occurred and at the same tidal height (approximately -1.5 ft below MLLW). We collected eight to 15 shoots from each quadrat (n=75) and measured their total length to the nearest mm. We calculated eelgrass biomass based on the ratio of total length to dry biomass (g m⁻²) from data collected from Raymond et al. (2021b). To explain variation in salmonid catch rates, we accounted for substrate and distance from anadromous streams, as sediment is important for seagrass and their ability to anchor in the sediment with their rhizomes and juvenile salmon abundance is likely related to distance from the anadromous stream. We classified primary and secondary sediment type adapted from Folk (1954). To account for the location of salmon bearing streams, we calculated straight-line distance from seine location to the mouth of known anadromous streams using ArcGIS and Alaska known anadromous stream catalog. The anadromous streams catalog is a geospatial layer maintained and updated by Alaska Department of Fish and Game and identifies over 20,000 streams, rivers, or lakes that are important for spawning and rearing of anadromous fishes (<https://www.adfg.alaska.gov/sf/sarr/awc/>, (Alaska Department of Fish and Game (ADFG) 2019). We completed two boat-based sea otter surveys to estimate sea otter density (no. km⁻²)

around each seine location. We surveyed the water area within 3.8 km of a site by boat traveling at 14 km hr⁻¹ around each beach seine site in 2017 and 2019, enumerating and geo-locating individual and rafts of sea otters. Surveys occurred a minimum of two weeks apart. Based on the varied coastline, we converted sea otter numbers to density by dividing by total area surveyed and averaging the two surveys.

We analyzed the total number of juvenile Chum (*O. keta*) and Pink Salmon (*O. gorbuscha*) caught per seine using a species-specific generalized linear model framework. Full models included all explanatory parameters with interactions between main parameters which included day of year, day of year squared, year, sea otter density, qualitative sediment classification, distance from anadromous stream, and eelgrass biomass. Squared day of year was included to incorporate the increase, peak, and then decline of juvenile salmon across months when sampling occurred. We used negative binomial error distribution and a log-link function to account for overdispersion in the catch data. Starting with the full model, we used backward selection and evaluated model fit using second order Akaike Information Criterion (AICc), Bayesian Information Criterion (BIC), and the model probability based on the weight of evidence using both AIC and BIC (AIC and BIC weights). Model predicted figures presented are back-transformed into the response space as predicted juvenile salmon catch for each species per beach seine set. All analyses were performed in RStudio R version 4.0.3 (R Core Team 2021).

2.4 Results

2.4.1 Habitat comparison use by juvenile salmon

Average number of juvenile salmon per seine varied for Chum and Pink salmon and by habitat type for the historic data. Average juvenile Chum Salmon abundance was similar

between eelgrass (10.2 ± 33.2) and understory kelp (10.6 ± 16.9) (Figure 2.2a). Whereas, average juvenile Pink Salmon trended to be more abundant in eelgrass (217 ± 615) than understory kelp (54.7 ± 165) (Figure 2.2b). Across month, both juvenile Chum and Pink Salmon declined, with the greatest catch occurring in April for both species (Figure 2.2a, Figure 2.2b).

Throughout southern Southeast Alaska in the historical NOAA surveys, after accounting for seasonality, the role of habitat varied by species. The final selected model for juvenile Chum and Pink Salmon included habitat and month as fixed effects and a random site effect for the intercept term (Supplementary Table 2.2, Supplementary Table 2.3). For both species, negative binomial distribution (Chum overdispersion parameter = 0.3, Pink overdispersion parameter = 0.2) minimized the AICc and BIC compared to using a zero-inflated negative binomial distribution. Chum Salmon was significantly more abundant in understory kelp beds compared to eelgrass meadows (Figure 2.3a; Table 2.1); whereas we observed no significant difference in juvenile Pink Salmon between habitat types (Figure 2.4a; Table 2.1). As expected, salmon abundance varied over time. Month significantly contributed to juvenile Chum Salmon abundance (Figure 2.3b; Table 2.1). The number of juvenile Chum Salmon peaked in mid-April to May and then decreased in June and July. Similarly, the abundance of juvenile Pink Salmon was significantly attributed to the month they were sampled (Figure 2.4b; Table 2.1). The greatest number of Pink Salmon caught in a single seine all occurred in eelgrass meadows in the months of April and May and in those five cases abundance was greater than 1,000 each time. Most of the juvenile Pink Salmon (82.7%) were caught in a small fraction of the total seines (6.9%).

Understory kelp and eelgrass meadows constitute different percentages of available coastal habitat in southern Southeast Alaska for juvenile salmon. Of the approximately 16,000

km of coastline in southern Southeast Alaska, continuous soft-brown kelps constitute 6,080 km (37.8%) of the coastline. Eelgrass coastal extent occupies 1,300 km (8%) of the coastline (represented in Figure 2.1a). Together, these two structured habitats represent nearly half of the coastal habitat available for juvenile salmon.

2.4.2 Chum and Pink Salmon abundance in eelgrass meadows

Across the 41 sites that we sampled along the western coast of Prince of Wales Island, the number of juvenile salmon was dominated numerically by Pink Salmon (*O. gorbuscha*) and Chum Salmon (*O. keta*), and thus we focus on these two species in our analyses. Average number of salmon caught was comparable between juvenile Chum Salmon (15.0 ± 28.2) and Pink Salmon (12.9 ± 49.8) and catch numbers ranged between 0-128 individuals for Chum Salmon and 0-287 for Pink Salmon. However, at a large percentage of sites no salmon were caught for either juvenile Chum Salmon (39% of sites) or juvenile Pink Salmon (58.5% of sites).

Environmental drivers of juvenile salmon were species specific. The model that best explained number of Chum Salmon included date, squared date, and sea otter density (Supplementary Table 2.5, overdispersion parameter = 0.3). Chum Salmon catch increased with increasing sea otter density, with sea otter density selected as part of the best fit model despite not significantly contributing to explaining juvenile Chum Salmon catch at the 95% significance level. However, this trend had large uncertainty and the confidence intervals overlapped with zero (Table 2.2, Figure 2.5b). Any patterns between sea otter density and Chum Salmon abundances were driven by only a few sites. Chum Salmon abundance and Julian day were related, with a peak of abundance end of May beginning of June (Figure 2.5a) and both parameters associated with date were significantly different from zero (Table 2.2).

Juvenile Pink Salmon had high abundance at just a few sites, and four environmental parameters contributed to explaining its variability. The best-fit model explaining the number of Pink Salmon included day of year, squared day of year, eelgrass biomass, sea otter density, and distance from anadromous stream (Supplementary Table 2.5, overdispersion parameter = 0.5). Similar to Chum Salmon, juvenile Pink Salmon abundance and day of year were related with a peak slightly earlier than Chum Salmon (Figure 2.6a). Both parameters associated with day of year were significantly different from zero (Table 2.2), indicating a non-linear relationship between catch rate and day of year. Sea otter density, eelgrass biomass, and distance from anadromous stream parameters were significantly different from zero (Table 2.2). Pink Salmon abundance had a positive relationship with sea otter density and distance from anadromous stream, but a negative relationship with increased eelgrass biomass (Figure 2.6b, c, d). Confidence bands ($\pm 95\%$) were large for all the parameters.

2.5 Discussion

In this study, we found juvenile Chum and Pink salmon (*O. gorbuscha* and *O. keta*) present in both eelgrass meadows and understory kelp beds, with Chum Salmon in greater abundance in understory kelp beds compared to eelgrass habitats. Environmental drivers in eelgrass meadows important for juvenile salmon were species-specific and the number of juvenile Chum Salmon were informed only by seasonality although including sea otter density improved model fit. The number of Juvenile Pink salmon increased with increasing sea otter density and distance from anadromous stream. Interestingly, we found that eelgrass biomass negatively influences juvenile Pink Salmon with fewer salmon encountered at greater biomass

values. We found that juvenile salmon use these habitats episodically with patchy and at times incredibly abundant groups of juvenile salmon encountered.

The roles of nearshore habitat as refuge and prey supply can be altered or modulated by the presence of an apex predator and potentially impact the associated fish assemblage. We observed different responses of salmon species to sea otter impacts, with a relationship for juvenile Pink Salmon, but not Chum Salmon. In nearshore habitats sea otters induce trophic cascades, which has led to clear indirect impacts of sea otters on fish assemblages. The reintroduction of sea otters increases the trophic level of adult copper and black rockfish in kelp forests as they switch to piscivory (Markel and Shurin 2015), increases species richness in eelgrass meadows, and shifts of the fish assemblage in understory kelp beds characterized by declines in black and brown rockfishes and increases in juvenile rockfishes and rock greenlings (Chapter 3). Longer occupation time of sea otters increases copper rockfishes (Silberg 2015) and declines in sea otters cause declines in rock greenlings (Reisewitz et al. 2006). Specifically within eelgrass meadows, sea otter recolonization is associated with increased biomass of meadows (Raymond et al. 2021b), boosted genetic diversity in meadows from disturbing beds while foraging clams (Foster et al. 2021), and enhanced eelgrass growth through removing belowground competitors (clams) (Saavedra 2021). These mechanisms connect sea otters and eelgrass through increased structure and biomass of eelgrass beds; therefore, indirect effects on fish communities are likely more apparent with fish species that reside longer than juvenile salmon in these nearshore habitats. This research took advantage of a gradient from low to high sea otter density, but we did not see the same gradient in the aboveground biomass of eelgrass meadows across our study sites, making it difficult to observe patterns in indirect effects of sea otters on juvenile salmon through changes in eelgrass biomass. Disentangling the myriad of

forces that impact nearshore habitats, the indirect impact of sea otters, and the difference in response of Chum and Pink Salmon makes it difficult to suggest if one species over the other will be more impacted by increased sea otter density. Additionally, the indirect signal of sea otters may not be clear because of the migratory nature of juvenile salmon, so if conditions are not adequate, i.e. if the habitat does not provide enough refuge, they get eaten and/or if prey are not available, they continue to migrate in search of prey.

The wide distribution of observations of juvenile salmon made it difficult to disentangle clear patterns in habitat preference and environmental drivers of juvenile salmon in eelgrass. In the historical NOAA surveys, nearly 79% of the total catch of juvenile Pink Salmon occurred at five eelgrass sites. In our contemporary work, we see similar patchy occurrence of juvenile salmon. While certain environmental variables are important for predicting juvenile salmon numbers, only a few sites with extremely abundant catches appear to drive this pattern. Intuitively we would have expected to see a positive relationship with eelgrass biomass if juvenile salmon are prioritizing refuge from predation (Semmens 2008) and a negative relationship between juvenile salmon and distance from anadromous stream. Instead, we see a weak, but opposite relationship between eelgrass biomass and distance from anadromous streams from what we expected for juvenile Pink Salmon and no relationship with Chum Salmon. These weak patterns could be attributed to not sampling a large enough gradient in our explanatory variables. We potentially did not sample from low enough to high enough eelgrass biomass and could miss the effect of extremely low or high eelgrass biomass on salmon through lack of informative contrast. In our study, average dry weight of leaf biomass ranged from 7.4 - 240.2 g m⁻². Our maximum biomass was just below median summertime dry weight of leaf biomass, 245 g m⁻², found in a metaanalysis of *Zostera marina* across its temperate ranges (Northern Europe,

Western USA, Eastern USA and Canada, Mexico, and Japan). This perhaps indicates that eelgrass meadows in southern Southeast Alaska may support greater leaf biomass than what we observed, with greater potential to influence juvenile salmon abundance.

Juvenile salmon may not be tied to the anadromous streams listed, as the Anadromous Waters Catalog (Alaska Department of Fish and Game (ADFG) 2019) contains a small fraction of the total watersheds that salmon species use and/or the juvenile salmon may originate from hatcheries rather than streams (Southern Southeast Regional Aquaculture Association (SSRAA) 2023). Of note, however, is that Pink Salmon are not released by hatcheries in southern Southeast Alaska and we observed patterns between anadromous streams only with juvenile Pink Salmon. The lack of association for Chum Salmon and anadromous streams may be influenced by hatchery releases.

Another factor driving our results could be catch efficiency. Beach seine sampling efficiency may be reduced with macrophytes present and can have large unpredictable variability in species catch causing difficulty and uncertainty when identifying patterns in nearshore fish communities (Pierce et al. 1990; Rozas and Minello 1997). While these are possible explanations for the weak relationships, with a few sites having much larger juvenile salmon abundances than others, this indicates that perhaps surveys across 100s of kilometers on juvenile salmon in eelgrass meadows is too vast to disentangle the complex relationship between quickly migrating species (moving from streams to open ocean in 2 - 3 months) and their reliance on the nearshore as stop-over habitats.

In southern Southeast Alaska, eelgrass and understory kelps compose just under half of available coastlines for juvenile salmon with Pink Salmon not distinguishing between habitats, but Chum Salmon more present in understory kelps. For juvenile Pink Salmon this indicates that

the presence alone of structured habitats, regardless of the type may be beneficial during migration to the open ocean compared to Chum Salmon which may be more reliant on understory kelps. Despite the smaller percentage of eelgrass habitat available (8%) compared to understory kelps (37.8%), we still see periodically high abundance of juvenile salmon within eelgrass demonstrating that less prevalent structured habitats can serve as crucial habitat. We may not have seen these patterns if the nearshore habitats were impacted by high anthropogenic disturbance, declining eelgrass meadows, or diminished food web stability. Likely the presence of these nearshore habitats and the complex and resilient ecosystem they support collectively supplies migratory habitat for juvenile salmon.

Juvenile salmon could utilize nearshore submerged vegetation for reasons unrelated to the environmental drivers explored in this study, in particular predator avoidance and prey availability could drive juvenile salmon in the nearshore. The ability to provide refuge differs between the habitat types studied here with most understory kelp beds in Southeast Alaska composed of large flat-lying *Saccharina* spp. and smaller bushy red and brown algae underneath the mats of bladed kelps and eelgrass blades that can extend up to a meter in the water column. Since juvenile salmon are generally surface-oriented the potential refuge benefit of understory kelps could be reduced compared to canopy kelps and eelgrass meadows. However, other studies found increased number of juvenile salmon with increasing macroalgae cover and near seagrass meadows compared to more open-water, rocky, and sandy habitats (Sharpe et al. 2019), which corroborates our findings of juvenile salmon use of both macroalgae/understory and eelgrass meadows with abundant groups of both juvenile Chum Salmon and Pink Salmon in both habitats. In addition, juvenile salmon are extremely reliant on prey sources and their outmigration timing is connected with prey availability (Orsi et al. 2000). Therefore, their use of

nearshore habitats could be connected to the diverse invertebrate and vertebrate community the submerged vegetation hosts. Certain sites having more productive sources of prey may explain some of the patchy distributions of juvenile salmon at some sites over others. Perhaps juvenile salmon convene among these structured habitats (eelgrass and kelps) due to the ability of the habitats to host high prey abundances similar to what is seen in eelgrass meadows in British Columbia (Kennedy et al. 2018). Future work may benefit from investigating diet composition and prey availability of salmon in addition to predator abundance rather than just the number of salmon present across habitat types throughout their early marine phase.

2.5.1 Conclusions

Nearshore habitats, including eelgrass meadows and understory kelps, serve as nursery habitats for commercially important fish species. We found juvenile salmon in both of these habitats, with juvenile Chum Salmon more abundant in understory kelp compared to eelgrass, while juvenile Pink Salmon show no preference. Juvenile salmon are ephemeral species in the nearshore, and thus the role that eelgrass and understory kelps facilitate for their development is difficult to disentangle from other environmental factors. The relationships among juvenile salmon and environmental metrics described in this study likely differ across regions within Southeast Alaska and at broader spatial scales. Regional (freshwater input, fjords, wave exposure, salmon productivity) and site (habitat structure, prey availability) specific metrics may all be impacting juvenile salmon use and presence in nearshore areas. Furthermore, other structured habitats like canopy kelp forests could provide similar refuge for salmon, or host to important prey species in the nearshore, indicating that all these structured habitats should be equally considered when identifying important coastal nurseries for juvenile salmon.

Regardless of habitat type present or structure of that habitat, juvenile salmon must navigate complex channels and coastlines before reaching the open ocean in Southeast Alaska. These corridors likely influence distance, duration, and migratory paths for juvenile salmon. As such juvenile salmon occur in patchy distributions where they are either nearly absent or present in extreme numbers. While emphasis on the nearshore as a critical habitat is warranted, perhaps more important are the availability of prey within the nearshore. Further studies could expand on this habitat-juvenile salmon association through including prey sampling and diet analysis to disentangle the role of prey availability versus predation avoidance in the nearshore. This current work reinforces the generalized use of nearshore submerged habitats by juvenile salmon during their transition and growth to the open ocean and highlights the need to consider various aspects of the early marine phase of juvenile salmon, the role of apex predators, the differential use of nearshore habitats, the impacts of environmental variability, and coastal development on the productivity of salmon.

2.6 Author contributions

Lia K. Domke, Rebecca J. Cates, Wendel W. Raymond and Ginny L. Eckert conceived the ideas and designed the methodology. Lia K. Domke collected data, performed formal analyses and visualization, and wrote the original draft. Rebecca J. Cates collected data and reviewed and edited the manuscript. Wendel W. Raymond collected data and reviewed and edited the manuscript. Ginny L. Eckert acquired funding, administered and supervised the project, collected data, and reviewed and edited the manuscript.

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2.9 Figures

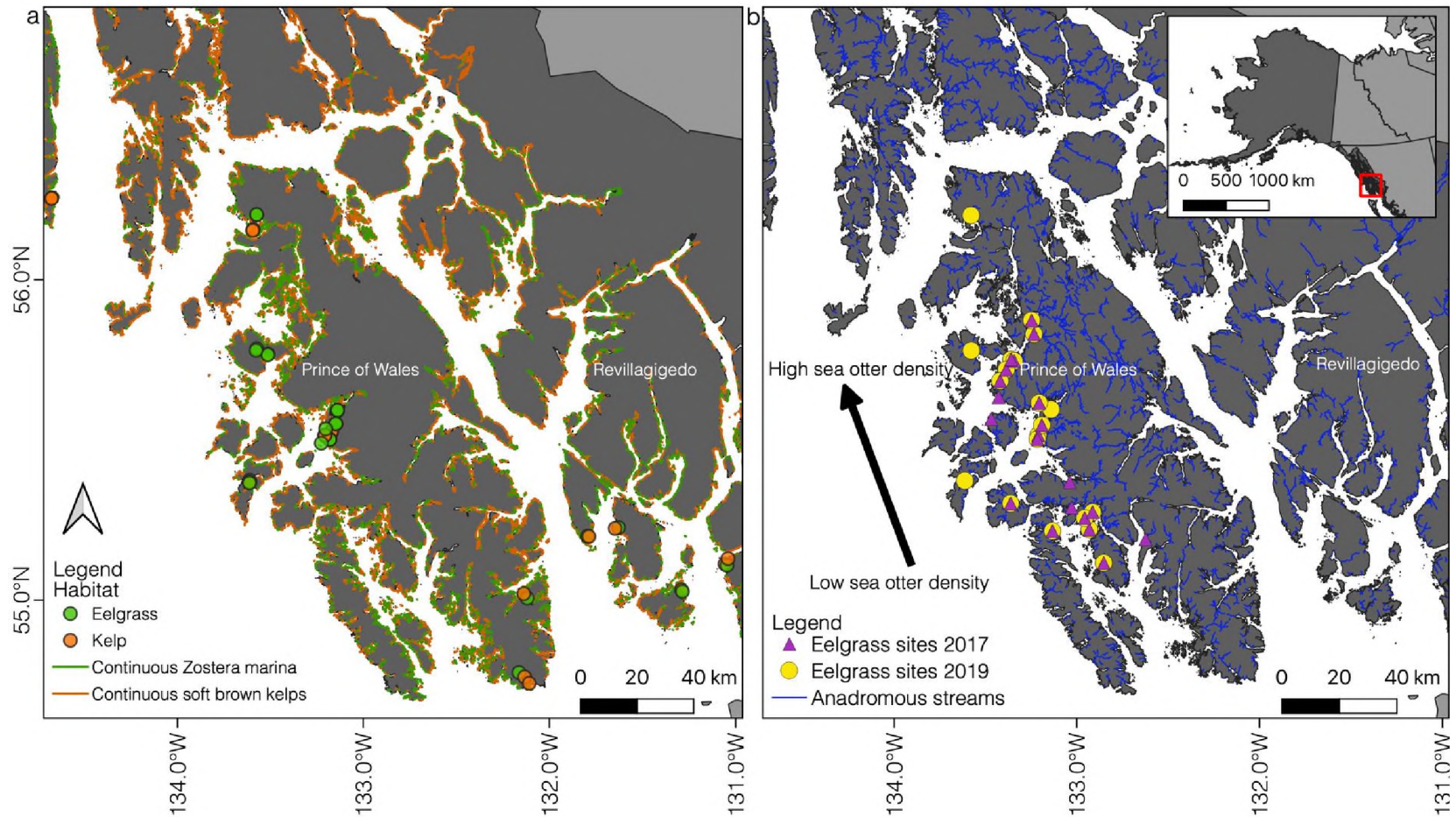


Figure 2.1. (a) Eelgrass (green) and understory kelp (orange) habitats from ShoreZone (Harper and Morris 2014) and historical NOAA sites sampled in southern Southeast Alaska (Johnson et al. 2012). (b) Eelgrass sites sampled in 2017 (purple triangle) and 2019 (yellow circle) with known anadromous streams (blue) from ADFG (2019).

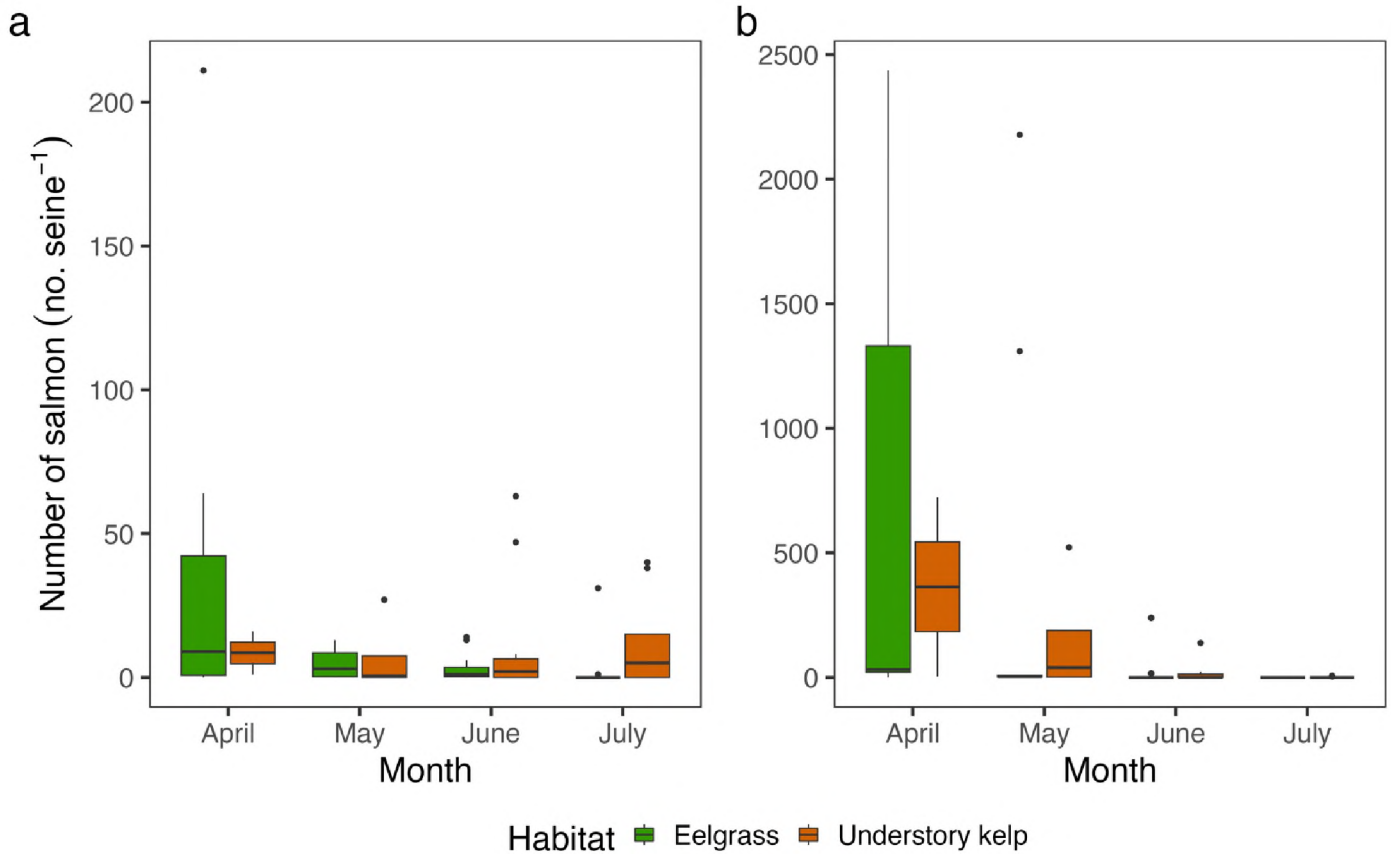


Figure 2.2. Boxplots of the number of juvenile Chum Salmon (a) and juvenile Pink Salmon (b) sampled across month and in two habitat types, eelgrass meadows (green) and understory kelp (orange). Center of boxplot represents the mean of the data with the lower and upper extent of the box representing the 25th and 75th percentiles. Boxplot whiskers extend from the first and third quartile no more than 1.5 times the interquartile range below and above the box. Outliers are black points outside of the interquartile range. Note the difference in y-axis scale.

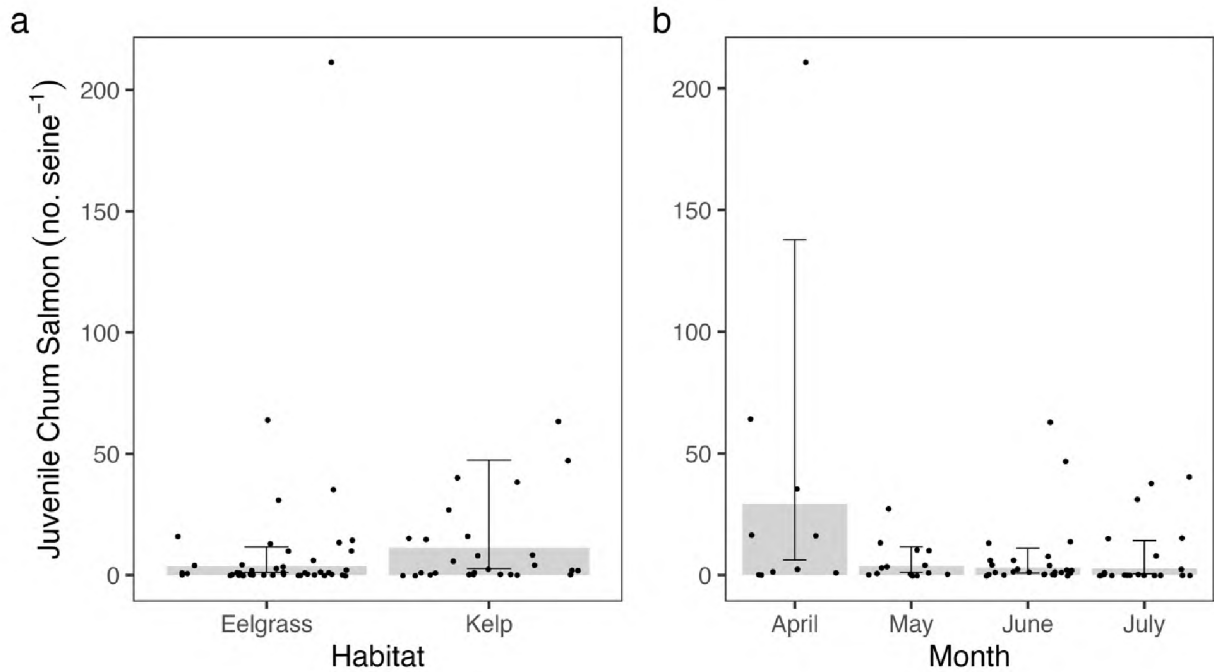


Figure 2.3. (a) Model predicted number of juvenile Chum Salmon (\pm 95% confidence interval) between habitat type (eelgrass meadows and understory kelp) while holding month constant on May and incorporating the average effect of site. (b) Model predicted number of juvenile Chum salmon across month (April - July) while holding habitat constant on eelgrass and incorporating the average effect of site. Points are the number of Chum Salmon per seine.

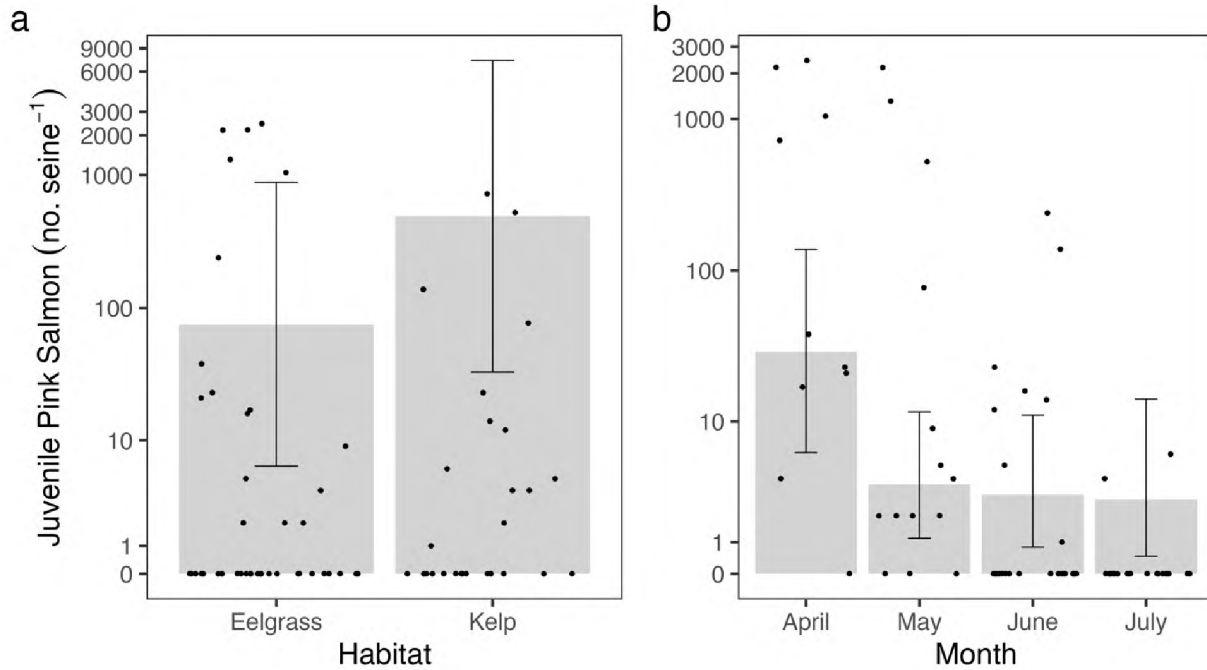


Figure 2.4. (a) Model predicted number of juvenile Pink Salmon (\pm 95% confidence interval) between habitat type (eelgrass meadows and understory kelp) while holding month constant on May and incorporating the average effect of site. (b) Model predicted number of juvenile Pink salmon across month (April - July) while holding habitat constant on eelgrass and incorporating the average effect of site. Points are the number of Pink Salmon per seine. Y-axis scale is a pseudo log scale to smoothly transition to linear scale at zero to better visualize the patterns across large and small catch numbers.

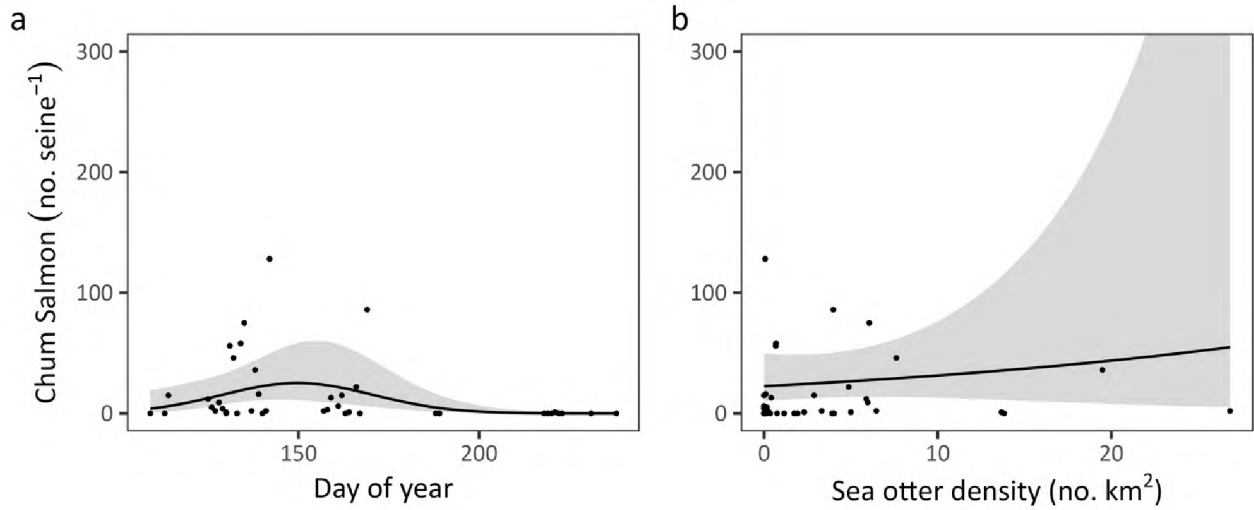


Figure 2.5. The relationship between Chum Salmon abundance and (a) day of year and (b) sea otter density. Black line indicates the relationship based on the best-fit model while holding the other explanatory variables at the median values with grey 95% confidence bands and number of Chum Salmon per seine (points).

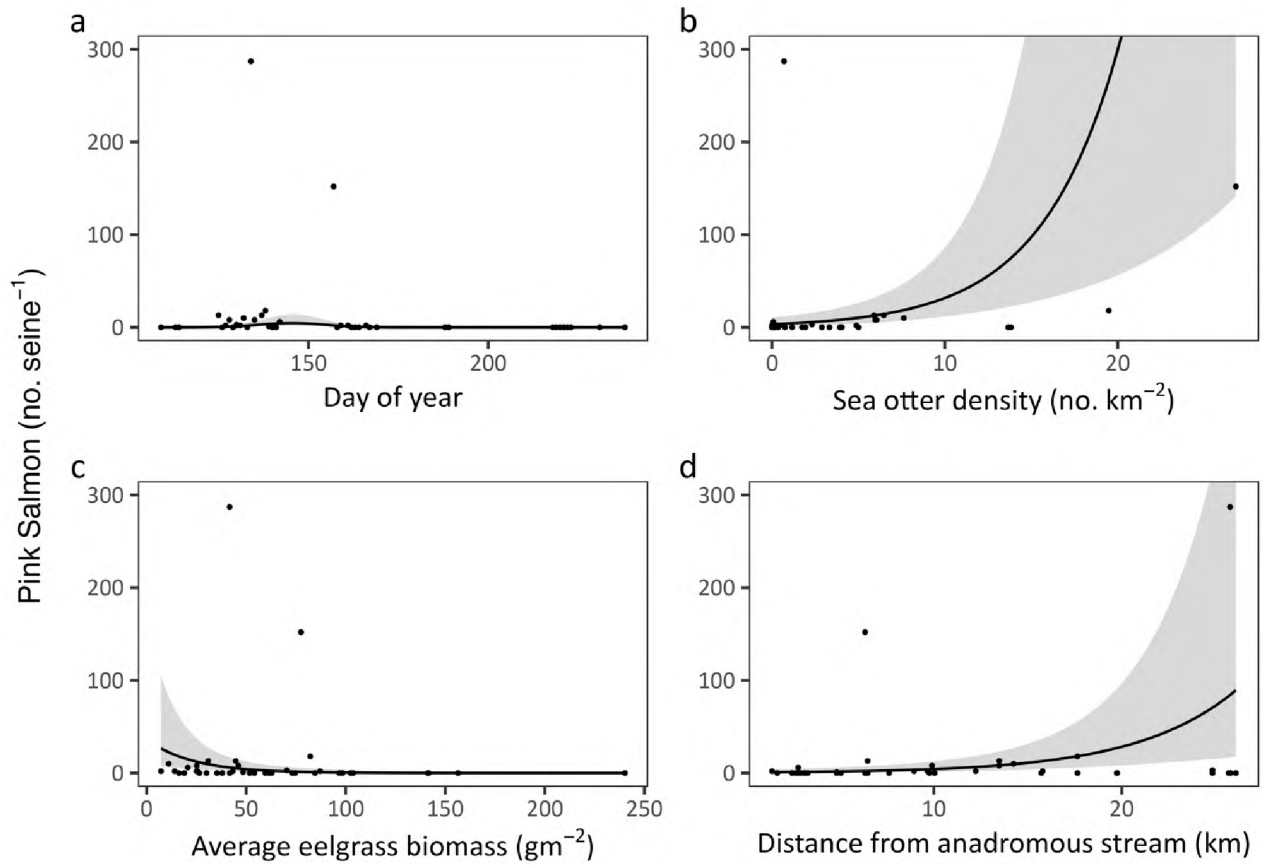


Figure 2.6. The relationship between Pink Salmon abundance and (a) day of year, (b) average sea otter density, (c) distance from anadromous stream, and (d) average eelgrass biomass. Black line indicates the relationship based on the reduced model while holding the other explanatory variables at the median value with grey 95% confidence bands and number of Pink Salmon per seine (points).

2.10 Tables

Table 2.1. Results of the best-fit model and the associated predictors for juvenile Chum Salmon (left) and juvenile Pink Salmon (right) from the historical NOAA surveys. The best-fit models included predictors that significantly ($\alpha=0.1$) contributed to explaining variability in juvenile salmon numbers per seine (bolded p-values) and those that did not contribute (not bolded p-values). Coefficients presented are in log space.

<i>Predictors</i>	Juvenile Chum Salmon				Juvenile Pink Salmon			
	<i>Estimate</i>	<i>Standard Error</i>	<i>Statistic</i>	<i>P-Value</i>	<i>Estimate</i>	<i>Standard Error</i>	<i>Statistic</i>	<i>P-Value</i>
(Intercept)	3.37	0.79	4.25	<0.001	6.18	1.28	4.83	<0.001
Habitat [Kelp]	1.14	0.61	1.86	0.062	1.88	1.36	1.38	0.167
Mon [May]	-2.08	0.9	-2.31	0.021	-1.87	1.58	-1.18	0.237
Mon [Jun]	-2.26	0.83	-2.74	0.006	-7.06	1.82	-3.88	<0.001
Mon [Jul]	-2.36	0.9	-2.63	0.009	-9.81	1.93	-5.08	<0.001
Random Effects								
σ^2	1.61	1.84						
τ_{00}	0.17 _{SiteID}	5.88 _{SiteID}						
N	42 _{SiteID}	42 _{SiteID}						
Observations	72	72						

Table 2.2. Summary table of the best-fit model and the associated predictors for juvenile Chum Salmon (left) and juvenile Pink Salmon (right) catch in contemporary seines in eelgrass meadows. The best-fit models included predictors that significantly ($\alpha=0.1$) to explaining variability in juvenile salmon catch (bolded p-values) and those that did not contribute (not bolded p-values). Coefficients are presented in log space.

<i>Predictors</i>	Juvenile Chum Salmon				Juvenile Pink Salmon			
	<i>Estimate</i>	<i>Standard Error</i>	<i>Statistic</i>	<i>P-Value</i>	<i>Estimate</i>	<i>Standard Error</i>	<i>Statistic</i>	<i>P-Value</i>
intercept	-22.11	8.77	-2.52	0.012	-123.97	38.97	-3.18	0.001
day of year	0.34	0.11	3.03	0.002	1.73	0.54	3.21	0.001
quadratic day of year	0	0	-3.28	0.001	-0.01	0	-3.22	0.001
average sea otter density	0.03	0.05	0.65	0.517	0.23	0.05	4.41	<0.001
average eelgrass biomass					-0.04	0.01	-3.19	0.001
distance from anadromous stream					0.18	0.05	3.81	<0.001
Observations	40	40						

2.11 Supplementary information

2.11.1 Supplementary tables

Supplementary Table 2.1. Seine locations, date and year of seine, and habitat sampled for objectives one and two.

Site	Site code	Latitude	Longitude	Habitat	Date (mm/dd/yy)	Year	Objective
Heceta Island	157	55.7581	-133.4708	eelgrass	7/17/99	1999	Historical
Heceta Island	158	55.7564	-133.4711	eelgrass	7/17/99	1999	Historical
Heceta Island	156	55.7758	-133.5319	eelgrass	7/17/99	1999	Historical
Heceta Island	155	55.7708	-133.5361	eelgrass	7/17/99	1999	Historical
Prince of Wales Island	145	55.5072	-133.1339	understory kelp	5/15/98	1998	Historical
Prince of Wales Island	145	55.5072	-133.1339	understory kelp	6/10/98	1998	Historical
Prince of Wales Island	146	55.5125	-133.1297	understory kelp	6/10/98	1998	Historical
Prince of Wales Island	146	55.5125	-133.1297	understory kelp	7/15/99	1999	Historical
Prince of Wales Island	145	55.5072	-133.1339	understory kelp	7/15/99	1999	Historical
Prince of Wales Island	146	55.5125	-133.1297	understory kelp	5/15/98	1998	Historical
Prince of Wales Island	177	56.1936	-133.5169	eelgrass	7/14/00	2000	Historical
Prince of Wales Island	178	56.195	-133.5167	eelgrass	7/14/00	2000	Historical
Prince of Wales Island	184	56.1483	-133.5378	understory kelp	7/14/00	2000	Historical
Prince of Wales Island	183	56.1453	-133.5408	understory kelp	7/14/00	2000	Historical
Prince of Wales Island	132	55.5772	-133.0944	eelgrass	5/12/98	1998	Historical
Prince of Wales Island	132	55.5772	-133.0944	eelgrass	6/11/98	1998	Historical
Prince of Wales Island	132	55.5772	-133.0944	eelgrass	4/14/98	1998	Historical
Prince of Wales Island	135	55.5	-133.1644	eelgrass	7/15/99	1999	Historical
Prince of Wales Island	136	55.5003	-133.1647	eelgrass	5/14/98	1998	Historical
Prince of Wales Island	136	55.5003	-133.1647	eelgrass	4/16/98	1998	Historical
Prince of Wales Island	136	55.5003	-133.1647	eelgrass	6/9/98	1998	Historical
Prince of Wales Island	135	55.5	-133.1644	eelgrass	5/14/98	1998	Historical

Supplementary Table 2.1 (contd)

Prince of Wales Island	135	55.5	-133.1644	eelgrass	4/16/98	1998	Historical
Prince of Wales Island	135	55.5	-133.1644	eelgrass	6/9/98	1998	Historical
Prince of Wales Island	131	55.5778	-133.0941	eelgrass	5/12/98	1998	Historical
Prince of Wales Island	131	55.5778	-133.0941	eelgrass	4/14/98	1998	Historical
Prince of Wales Island	131	55.5778	-133.0941	eelgrass	6/11/98	1998	Historical
Prince of Wales Island	141	55.5361	-133.1056	eelgrass	5/13/98	1998	Historical
Prince of Wales Island	140	55.5011	-133.1675	understory kelp	4/16/98	1998	Historical
Prince of Wales Island	141	55.5361	-133.1056	eelgrass	4/15/98	1998	Historical
Prince of Wales Island	140	55.5011	-133.1675	understory kelp	7/15/99	1999	Historical
Prince of Wales Island	141	55.5361	-133.1056	eelgrass	6/12/98	1998	Historical
Prince of Wales Island	140	55.5011	-133.1675	understory kelp	5/14/98	1998	Historical
Prince of Wales Island	140	55.5011	-133.1675	understory kelp	6/9/98	1998	Historical
Prince of Wales Island	142	55.5358	-133.1053	eelgrass	6/12/98	1998	Historical
Prince of Wales Island	142	55.5358	-133.1053	eelgrass	7/15/99	1999	Historical
Prince of Wales Island	141	55.5361	-133.1056	eelgrass	7/15/99	1999	Historical
Prince of Wales Island	142	55.5358	-133.1053	eelgrass	4/15/98	1998	Historical
Prince of Wales Island	142	55.5358	-133.1053	eelgrass	5/13/98	1998	Historical
Prince of Wales Island	138	55.4875	-133.1414	eelgrass	4/17/98	1998	Historical
Prince of Wales Island	138	55.4875	-133.1414	eelgrass	6/10/98	1998	Historical
Prince of Wales Island	138	55.4875	-133.1414	eelgrass	5/13/98	1998	Historical
Prince of Wales Island	136	55.5003	-133.1647	eelgrass	7/15/99	1999	Historical
Prince of Wales Island	137	55.4872	-133.1414	eelgrass	5/13/98	1998	Historical
Prince of Wales Island	137	55.4872	-133.1414	eelgrass	6/10/98	1998	Historical
Prince of Wales Island	137	55.4872	-133.1414	eelgrass	4/17/98	1998	Historical
Prince of Wales Island	139	55.5008	-133.1672	understory kelp	5/14/98	1998	Historical
Prince of Wales Island	139	55.5008	-133.1672	understory kelp	6/9/98	1998	Historical

Supplementary Table 2.1 (contd)

Prince of Wales Island	139	55.5008	-133.1672	understory kelp	7/15/99	1999	Historical
Prince of Wales Island	139	55.5008	-133.1672	understory kelp	4/16/98	1998	Historical
Gravina Island	616	55.1551	-131.7421	understory kelp	6/19/07	2007	Historical
Gravina Island	617	55.1561	-131.7498	eelgrass	6/19/07	2007	Historical
Prince of Wales Island	598	54.7401	-132.1536	eelgrass	6/14/07	2007	Historical
Prince of Wales Island	599	54.7259	-132.1241	understory kelp	6/14/07	2007	Historical
Prince of Wales Island	596	54.9711	-132.0924	eelgrass	6/13/07	2007	Historical
Prince of Wales Island	601	54.7051	-132.1005	understory kelp	6/14/07	2007	Historical
Prince of Wales Island	595	54.9856	-132.1098	understory kelp	6/13/07	2007	Historical
Annette Island	613	55.176	-131.5972	understory kelp	6/18/07	2007	Historical
Annette Island	614	55.1782	-131.5791	eelgrass	6/18/07	2007	Historical
	605	55.0635	-130.9917	understory kelp	6/15/07	2007	Historical
Duke Island	606	54.9744	-131.2538	understory kelp	6/16/07	2007	Historical
	603	55.0426	-130.9995	eelgrass	6/15/07	2007	Historical
Duke Island	607	54.9684	-131.2492	eelgrass	6/16/07	2007	Historical
Ballena Island	337	55.4764	-133.1881	eelgrass	5/14/98	1998	Historical
Prince of Wales Island	338	55.5208	-133.1617	eelgrass	5/15/98	1998	Historical
	602	55.047	-131.0105	understory kelp	6/15/07	2007	Historical
Baker Island	107	55.3658	-133.5856	eelgrass	7/16/99	1999	Historical
Baranof Island	112	56.2553	-134.6633	understory kelp	7/12/00	2000	Historical
Baranof Island	111	56.2536	-134.6653	understory kelp	7/12/00	2000	Historical
Baker Island	110	55.3597	-133.5878	understory kelp	7/16/99	1999	Historical
Baker Island	109	55.3597	-133.5883	understory kelp	7/16/99	1999	Historical
Baker Island	108	55.3575	-133.5869	eelgrass	7/16/99	1999	Historical
Blanquizal Point	BLAQ_A	55.62082	-133.38664	eelgrass	8/19/17	2017	Contemporary
Chusini Cove	CHUS_A	55.80692	-133.171	eelgrass	6/13/17	2017	Contemporary
Dunbar Inlet	DUNB_A	55.0848	-132.826	eelgrass	7/7/17	2017	Contemporary
Dunbar Inlet	DUNB_A	55.0848	-132.826	eelgrass	5/6/19	2019	Contemporary
Farallon Bay	FARA_A	55.19112	-133.10531	eelgrass	8/11/17	2017	Contemporary
Farallon Bay	FARA_A	55.19112	-133.10531	eelgrass	5/22/19	2019	Contemporary
Garcia Bay	GARC_A	55.552669	-133.43139	eelgrass	8/6/17	2017	Contemporary

Supplementary Table 2.1 (contd)

Guktu Bay	GUKT_A	55.739816	-133.31202	eelgrass	8/9/17	2017	Contemporary
Guktu Bay	GUKT_A	55.739816	-133.31202	eelgrass	5/18/19	2019	Contemporary
Hetta Cove	HETA_A	55.155625	-132.58993	eelgrass	8/10/17	2017	Contemporary
Kaguk Cove	KAGK_A	55.73361	-133.29	eelgrass	7/8/17	2017	Contemporary
Kaguk Cove	KAGK_A	55.73361	-133.29	eelgrass	6/6/19	2019	Contemporary
Natzuhini Bay	NATZ_A	55.25051	-132.883	eelgrass	6/11/17	2017	Contemporary
Natzuhini Bay	NATZ_A	55.25051	-132.883	eelgrass	6/16/19	2019	Contemporary
Naukati Bay	NAUK_A	55.862405	-133.19072	eelgrass	8/8/17	2017	Contemporary
Naukati Bay	NAUK_A	55.862405	-133.19072	eelgrass	5/21/19	2019	Contemporary
North Fish Egg Island	NFEI_A	55.49709	-133.17	eelgrass	5/10/17	2017	Contemporary
North Fish Egg Island	NFEI_A	55.49709	-133.17	eelgrass	4/19/19	2019	Contemporary
Nossuk Bay	NOSK_A	55.7073	-133.342	eelgrass	5/15/17	2017	Contemporary
Nossuk Bay	NOSK_A	55.70818	-133.34164	eelgrass	4/24/19	2019	Contemporary
Port Refugio	REFU_A	55.282137	-133.33403	eelgrass	8/26/17	2017	Contemporary
Port Refugio	REFU_A	55.282137	-133.33403	eelgrass	5/19/19	2019	Contemporary
Shinaku Inlet	SHIN_A	55.59929	-133.16	eelgrass	6/12/17	2017	Contemporary
Shinaku Inlet	SHIN_A	55.59929	-133.16	eelgrass	5/17/19	2019	Contemporary
Soda Bay	SODA_A	55.26366	-132.995	eelgrass	5/11/17	2017	Contemporary
South Wadleigh Island	SWAD_A	55.52904	-133.147	eelgrass	6/8/17	2017	Contemporary
South Wadleigh Island	SWAD_A	55.52904	-133.147	eelgrass	5/10/19	2019	Contemporary
Trocadero Bay	TROC_A	55.344914	-133.0011	eelgrass	8/7/17	2017	Contemporary
Baker Island	BAKE_A	55.3575	-133.58694	eelgrass	6/18/19	2019	Contemporary
Chusini Cove	CHUS_B	55.81849	-133.1794	eelgrass	5/8/19	2019	Contemporary
Goats mouth inlet	GOAT_A	55.19286	-132.9	eelgrass	5/13/17	2017	Contemporary
Goats mouth inlet	GOAT_A	55.192784	-132.90011	eelgrass	4/23/19	2019	Contemporary
Klawock Airport	KLWA_A	55.577767	-133.0941	eelgrass	5/7/19	2019	Contemporary
South Fish Egg Island	SFEI_A	55.48442	-133.175	eelgrass	5/14/17	2017	Contemporary
South Fish Egg Island	SFEI_A	55.48442	-133.17549	eelgrass	5/20/19	2019	Contemporary
Salt Lake Bay	SALA_A	55.67264	-133.378	eelgrass	5/12/17	2017	Contemporary
North Pass	NPAS_A	55.22962	-132.925	eelgrass	6/10/17	2017	Contemporary
Heceta Island	HECA_A	55.7758333	-133.53194	eelgrass	6/15/19	2019	Contemporary
North Pass	NPAS_B	55.229743	-132.92405	eelgrass	5/9/19	2019	Contemporary
Salt Lake Bay	SALA_A	55.67565	-133.3735	eelgrass	5/5/19	2019	Contemporary
Calder Bay	CALD_A	56.193611	-133.51694	eelgrass	6/7/19	2019	Contemporary

Supplementary Table 2.2. Candidate models for number of juvenile Chum Salmon (No. Chum Salmon) selected for goodness of fit evaluation using second order Akaike Information Criterion (AICc), and Bayesian Information Criterion (BIC). Random effect structure was tested first with generalized linear mixed model (glmm) with a negative binomial error distribution (NB) (selected random effect structure is underlined). Models tested the role of habitat type (eelgrass or understory kelp) and month in a glmm framework either a negative binomial error distribution (NB) or zero-inflated negative binomial error distribution (ZINB). All models included random effect of site. Bolded model is the best-fit model.

Effect structure testing	Candidate models	Model type	AICc	BIC	ΔBIC	ΔAICc
<u>Random</u>	<u><i>No. Chum Salmon ~ Habitat + Month + site (random ϵ_{jfec1})</i></u>	<u>NB</u>	<u>399.14</u>	<u>413.32</u>	<u>0</u>	<u>0</u>
Random	<i>No. Chum Salmon ~ Habitat + Month (random ϵ_{jfec1}) + site (random ϵ_{jfec1})</i>	NB	404.73	415.2	1.88	5.59
Fixed	<i>No. Chum Salmon ~ Habitat + Month + site (random ϵ_{jfec1})</i>	NB	401.43	415.62	0	0
Fixed	<i>No. Chum Salmon ~ Habitat + Month + site (random ϵ_{jfec1})</i>	ZINB	403.97	419.89	4.28	2.54

Supplementary Table 2.3. Candidate models for number of juvenile Pink Salmon (No. Pink Salmon) selected for goodness of fit evaluation using second order Akaike Information Criterion (AICc), and Bayesian Information Criterion (BIC). Random effect structure was tested first with generalized linear mixed model (GLMM) with a negative binomial error distribution (NB) (selected random effect structure is underlined). Models tested the role of habitat type (eelgrass or understory kelp) and month in a GLMM framework either a negative binomial error distribution (NB) or zero-inflated negative binomial error distribution (ZINB). All models included random effect of site. Bolded model is the best-fit model.

Effect structure testing	Candidate models	Model type	AICc	BIC	ΔBIC	ΔAICc
<u>Random</u>	<u><i>No. Pink Salmon ~ Habitat + Month + site (random ϵ_{jfec1})</i></u>	<u>NB</u>	<u>413.04</u>	<u>427.23</u>	<u>0</u>	<u>0</u>
Random	<i>No. Pink Salmon ~ Habitat + Month (random ϵ_{jfec1}) + site (random ϵ_{jfec1})</i>	NB	427.85	438.32	11.09	14.81
Fixed	<i>No. Pink Salmon ~ Habitat + Month + site (random ϵ_{jfec1})</i>	NB	421.18	435.37	0	0
Fixed	<i>No. Pink Salmon ~ Habitat + Month + site (random ϵ_{jfec1})</i>	ZINB	423.72	439.65	4.28	2.54

Supplementary Table 2.4. Candidate models from negative binomial generalized linear model (GLM) regression results testing the effects of day of year (date), quadratic date (date²), sea otter density (s. otter), qualitative primary (sed1) and secondary (sed2) sediment scores, seagrass biomass (eelgrass), straight-line distance from anadromous streams (stream distance), and categorical year (year) on total number of juvenile Chum Salmon caught per seine. Best-fit model (in bold) as indicated by Akaike Information Criterion (AICc), change in AICc (Δ AICc) AIC weight of evidence that the given model is the most parsimonious (AICc Wt), Bayesian Information Criterion (BIC), change in BIC (Δ BIC), BIC weight of evidence (BIC Wt).

Candidate models	df	AICc	Δ AICc	AICcWt	BIC	Δ BIC	BICWt
No. Chum Salmon ~ date + I(date²) + s. otter	5	242.19	0	0.35	248.87	0	0.44
No. Chum Salmon ~ date + I(date ²) + s. otter + sed2	6	242.34	0.15	0.33	249.93	1.06	0.26
No. Chum Salmon ~ sed1 + date + I(date ²) + s. otter	6	243.29	1.11	0.2	250.88	2.02	0.16
No. Chum Salmon ~ sed1 + eelgrass + date + I(date ²) + s. otter	7	245.96	3.78	0.05	254.28	5.42	0.03
No. Chum Salmon ~ date + I(date ²)	4	246.2	4.01	0.05	251.94	3.08	0.1
No. Chum Salmon ~ sed1 + eelgrass + date + I(date ²) + s. otter + stream distance	8	248.91	6.72	0.01	257.77	8.91	0.01
No. Chum Salmon ~ year + sed1 + eelgrass + date + I(date ²) + s. otter + stream distance	9	250.87	8.69	0	260.07	11.21	0
No. Chum Salmon ~ year * sed1 * date + I(date ²) + s. otter + eelgrass + stream distance	13	260.11	17.93	0	268.07	19.20	0
No. Chum Salmon ~ year * sed1 * eelgrass * date + I(date ²) + s. otter + stream distance	20	295.24	53.05	0	284.80	35.94	0

Supplementary Table 2.5. Candidate models from negative binomial generalized linear model (GLM) regression results testing the effects of day of year (date), quadratic date (date²), sea otter density (s. otter), qualitative primary (sed1) and secondary (sed2) sediment scores, seagrass biomass (eelgrass), straight-line distance from anadromous streams (stream distance), and categorical year (year) on total number of juvenile Pink Salmon caught per seine. Best-fit model (in bold) as indicated by Akaike Information Criterion (AICc), change in AICc (Δ AICc) AIC weight of evidence that the given model is the most parsimonious (AICc Wt), Bayesian Information Criterion (BIC), change in BIC (Δ BIC), BIC weight of evidence (BIC Wt).

Candidate models	df	AICc	Δ AICc	AICcWt	BIC	Δ BIC	BICWt
<i>No. Pink Salmon ~ date + I(date²) + eelgrass + s. otter + stream distance</i>	7	159.35	0	0.67	167.67	0	0.73
<i>No. Pink Salmon ~ date + I(date²) + eelgrass + s. otter + stream distance + sed2</i>	8	162.31	2.96	0.15	171.18	3.48	0.13
<i>No. Pink Salmon ~ date + I(date²) + eelgrass + s. otter + stream distance + sed1</i>	8	162.37	3.03	0.15	171.24	3.58	0.12
<i>No. Pink Salmon ~ year + date + I(date²) + eelgrass + s. otter + stream distance + sed1</i>	9	165.70	6.35	0.03	174.90	7.13	0.02
<i>No. Pink Salmon ~ date + I(date²) + eelgrass + stream distance</i>	6	173.45	14.10	0	181.26	13.35	0
<i>No. Pink Salmon ~ year * sed1 * eelgrass * date + I(date²) + s. otter + stream distance</i>	20	218.15	58.80	0	207.72	39.78	0

Chapter 3: Shifts in nearshore fish assemblages following reintroduction of an apex predator²

3.1 Abstract

The reintroduction and expansion of sea otters (*Enhydra lutris*) in Southeast Alaska provides an opportunity to explore the role of an apex predator on biodiversity and species composition. We employed a before-after-control-impact framework to quantify changes associated with sea otters in the richness, diversity, evenness, and species composition of nearshore fish assemblages. The impacts of sea otters differed among eelgrass and understory kelp habitats. Fish species richness in eelgrass meadows (*Zostera marina*) increased over time where sea otters recolonized but remained stable in areas without sea otter recolonization. Occurrence of flatfish (*Pleuronectidae*), greenlings (*Hexagrammidae*), and rockfish (*Sebastidae*) increased after sea otters recolonized and contributed to the observed increased richness in eelgrass. Species diversity, evenness, and composition of the fish assemblage within eelgrass meadows were not distinguishable between areas with and without sea otter recolonization. In contrast, in understory kelp beds the fish assemblage composition shifted in areas when sea otters recolonized, characterized by declines in bay pipefish (*Syngnathus leptorhynchus*), rockfish, and juvenile greenling. We did not detect a change in species richness, diversity, or evenness. Mechanisms for increased richness within eelgrass meadows, could be from indirect impacts of sea otters who may facilitate prey availability changes, habitat alterations, or increased niche

² Lia K. Domke, Rebecca J. Cates, Ginny L. Eckert. (2023) Shifts in nearshore fish assemblages following reintroduction of an apex predator. Prepared for submission to *Ecology*

diversity allowing new species to establish themselves in the meadows or a combination therein. Species present after sea otter recolonization existed in low abundances only, aside from rock greenling (*Hexagrammos lagocephalus*), rock sole (*Lepidopsetta* spp.), and *Arctedius* sculpin. Within understory kelp beds, through trophic connections sea otters modify algal abundances and presence of algal species which we hypothesize may indirectly lead to the shifts in fish species composition – as certain species may be more reliant on the habitat provisioned by large-bladed kelps. This work reinforces the role of apex predators as important to structuring nearshore marine fish assemblages.

3.2 Introduction

Top-down effects of apex predators have profound impacts on ecosystems through complex, subtle, and difficult to discern direct and indirect food web interactions (Hairston et al. 1960, Paine 1980, Estes and Duggins 1995). These effects may be underappreciated or unobserved until a predator becomes rare or absent, and ecosystem phase shifts occur (Sutherland 1990). Examples of changes in apex predators and ecosystem shifts are observed in tundra, temperate nearshore marine, coral reefs, and river and lake ecosystems (Paine 1980, Estes and Duggins 1995, Carpenter et al. 2001, Ripple and Beschta 2003, Croll et al. 2005, Sandin et al. 2008). Natural experiments, such as the reintroduction of apex predators, allow for novel research delineating the role of predators. Here we investigate indirect effects of the recolonization of sea otters in Southeast Alaska after previous extirpation.

Sea otters (*Enhydra lutris*) are a well-known keystone species and apex predator altering invertebrate communities and impacting nearshore submerged vegetation; however, few studies investigate indirect effects on fish assemblages. Within canopy kelp forests, sea otters consume

invertebrate herbivores and release kelp from herbivory, leading to an increase in canopy kelps (Estes and Duggins 1995). The keystone role of sea otters in seagrass meadows is more complex. Sea otters in Elkhorn Slough, California mitigate the bottom-up effect of nutrient loading through a four-level trophic cascade (Hughes et al. 2013). Sea otters consume mesopredators (crabs), which increases invertebrate epifauna (isopods and sea slugs) and decreases the total epiphyte load on eelgrass blades, ultimately increasing the health of eelgrass (Hughes et al. 2013). In Southeast Alaska sea otters are correlated with an increase in eelgrass meadow biomass, but not all the documented relationships in the California trophic cascade exist (Raymond et al. 2021). Eelgrass transplant experiments between low and high sea otter abundance sites show increased eelgrass shoot mass and rhizome elongation, indicating a potential relationship between sea otters, belowground competitors, and eelgrass growth (Saavedra 2021). Additionally, disturbance from sea otters digging for clams is associated with increased eelgrass genetic diversity through boosting sexual rather than asexual reproduction of the plants (Foster et al. 2021). Researchers have identified a few indirect effects of sea otters on fish communities primarily in canopy kelp forests (Reisewitz et al. 2006, Markel and Shurin 2015, Silberg 2015). Documented responses to sea otter reintroduction include changes in both increases (e.g. copper rockfish; (Markel and Shurin 2015, Silberg 2015), decreases (e.g. rock greenling; (Reisewitz et al. 2006), and no change (kelp greenling; (Silberg 2015) in abundance as well as shifts in trophic position and diet (Markel and Shurin 2015).

While few studies have described the indirect connections between sea otters, nearshore habitats, and the associated fish assemblage, coastal regions form important habitat for migratory, resident, and juvenile fish species. Submerged underwater vegetation, such as kelp or seagrass, serves as nursery habitat, enhances juvenile fish density, provides protection, food

availability, or spawning grounds (Beck et al. 2001, Lefcheck et al. 2019). Herring (*Clupea pallasii*) often use submerged vegetation as spawning habitat during late spring (Haegele 1985). Juvenile rockfish (*Sebastes* spp.) in Southeast Alaska use shallow nearshore vegetated habitat, both understory kelps and eelgrass, for habitat during the summer and early fall (Murphy et al. 2000). Juvenile rockfish recruit to nearshore shallow habitats before moving out into deeper waters (Love et al. 1991, Murphy et al. 2000). For Pacific Salmon (*Oncorhynchus* spp.) nearshore habitats such as estuaries and eelgrass meadows are highlighted as important habitats for juveniles during the physiologically difficult and life-threatening transition from freshwater to marine waters (Levings 1994, Thorpe 1994, Shaffer 2004, Dumbauld et al. 2015, Kennedy et al. 2018). Eelgrass can provide ample prey, protection from predation, and reduced currents during outmigration (Simenstad et al. 1982, Murphy et al. 2000, Semmens 2008, Johnson et al. 2012, Kennedy et al. 2018). Generally, juvenile salmon are present in higher densities in vegetated habitats than unvegetated habitats. Finally, resident species such as sculpins (*Cottidae*), flatfishes (*Pleuronectidae*), gunnels (*Pholidae*), among others are all present in Southeast Alaskan eelgrass meadows and understory kelp beds (Johnson et al. 2012).

Here we employ a natural experiment associated with sea otter recolonization to evaluate the role of habitat, time, and recolonization of sea otters on fish assemblages. We use a before-after control-impact (BACI) framework to control for temporal variability and identify signals of change in fish assemblages associated with the recolonization of sea otters. We use nearshore fish surveys to evaluate the indirect effect of sea otters in two nearshore submerged marine vegetated habitats on fish assemblages through changes to fish species diversity, evenness and richness and the overall fish species composition.

3.3 Methods

3.3.1 Study area

We use fish surveys conducted in southern Southeast Alaska, focusing on the areas around Prince of Wales Island, Revillagigedo Island, and surrounding smaller islands during the summer months between May - August (Figure 3.1). This region is composed of over 1,000 small and large islands with coastal mountains separated by deep channels and fjords (O'Clair et al. 1997). The outer islands near Revillagigedo and Prince of Wales have similar oceanographic conditions (north-south temperature gradient and inshore-outside salinity gradient) and fish species distribution as described in Johnson et al. (2012). Wave-exposure ranges from very protected to exposed, with a diversity of habitats including highly exposed rocky habitats to low-energy soft-sediment estuaries and protected bays. In high-energy areas, bedrock and cobble beaches have understory (*Laminaria* and *Saccharina* among others) and canopy (*Nereocystis luetkeana* and *Macrocystis pyrifera*) kelps. Low-energy areas and protected bays have expansive and narrow, fringing seagrass meadows (*Zostera marina* and *Phyllospadix sp.*) in low intertidal to subtidal zones.

3.3.2 Fish assemblage composition and abundance

To compare the fish assemblage changes across time and in the presence of an apex predator, we resampled 22 sites (11 eelgrass, 11 understory kelp) between May - August in 2019 and 2021 (Figure 3.1, Table 3.1) that were previously seined by NOAA National Marine Fisheries Service (NMFS) between 1998-2007. Sites were resampled on average within 12 days (± 31) of the original sample date to best account for seasonality in the fish assemblage. Beach seine methods were identical (see Johnson et al. 2012) and used a 37 m long net that tapered in

width from 10 m in the center to 5 m in the sides with variable mesh, 32 mm square mesh along sides, decreasing to 6 mm square mesh towards the center with a 3.2 mm square mesh in the middle. We set the net by boat, brought the net into shore, identified all fish to lowest possible taxonomic level, counted all individuals, and measured a subsample (n=30) to fork length or total length (depending on the species) to the nearest mm. The proportion of measured fish by site and species were used to assign lengths to the unmeasured fish. All contemporary seines occurred around the negative low tides of the month (-0.03 to -1.0 m below mean lower low water, MLLW). The NMFS surveys occurred during daylight low tides and happened within 2 hours of low tide (+1.0 to - 1.5 m below MLLW). At each site, we measured temperature, salinity, and dissolved oxygen at the surface and 1 m deep using a YSI Pro2030 meter. We caught 15,622 individual fish and identified over 65 unique species or species groups.

3.3.3 Sea otter presence

We categorized historical and contemporary presence or absence of sea otters at seine sites using data from standardized aerial surveys of sea otters in Southeast Alaska conducted by the US Geological Survey (USGS) and US Fish and Wildlife Service (USFWS) in 1997, 2003, and 2010 along with our personal observations of sea otters in the study region in 2014 and 2021 (Esslinger and Bodkin 2009, USFWS 2014). We determined whether sea otters were present or absent during historical sampling based on the year the beach seine occurred and the spatial extent of sea otters from surveys. Most seines occurred within 1-2 years of an aerial survey. Of the 11 beach seines in each habitat, sea otters were absent during the historical and contemporary seines at six sites. Five sites in each habitat had sea otters recolonize the area after the historical

seines and before the contemporary seines based on the extent of sea otter from the USFWS survey and personal observations of sea otter presence while beach seining.

3.3.4 Analytical approach

We utilized a *before-after control-impact* (BACI) statistical framework to investigate changes in richness, diversity, and fish assemblages with time and reintroduction of apex predators and the interaction of time and presence of apex predators. This framework allows us to disentangle the effects of time and sea otters on fish assemblages.

We measured the fish community biodiversity with common indices including richness, diversity, evenness, species accumulation curves, and overall multivariate fish assemblages. Species richness (S) represents the total number of species regardless of the abundance of each species. Shannon diversity index (H') (eq. 1) incorporates the number of species present in a community and their relative evenness where 0 represents a community with only one species (Shannon and Weaver 1949). Shannon diversity is sensitive to species richness and is inflated by rare species. H' is calculated by summing the product of the proportion of each species (p_i) and natural log of the proportion of i th species (p_i) from i to S (species richness).

$$H' = - \sum_{i=1}^S p_i \ln p_i \quad (1)$$

Pielou's evenness index (J') (eq. 2) incorporates the abundance of each species and ranges from 0 to 1, where J' close to zero represents a community strongly dominated by a single species and J' close to 1 is when all species are present in equal abundances in the community (Pielou 1966). J' is calculated from the Shannon diversity index (H') divided by the natural logarithm of species richness.

$$J' = H' / \ln(S) \quad (2)$$

Species accumulation curves use random resampling to estimate the expected richness and its standard deviation as the number of sites sampled increases. In addition, we calculated a multivariate measure to understand changes in species composition among sites and sea otter occupation, by determining the similarity or different of sites based on the scaled abundance of fish species at each site.

We first compared diversity, richness, and evenness across time, sea otter presence, and the interaction between time and sea otter presence. We used linear random effects models to quantify the Gaussian response (either diversity, richness, or evenness) with a random effect of site and fixed effects for the factors of time (categorical) and sea otter presence (categorical). We compared model fit using maximum likelihood that allowed a random slope of time and random intercept with just a random intercept. The random effect structure was tested using a likelihood ratio test and the best model refit using Restricted Maximum Likelihood (REML) to better estimate model parameters. For species richness, diversity, and evenness in both habitats, the best fit model for both habitats had a random intercept structure for site and included both time, sea otter presence, and the interaction between time and sea otter presence. We then tested for a significant difference in overall means of the fixed effects ($\alpha = 0.1$). If different, we then determined which combination of levels of the fixed effects contributed to the difference in means using post-hoc emmeans procedure (Lenth 2023).

In addition, we visualized species accumulation curves by calculating the expected species richness across the four groups of the combination of sea otter presence and time (before no sea otters, after no sea otters, before sea otter recolonization, and after sea otter recolonization) in both habitat types. The standard deviation estimated from random permutations for each group and habitat was then calculated.

Next, we examined how the fish assemblage differs temporally and with sea otter presence within eelgrass and understory kelp habitats. We standardized fish catch relative to species' maximum catch across samples to downweight numerous species and then calculated pairwise Bray-Curtis dissimilarity by site for the scaled and untransformed species abundance data (Bray and Curtis 1957, Jongman et al. 1995). We tested the assumption of homogeneity of dispersion using 'betadisper' function in the vegan package (R package) for subsequent permutation-based tests of differences between time and sea otter presence (McArdle and Anderson 2001, Anderson 2006, Oksanen et al. 2022). We evaluated differences in species composition between sea otter presence, time, and the interaction of time and sea otter presence with blocks by site to account for resampling using the 'adonis2' function in the vegan package which performs permutation-based analysis of variance (PERMANOVA) (Oksanen et al. 2022). If a significant difference in overall species composition existed ($\alpha = 0.1$), we used sequential post-hoc pairwise tests to determine which combination of factors were different from each other with site included as a fixed effect to account for resampling by location. We visualized species composition using non-metric multidimensional scaling (nMDS) and plotted species vectors that significantly correlated with each axis. This was done for each habitat type.

For combinations of time and sea otter presence that were significantly different from each other we used similarity percentage (SIMPER) breakdown to determine which species may be driving the difference between the presence of sea otters and sampling time frame. SIMPER analysis compares the groups in pairwise fashion and identifies which species may be contributing most to the average between group dissimilarity based on the Bray-Curtis dissimilarity (Clarke 1993). The percent contribution of species is caused both by the within and between-fixed effect variation in species abundances. For the species that significantly

contributed to the dissimilarity in the fish assemblage we visualized changes in their average abundance before and after sea otter recolonization. All analyses were done in R v 4.1.2 (R Core Team 2021).

3.4 Results

3.4.1 Species richness

Fish species richness in eelgrass meadows increased over time at sites where sea otters recolonized but not in sites without sea otters (Figure 3.2a, Table 3.1), as demonstrated by a significant interaction effect of sea otters and time (p-value = 0.08, Table 3.1). Post-hoc comparisons of interaction effects (i.e. time x sea otter presence) indicated a non-significant (p-value = 0.15; Table 3.1) difference between before and after sea otter recolonization. No temporal difference existed in richness in the region without sea otter recolonization (p-value = 0.98; Table 3.1). Richness in sites before sea otter recolonized averaged 13 (\pm 2.8) and richness after sea otter recolonization averaged 19.2 (\pm 3.5). Despite large among site variation in eelgrass (\pm 4.9), we still observe an interaction effect of time and sea otter presence on fish species richness in eelgrass beds.

Across all sites, we observed a net change of 20 species following sea otter recolonization in eelgrass meadows (detected 24 new species, failed to detect four species). Additional species observed included groups of small sculpins (juvenile Cabezon, *Scorpaenichthys marmoratus*, Roughback Sculpin, *Chitonotus pugetensis*), a few species of greenlings (Masked Greenling, *Hexagrammos octogrammus*, Rock Greenling, *Hexagrammos lagocephalus*, and Painted Greenling *Oxylebius pictus*), flatfish species (Starry Flounder, Sanddabs, *Citharichthys* spp., Soles) and juvenile Rockfishes (*Sebastes* spp.) among others.

Richness at sites where sea otters were absent during both surveys averaged 17.2 (± 4.9) historically and 16.3 (± 6.1) in modern surveys.

Species accumulation curves in eelgrass meadows highlight that richness was different at sites where sea otters recolonized compared to where sea otters are still absent, by the lack of overlap between the species accumulation curves and their confidence intervals (Figure 3.3a). While species richness increased with sea otter recolonization and time, species accumulation curves indicated that total species richness for eelgrass meadows were not fully captured (Figure 3.3a). Sampling five to six sites per group was insufficient to completely sample all the species likely present within eelgrass meadows across time and with the reintroduction of sea otters in this region.

Within understory kelp beds fish species richness increased over time (p-value = 0.04, Figure 3.2b, Table 3.1) but did not vary with sea otter presence (p-value = 0.99) or the interaction of sea otters and time (p-value = 0.54; Table 3.1) and had large among site variation (± 7.8). In regions without sea otter recolonization richness increased over time from 10.5 (± 4.6) to 15.2 (± 5.2) and in areas with sea otter recolonization richness increased slightly from 12.4 (± 3.1) to 15.2 (± 4.1) in the contemporary samples. The species richness accumulation curves appear to saturate more than in eelgrass meadows indicating a better sampling depth for understory kelp bed fish community richness, but do not indicate a difference in fish species richness in understory kelp beds (Figure 3.3b).

3.4.2 Diversity and evenness

Shannon-Weiner diversity index and Pielou's evenness did not change over time, with sea otter presence, or their interaction in either habitat type (Figure 3.2c, d, e, f, Table 3.2, Table

3.3). Diversity values were variable at each site but overall averaged 1.6 (± 0.2) in eelgrass meadows and 1.6 (± 0.3) in understory kelp beds. Apparent declines in evenness in understory kelp beds across time were not significant (p -value = 0.23). Evenness values were similar between habitats and averaged 0.6 (± 0.1) in eelgrass and 0.6 (± 0.1) in understory kelp beds.

3.4.3 Fish assemblage composition

The understory kelp fish assemblage significantly changed between before and after sea otter recolonization as illustrated with a significant interaction effect on fish assemblage (PERMANOVA, Marginal $R^2 = 1.33$, Pseudo F-statistic = 1.31, p -value = 0.04, Figure 3.4). We detected no difference in within-group dispersion (F-statistic = 0.54, p -value = 0.66). A subsequent post-hoc pairwise comparison of the interaction effect found that this difference in the fish assemblage was driven by a change in assemblage at sites where sea otters recolonized (Marginal $R^2=0.96$, Pseudo-F statistic = 1.95, p -value = 0.03) and a significant effect of site (Marginal $R^2=0.67$, Pseudo-F statistic = 2.72, p -value = 0.001). No difference in the fish assemblage composition among sites without sea otter recolonization was detected (Marginal $R^2=0.10$, Pseudo-F statistic = 1.53, p -value = 0.14). The effect of sea otters and time was visualized with non-metric multidimensional scaling (nMDS) adequately in two-dimensions (2D stress = 19%), with anything below 20% considered sufficient to represent the multivariate data in reduced dimensions (Kruskal 1964). Species abundances were significantly correlated with nMDS axes (p -value < 0.05), with the length of the vectors associated with the magnitude of the relationship.

The difference between species composition among the sites where sea otters recolonized was driven by several fish species (based on SIMPER analysis with p -value < 0.1, Table S 3.1)

including rockfish species (Copper, Black, and Brown Rockfish, *Sebastes* spp.), greenlings (Kelp and Rock Greenlings, *Hexagrammidae* spp.), small sculpins (Great and Northern Sculpins, Family *Cottoidea*), and Bay Pipefish (*Syngnathus leptorhynchus*) (Figure 3.6, Table S 3.2).

The eelgrass meadow fish assemblage did not differ with time, sea otter presence, or their interaction (PERMANOVA, Marginal $R^2=0.18$, Pseudo-F statistic = 1.43, p-value = 0.12, Figure 3.5). Similar to understory kelp beds, we detected no within group dispersion (F-statistic = 0.90, p-value = 0.46). Several species were significantly correlated with the nMDS axes (p-value < 0.1) including Sturgeon Poacher (*Podothecus accipenserinus*), Shiner Perch (*Cymatogaster aggregata*), Pacific Sand Lance (*Ammodytes hexapterus*), Pacific cod (*Gadus macrocephalus*), and Pacific Sanddab (*Citharichthys sordidus*).

3.5 Discussion

Sea otters are known keystone predators that have direct and indirect impacts in ecosystems in canopy kelp forests, seagrass meadows, and on nearshore fish assemblages. Our study found an increase in fish species richness in eelgrass meadows with 24 new species across all sites present after sea otters recolonized. Sea otters had a different impact within understory kelp beds; we saw a shift in the fish assemblage characterized by declines in abundance of a few species (Black and Brown Rockfish species, Northern Sculpins, and Red Irish Lords) and an increased occurrence of *Artedius* sculpins, and juvenile rockfish. In both eelgrass and understory kelp beds Rock Greenlings (*Hexagrammos lagocephalus*) increased in abundance. This species has previously shown positive indirect relationships with sea otters and is connected with the sea otter – urchin – kelp trophic relationships in canopy kelp forests in the Aleutian Chain (Reisewitz et al. 2006). Previous research focused on canopy kelp forests and assessed either changes in

trophic levels or increases in abundance or biomass of individual fish species (Reisewitz et al. 2006, Markel and Shurin 2015, Silberg 2015). The indirect effects of sea otters with this study are described in two nearshore habitats, eelgrass and understory kelp beds in Southeast Alaska, and contributes to a priority research area of indirect effects of sea otters (Davis et al. 2019). Our study contributes to the ongoing field of research on the indirect impact of sea otters on nearshore marine ecosystems and expands our understanding of the consequences of recolonization of sea otters on a suite of nearshore fish species and overall fish assemblage.

3.5.1 Eelgrass meadows

Reintroduction of sea otters in southern Southeast Alaska has an important structuring role in nearshore fish assemblages but the effect varies by habitat type. Within eelgrass meadows, sea otter presence indirectly increased species richness but did not impact other metrics of diversity, evenness, or the overall assemblage composition. The interaction of time and sea otter presence increased species richness. Species richness at sites without sea otters did not change (historic survey: 17.2 ± 4.9 ; modern survey: 16.3 ± 6.1) compared to the increase in richness after sea otter recolonized (from 13 ± 2.8 to 19.2 ± 3.5).

The increase in species richness within eelgrass meadows in Southeast Alaska is dominated by flatfish species, juvenile rockfishes, juvenile greenlings, and other small sculpins. As sea otters enhance the genetic diversity of eelgrass meadows (Foster et al. 2021), improve eelgrass growth through reduction in belowground competitors (Saavedra 2021), and increase the eelgrass meadows biomass (Raymond et al. 2021), the synergistic effects of these changes are likely responsible for the changes in the fish assemblage we see in this study. Possible mechanisms for the increase in richness could include changes in prey quality or type, better

habitat condition for refuge, or changes in niches diversity, although other forces may influence nearshore fish assemblages as well.

Prey availability for the fish assemblage within eelgrass meadows in Southeast Alaska could be controlled by top-down or bottom-up processes. Southeast Alaska has lower grazer abundance than other regions (i.e. California) with a clear trophic cascade between sea otters and grazers (Hughes et al. 2013, Raymond et al. 2021). Within eelgrass meadows in Southeast Alaska, Raymond et al (2021) found no difference in grazer biomass across a gradient of sea otter density. It is not clear if a robust fish community is suppressing the grazer population, or the grazer population is resource limited, making it difficult to disentangle the food web dynamics of nearshore fish assemblages. As juvenile migrants, many of the species move among nearshore and offshore habitats and may rely on prey sources from a variety of habitats (Olson et al. 2019, Chittaro et al. unpubl manuscript).

Another important metric for nearshore fish assemblages may be habitat quality of eelgrass meadows and changes to habitats may impact nearshore fish assemblages since fish use these habitats as refuge. This study is unable to measure decadal changes in eelgrass biomass, extent, or leaf size; however, we may expect certain fish species to be more successful in eelgrass meadows after sea otter recolonization based on known changes to meadows related to sea otter presence. Specific nearshore fish species may be evolutionarily better adapted for certain habitat conditions and qualities based on individual body size, swimming ability, life-history traits among others. For example, anthropogenic disturbance in British Columbia eelgrass meadows shifted species compositions from specialist to more generalist fish species. Specialist fishes with lower swimming ability, intolerance to environmental change, or egg guarding characteristics (e.g. juvenile rockfishes (*Sebastidae*), Bay Pipefish (*Syngnathus leptorhynchus*),

Tubesnouts (*Aulorhynchus flavidus*), and Penpoint Gunnels (*Apodichthys flavidus*)) were less abundant in high anthropogenic disturbed sites indicating that they were no longer suited for highly disturbed conditions (Iacarella et al. 2018). After sea otters recolonized eelgrass meadows, we found increased occurrence of Penpoint Gunnels, rockfish species, and greenling species indicating that these meadows may be better suited for lower swimming ability fish that tend to maintain a smaller range than other fish species. We hypothesize that this may be connected to increased eelgrass cover and/or density that reduces currents and may allow for fish with poor swimming ability to occupy meadows (Eckman 1983).

Changes to niche spaces through physical alteration to eelgrass meadows may increase species richness in eelgrass meadows. As sea otters physically disturb eelgrass meadows while foraging, they may encourage an increase in eelgrass-associated fish species. Perhaps through moderate disturbance to eelgrass meadows sea otters enhance richness. The majority of the new species present after recolonization were present in low abundances across all sites. Only a few species were decidedly more abundant after sea otters were present: Rock Greenling, Rock Sole, and *Artedius* sculpin (Figure S1). While sea otter disturbance may open niche spaces for some fish species, the absence of Lingcod (*Cphiodon elongatus*), Tubesnouts (*Aulorhynchus flavidus*), Alaskan Ronquil (*Bathymaster caeruleofasciatus*), and Northern Sculpins (*Icelinus borealis*) at sites where sea otters recolonized highlight that certain species may benefit disproportionately from sea otter recolonization.

One difficulty we encountered was that sampling at five to six sites per group may not have been enough to capture all the species present within the meadows as indicated by the species accumulation curves. An additional three to five sites would likely be required to fully sample the eelgrass fish community richness in southern Southeast Alaska. Potentially, some of

the difference in species richness seen in this study can be attributed to sampling different subsets of the fish assemblage before and after sea otters recolonized.

The prey availability for nearshore species, the quality of eelgrass habitat, and increased niche spaces are likely connected for nearshore fish species. Healthier and larger sized eelgrass meadows may support more and higher diversity of prey species for nearshore fish (Bell and Westoby 1986). Denser eelgrass meadows may provide better cover and refuge for juvenile species within meadows and prevent predation, as seen for juvenile Chinook salmon from birds (Semmens 2008). Moderate levels of disturbance may allow for varied niche spaces and enhance richness in both fish and prey species. The collective and individual impacts of these changes may be responsible for the presence of different species in eelgrass meadows after sea otters are reintroduced.

3.5.2 Understory kelp beds

Within understory kelp beds, fish assemblages in locations where sea otters recolonized differed when compared to those without sea otters, but richness, diversity, or evenness did not change. Interestingly, it was the decline of several fish species post sea otter recolonization that drove the changes seen in the fish assemblage. Bay Pipefish (*Syngnathus leptorhynchus*); Black, Brown, and Copper Rockfishes (*Sebastes* spp.); greenlings (*Hexagrammidae* spp.); and Red Irish Lords (*Hemilepidotus* spp.) all declined in sites with sea otters present. Small sculpins — like those in the *Artedius* family — increased, along with Rock Greenlings and unidentified species of juvenile rockfishes (*Sebastes* spp.). The abundance of these temperate rocky reef fish can be dependent on various factors including indirect effects from apex predators, trade-offs by life-history traits, forage strategies, habitat quality, size, and algae species present. Simenstad et al.

(1977) hypothesized that sea otters would impact fish assemblages through either direct consumption, through provisioning a robust three-dimensional habitat, and/or through nutritional fueling. Sea otters infrequently directly consume finfish when nutritionally dense invertebrates are available, and fish do not constitute a significant portion of their diet (Szpak et al. 2012). Therefore, reasonable hypotheses for the relationship between sea otters and finfish assemblages include changes to prey availability as well as habitat quality, size, and algae species present.

Previous work in kelp forests predict increases in juvenile rockfish species with longer sea otter occupation time (Silberg 2015); however, we do not see a clear increase across all rockfishes in understory kelp beds. We expect rockfish abundance to increase in better habitat or with increased food availability, however, Copper, Black, and Brown Rockfishes all decreased. We would have expected rockfish abundance to increase if the habitat or resources improved in understory kelp beds. Further research may benefit from considering the availability of quality prey resources for nearshore fish.

Instead, we hypothesize that indirect changes to understory kelp habitat itself may be driving the associated change in fish assemblages. While habitat quality data was not available at the sites seined before sea otter recolonization, the habitat at sites after sea otter expansion were dominated by *Saccharina* spp. (primarily *Saccharina latisima* and *Saccharina groenlandica*). In other regions, sea otter presence and reinvasion cause changes to understory and canopy-forming kelps with declines of grazers including shifts from annual algae species (*Desmarestia* spp) followed by “old-growth” perennials (*Pterygophora californica* or *Laminaria setchellii*) (Watson and Estes 2011) or transitions from multi-species algae configurations to single-species beds dominated by *Saccharina groenlandica* (Duggins 1980). The prevalence of *Saccharina* spp. we observed may be indicative of sea otter reintroduction and connected to the shift in species with

declines in Bay Pipefish and several rockfish species while small *Artedius* sculpins and Rock Greenlings increased. This is consistent with other studies that connect certain fish species (rock greenlings) with indirect sea otter trophic connections (Reisewitz et al. 2006).

Non-biological factors may confound the fish assemblage signal we observed in this study. If the recolonization of sea otter increased or allowed kelp species to proliferate and increase in biomass, it may change the sampling efficiency of the net. Rockfish declines seen in the understory kelp beds may be linked to an inability to efficiently seine beds with large *Saccharina* blades. Greenlings and rockfishes may be more difficult to sample with conventional beach seine techniques in dense algae patches. Perhaps another method like baited cameras, environmental DNA or underwater visual surveys would better capture presence of species in dense and complex understory kelp beds. However, without better habitat data from the before sea otter recolonization we cannot determine if sampling efficiency or habitat biomass were significantly different.

Sea otters are one factor amongst many leading to variation in understory kelp assemblages. Algal recruitment, succession, and wave exposure all contribute to kelp forest patchiness (Watson and Estes 2011). Natural demographic cycles including senescence and episodic recruitment of annual kelp species can change the composition of the algal bed. Therefore, detecting the role of sea otters, amongst many processes can require longer-term studies of both habitat and fish assemblages than what was undertaken here.

3.5.3 Conclusions

To date, few studies have investigated changes in fish assemblages associated with sea otter reintroduction within the context of Southeast Alaska's unique temperate ecosystem. Using

a before-after controlled impacted framework is a powerful way to disentangle the effects of sea otters and potential changes in habitat or fish populations over time. We see changes in richness within eelgrass meadows and fish assemblages in understory kelp beds over time; however, the mechanisms driving this shift in assemblage are not yet clear. Forces influencing fish abundances are likely species-specific as evidenced by which fish are driving changes in the understory kelp beds and eelgrass meadows and their subsequent changes in abundances.

The results of this study rely on the consistency of the sea otter trophic connections that have been described elsewhere applying in Southeast Alaska. We assume that when sea otters reduce the grazer population that the habitat — either kelp or eelgrass — is impacted and those changes to the habitat then affect the fish assemblage. Work from the Aleutian Islands to California corroborate the general link between sea otter presence and vegetated habitats (Estes and Duggins 1995, Watson and Estes 2011, Hughes et al. 2013, Raymond et al. 2021) and support this assumption. However, we lack habitat and invertebrate abundance data from before sea otters recolonized the area so we therefore cannot describe the mechanism for shifts in the nearshore fish assemblage at our sites.

This research illustrates the feasibility of resampling locations across time and underscores the benefit of maintaining robust and open data sources. Sites were relocated using GPS and resampled after 12-23 years, within the same month, and during a similar low tide cycle. Despite the difficulty in maintaining consistent effort and sampling efficiency, we were successful in identifying sites, utilizing the same net, and following previous methods.

This work highlights the indirect effect of sea otters on nearshore fish assemblages. Thus far, we know that sea otters compete with humans and can detrimentally impact commercial, subsistence, and personal shellfish fisheries as well as deplete nearshore Dungeness crab

abundances and size (Larson et al. 2013, Hoyt 2015, Ibarra 2021, Cates 2022). In Southeast Alaska we see positive indirect effects of sea otters in the expanse of eelgrass meadows and presence of canopy kelp forests (Raymond et al. 2021).

Further work should attempt to disentangle the mechanisms driving these patterns in nearshore fish assemblages. Eelgrass meadows and understory kelp beds compose a large portion of the nearshore regions in southern Southeast Alaska; therefore, the geographical extent of indirect impacts of sea otters is vast. These indirect impacts on nearshore fish assemblages are likely influenced by the mosaic of nearshore habitats that form important nutrient subsidies from one to another (Olson et al. 2019) and can occur over long time frames of sea otter recolonization and changing trophic dynamics (Watson and Estes 2011). As sea otter populations in Southeast Alaska continue to grow, understanding the long-term dynamics of nearshore habitats, invertebrate, and vertebrate communities and their influences on fish populations will be critical for successful management.

Sea otters modify the coastline they inhabit and have widespread impacts through intricate and complex food web interactions. With the reintroduction of sea otters and their subsequent expansion, understanding the socio-ecological, economic, and environmental impact will continue to be integral to the management of marine resources and our understanding of ecosystem processes.

3.6 Author contributions

Lia K. Domke, Rebecca J. Cates, and Ginny L. Eckert conceived the ideas and designed the methodology. Lia K. Domke collected data, performed the formal analyses and visualization, and wrote the original draft. Rebecca J. Cates collected data and reviewed and edited the manuscript.

Ginny L. Eckert acquired funding, administered and supervised the project, collected data, and reviewed and edited the manuscript.

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3.9 Figures

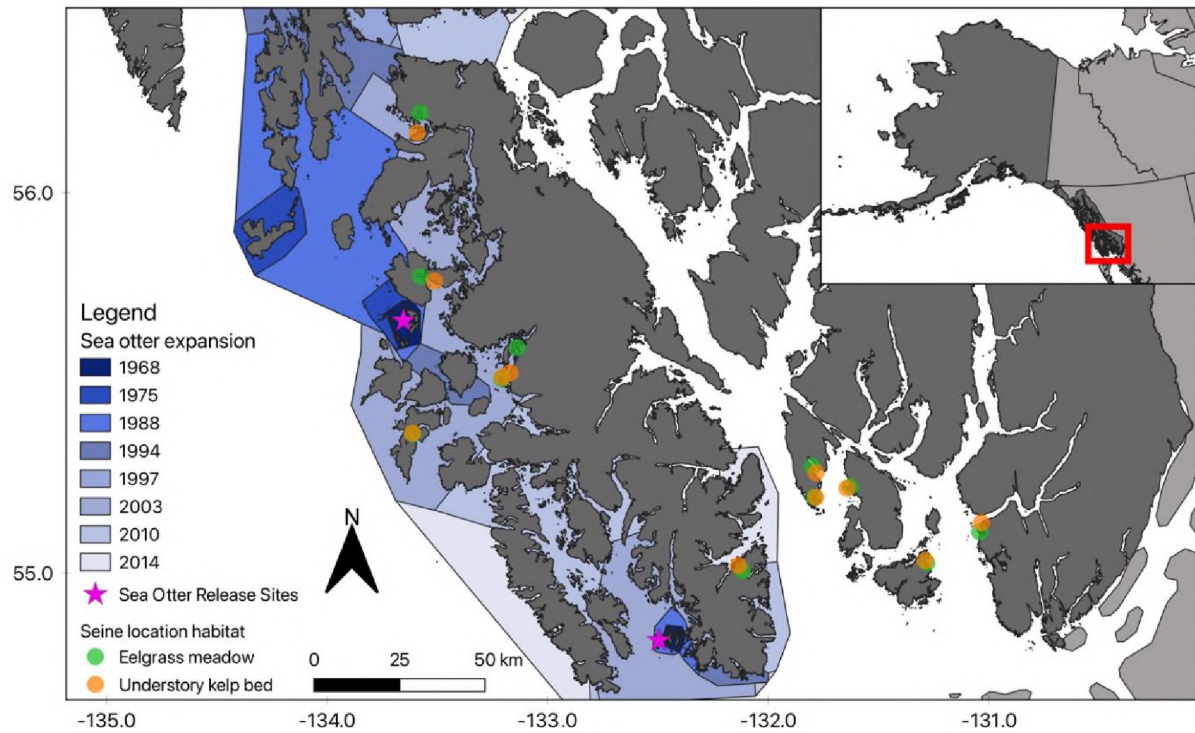


Figure 3.1. Study area including Prince of Wales Island and Revillagigedo Island. Sea otter reintroductions sites are indicated by pink stars and sea otter colonization over time (1969-2014) is indicated with blue shaded polygons. Seine locations re-sampled from the NOAA Atlas of nearshore fishes from 1998-2007 are indicated by colored circles (eelgrass = green, understory kelp = orange).

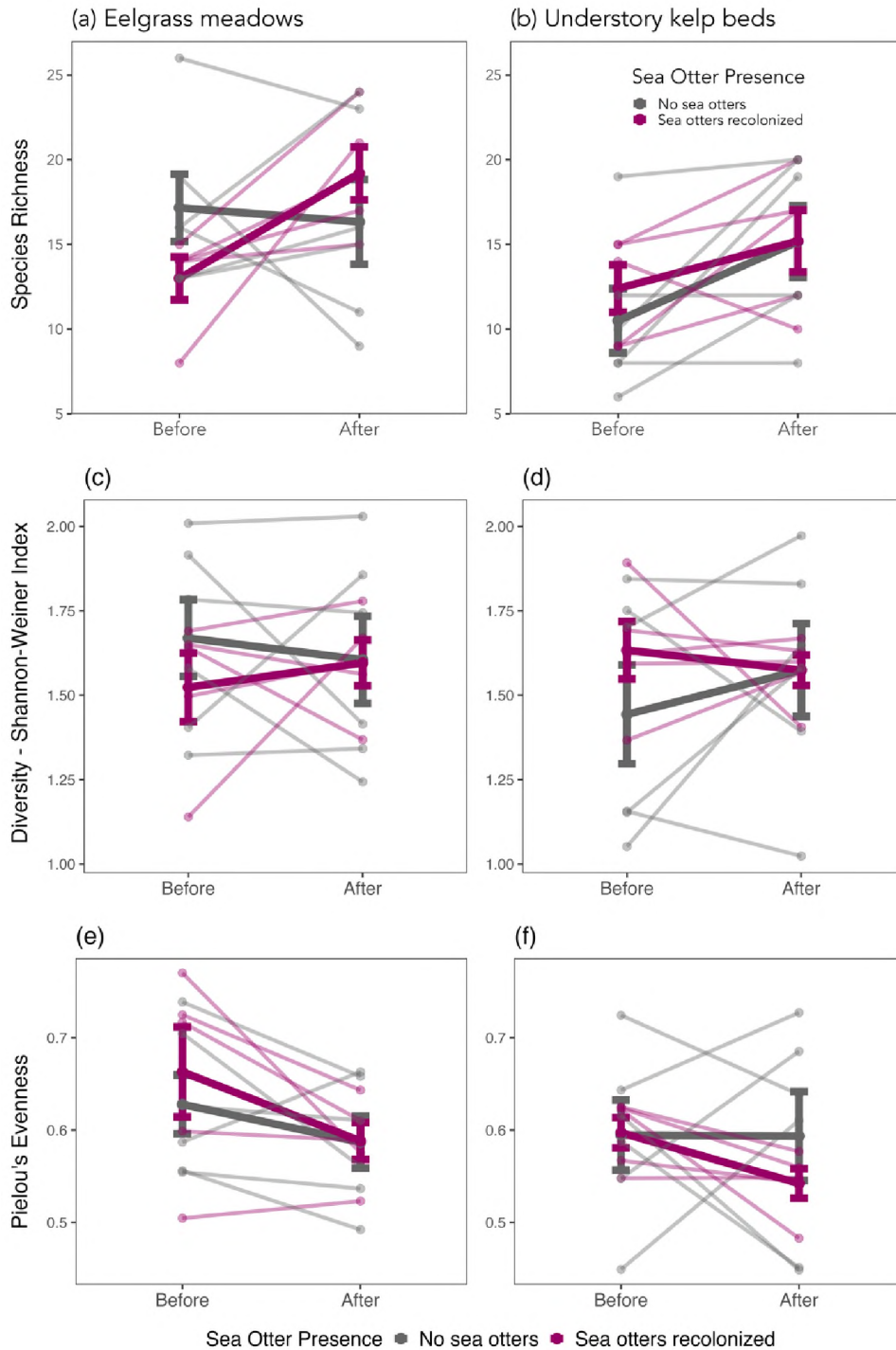


Figure 3.2. Changes in species richness (a-b), diversity (c-d), and evenness (e-f) in eelgrass (a, c, e) and understory kelp (b, d, f) habitats at sites sampled in 1990s (before) and 2019 and 2021 (after) in areas where sea otters did (purple) and did not (gray) recolonize. Dark lines connect the mean values and error bars represent the standard error of those values. Faint lines connect the individual sites that were resampled in each group.

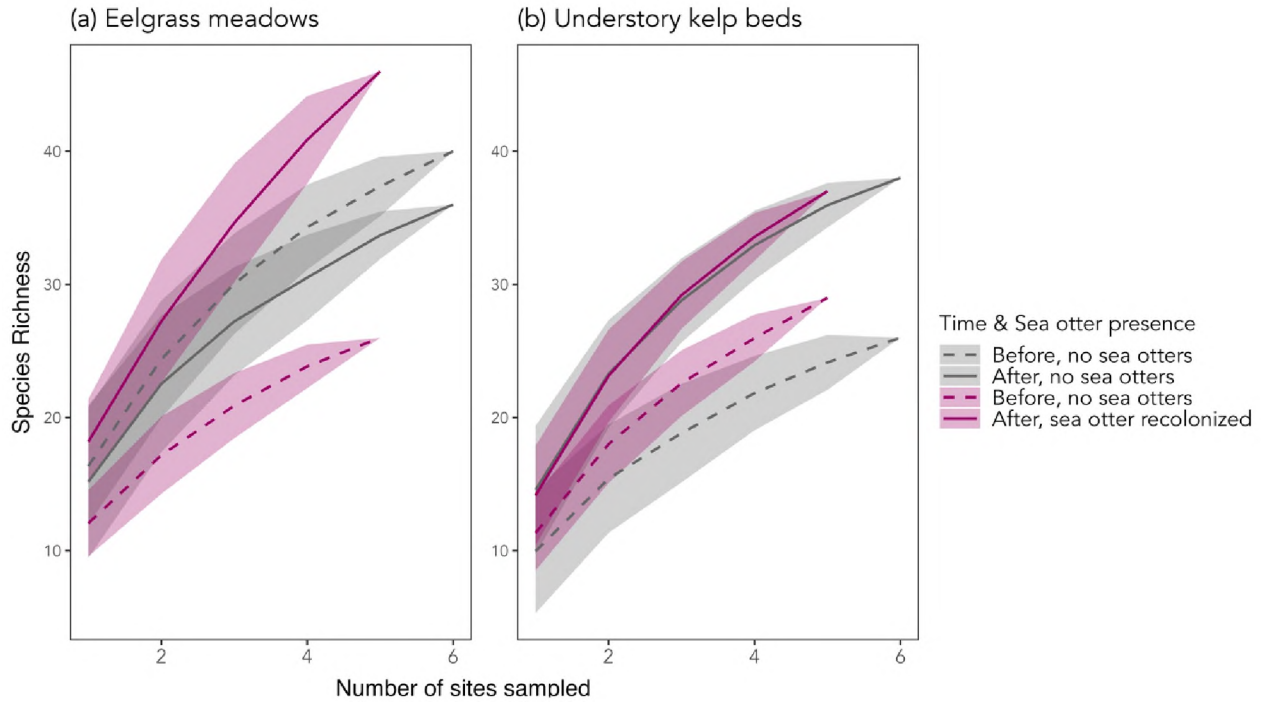


Figure 3.3. Species accumulation curves for (a) eelgrass meadows and (b) understory kelp beds based on sites sampled in the 1990s (dashed lines) and 2019 and 2021 (solid lines) in areas where sea otters recolonized (purple) and in areas where sea otters did not recolonize (gray).

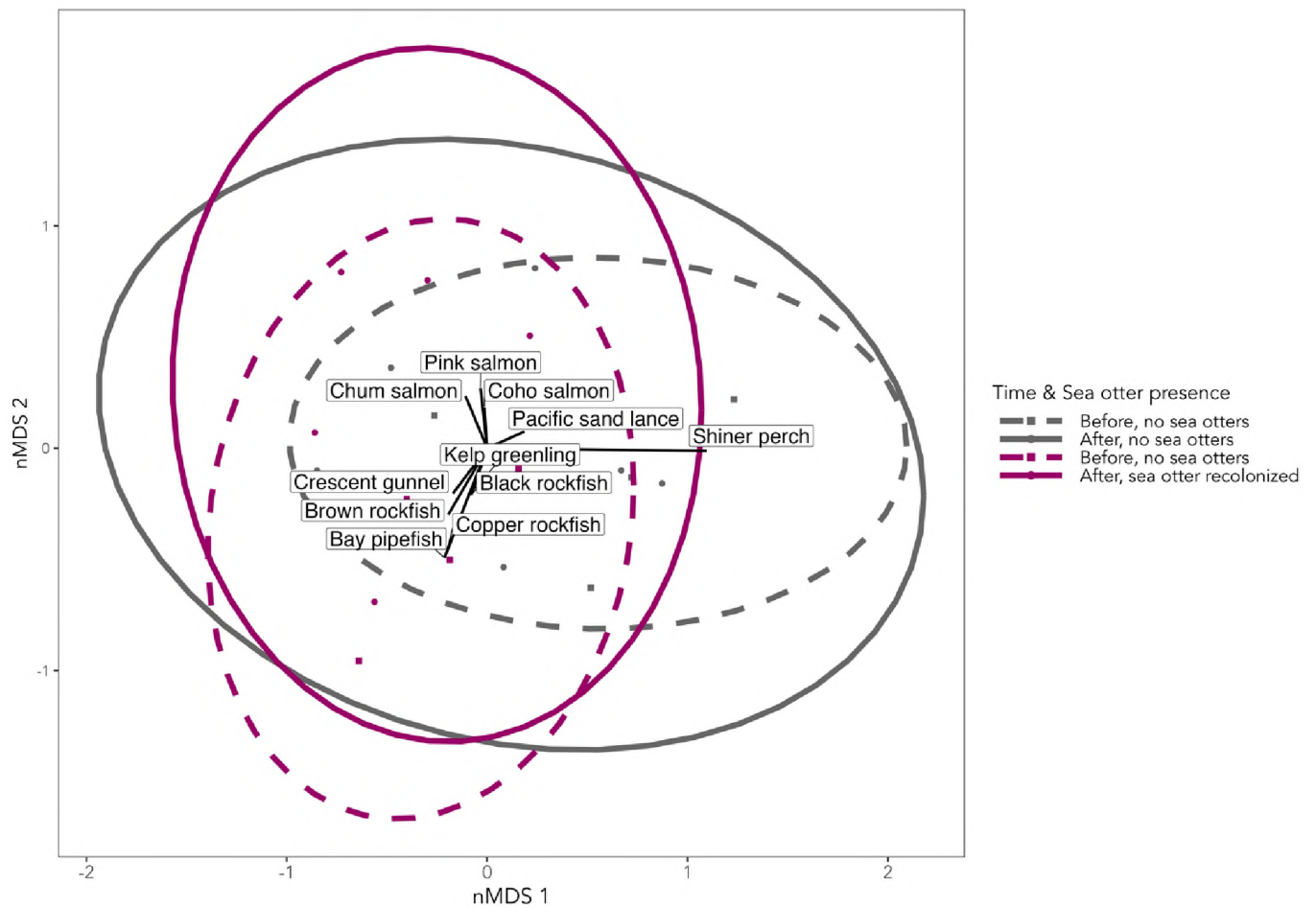


Figure 3.4. Non-metric multidimensional scaling plot of species composition in understory kelp beds of each site (shown by points) with ellipses representing the 95% confidence region for each group of sites (2D stress = 19%). Square points and dashed ellipses indicate sites sampled before sea otter recolonization and round point and solid ellipses represent sites after. Purple points and ellipses represent sites where sea otter recolonized in the after time frame, and gray points and ellipses represent sites where sea otters still have not recolonized. Vectors indicate the species that are significantly correlated with the nMDS axes (p -value < 0.05), with the length of the lines indicating the strength of the relationship.

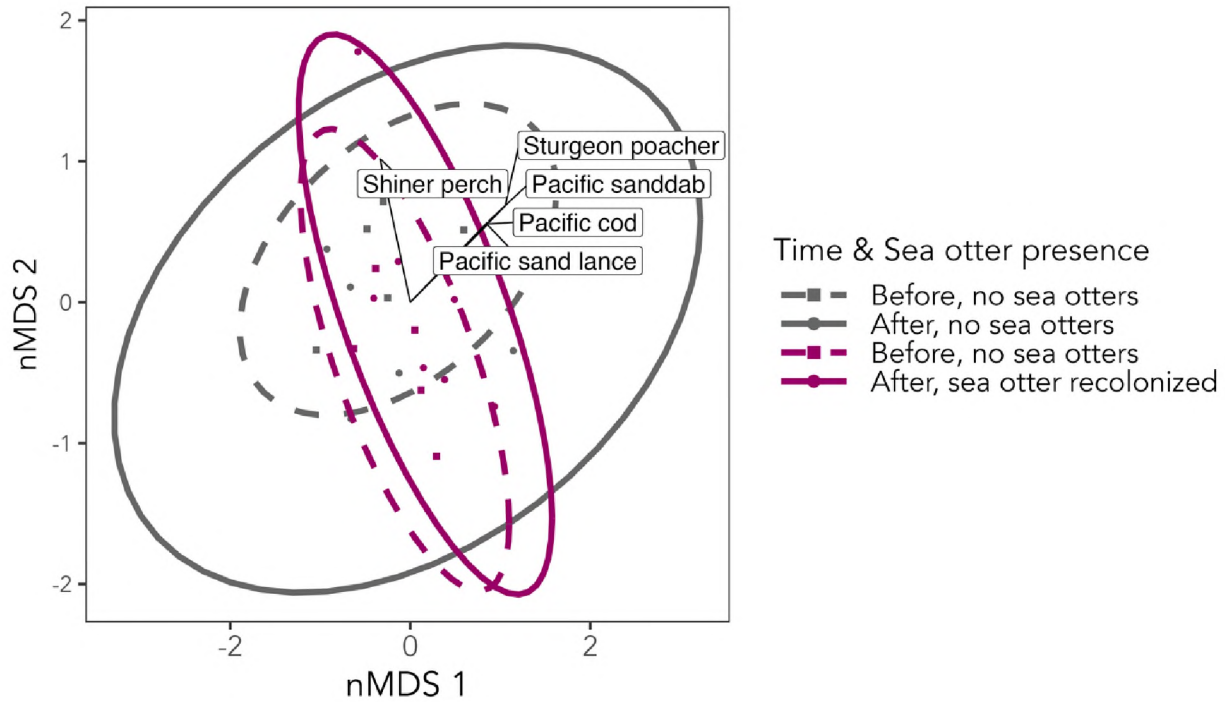


Figure 3.5. Non-metric multidimensional scaling plot of species composition in eelgrass meadows of each site (shown by points) with ellipses representing the 95% confidence region for each group of sites (2D stress = 15.2%). Square points and dashed ellipses indicate sites sampled before sea otter recolonization and round point and solid ellipses represent sites after. Purple points and ellipses represent sites where sea otter recolonized in the after time frame, and gray points and ellipses represent sites where sea otters still have not recolonized. Vectors indicate the species that are significantly correlated with the nMDS axes (p -value < 0.05), with the length of the lines indicating the strength of the relationship.

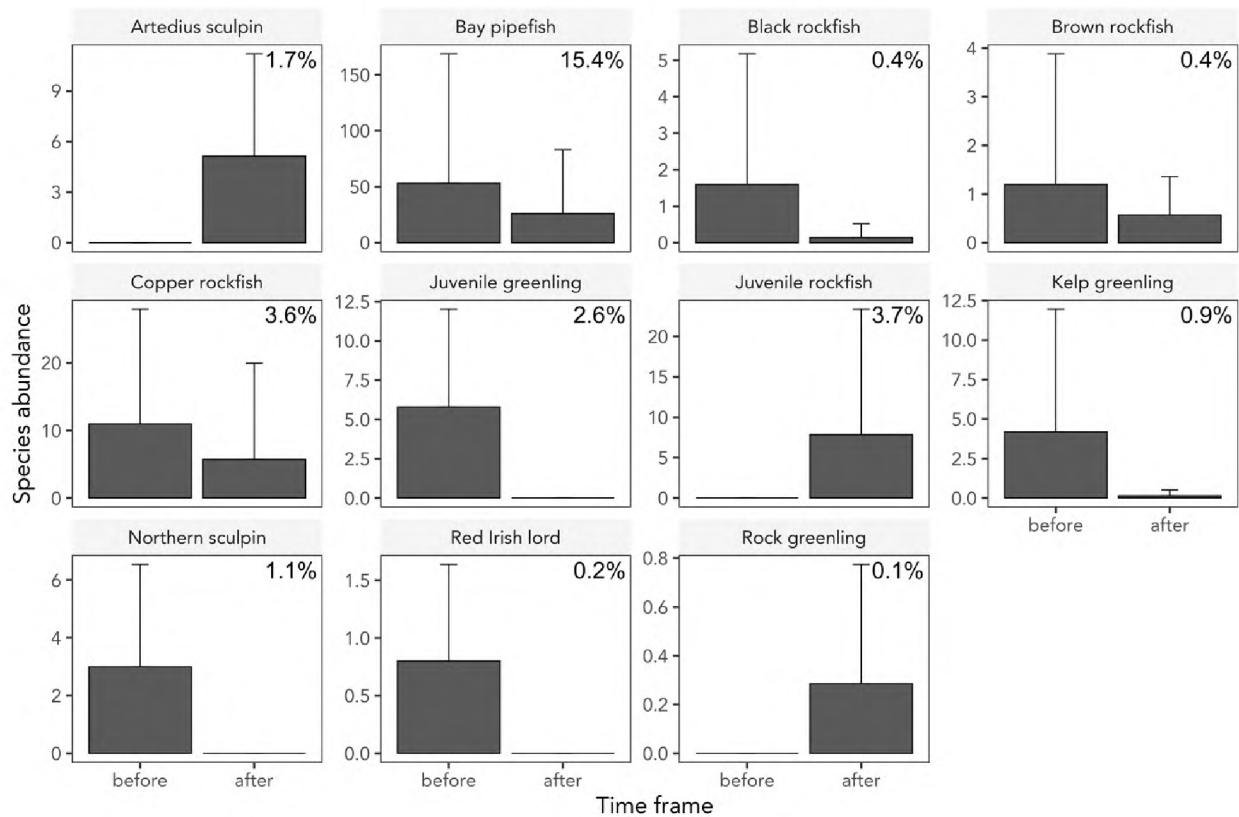


Figure 3.6. Average abundance (\pm SD) of key species in understory kelp beds driving the difference between species composition in sites where sea otters recolonized. Percent values in each panel represent the contribution of each species to the difference between the fish assemblage before and after sea otter recolonization in understory kelp beds.

3.10 Tables

Table 3.1. Summary table of the linear mixed effect models for eelgrass (on left) and understory kelp (right) testing the fixed effect of time (before and after), sea otter presence (no sea otters, and sea otter recolonization), and interaction of time and sea otter presence on species richness in each habitat type. Model includes random effects of site (bay_ID). Reference levels are indicated by square brackets.

<i>Predictors</i>	Eelgrass richness				Understory kelp richness			
	<i>Estimates</i>	<i>Standard Error</i>	<i>P-Value</i>	<i>df</i>	<i>Estimates</i>	<i>Standard Error</i>	<i>P-Value</i>	<i>df</i>
intercept	16.33	1.89	< 0.001	9.00	15.17	1.79	< 0.001	9.00
before after [before]	0.83	2.36	0.732	9.00	-4.67	1.95	0.041	9.00
no sea otters, sea otters recolonized [sea otters recolonized]	2.87	2.81	0.334	9.00	0.03	2.66	0.990	9.00
before after [before] x no sea otters, sea otters recolonized [sea otters recolonized]	-7.03	3.49	0.075	9.00	1.87	2.90	0.536	9.00
Random Effects								
σ^2	16.65				11.45			
τ_{00}	4.85 bay_ID				7.79 bay_ID			
N	11 bay_ID				11 bay_ID			
Observations	22				22			
Marginal R ² / Conditional R ²	0.223 / NA				0.272 / NA			

Table 3.2. Summary table of the linear mixed effect models for eelgrass (on left) and understory kelp (right) testing the fixed effect of time (before and after), sea otter presence (no sea otters, and sea otter recolonization), and interaction of time and sea otter presence on Shannon-Weiner diversity index in each habitat type. Model includes random effects of site (bay_ID). Reference levels are indicated by square brackets.

<i>Predictors</i>	Eelgrass diversity				Understory kelp diversity			
	<i>Estimates</i>	<i>Standard Error</i>	<i>P-Value</i>	<i>df</i>	<i>Estimates</i>	<i>Standard Error</i>	<i>P-Value</i>	<i>df</i>
intercept	1.60	0.10	<0.001	9.00	1.57	0.11	<0.001	9.00
before after [before]	0.06	0.13	0.631	9.00	-0.13	0.13	0.340	9.00
no sea otters, sea otters recolonized [sea otters recolonized]	-0.01	0.16	0.954	9.00	-0.00	0.17	0.998	9.00
before after [before] x no sea otters, sea otters recolonized [sea otters recolonized]	-0.14	0.19	0.495	9.00	0.19	0.19	0.351	9.00
Random Effects								
σ^2	0.05				0.05			
τ_{00}	0.02 bay_ID				0.03 bay_ID			
ICC	0.24				0.34			
N	11 bay_ID				11 bay_ID			
Observations	22				22			
Marginal R ² / Conditional R ²	0.040 / 0.270				0.063 / 0.381			

Table 3.3. Summary table of the linear mixed effect models for eelgrass (on left) and understory kelp (right) testing the fixed effect of time (before and after), sea otter presence (no sea otters, and sea otter recolonization), and interaction of time and sea otter presence on Pielou’s evenness in each habitat type. Model includes random effects of site (bay_ID). Reference levels are indicated by square brackets.

<i>Predictors</i>	Eelgrass evenness				Understory kelp evenness			
	<i>Estimates</i>	<i>Standard Error</i>	<i>P-Value</i>	<i>df</i>	<i>Estimates</i>	<i>Standard Error</i>	<i>P-Value</i>	<i>df</i>
intercept	0.59	0.03	<0.001	9.00	0.59	0.03	<0.001	9.00
before after [before]	0.00	0.05	0.981	9.00	0.04	0.03	0.235	9.00
no sea otters, sea otters recolonized [sea otters recolonized]	-0.05	0.05	0.333	9.00	0.00	0.05	0.979	9.00
before after [before] x no sea otters, sea otters recolonized [sea otters recolonized]	0.05	0.07	0.456	9.00	0.03	0.05	0.496	9.00
Random Effects								
σ^2	0.01				0.00			
τ_{00}	0.00 _{bay_ID}				0.00 _{bay_ID}			
ICC	0.05				0.49			
N	11 _{bay_ID}				11 _{bay_ID}			
Observations	22				22			
Marginal R ² / Conditional R ²	0.070 / 0.116				0.141 / 0.561			

3.11 Supplementary information

3.11.1 Supplementary figures

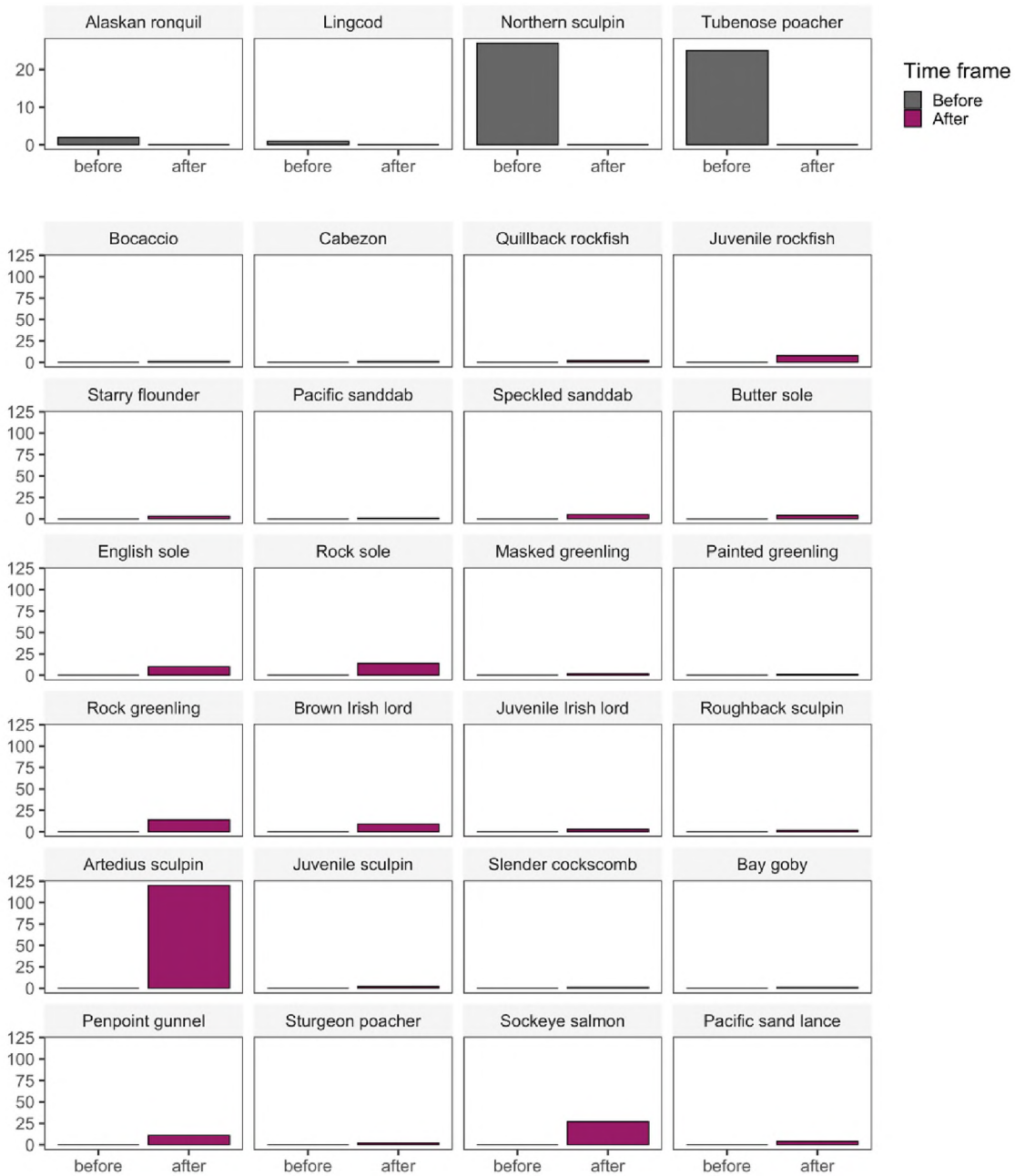


Figure S 3.1. Total abundance of species that were present in one time frame that were not present in the other within eelgrass meadows. The first four panels are species present before that were not present after sea otter recolonization. The remaining 24 panels were species that were present after sea otter recolonization and not before. Note the different y-axis scale.

3.11.2 Supplementary tables

Table S 3.1. Summary table of permutation-based ANOVA (PERMANOVA) to test if the interaction between time and sea otter recolonization impacts the fish assemblage composition in understory kelp beds. Permutations were performed with blocks to account for resampling at sites.

	<i>DF</i>	<i>Marginal R²</i>	<i>Sum of squares</i>	<i>Psuedo-F statistic</i>	<i>P-value</i>
<i>Before After x No sea otters, Sea otters</i>	3	1.3271	0.16471	1.3146	0.038
<i>Residual</i>	20	6.7302	0.83529		
<i>Total</i>	23	8.0571	1.000		

Table S 3.2. SIMPER analysis describing the species the significantly (p -value < 0.1) contribute to the difference between before and after sites with sea otters present in understory kelp beds.

Average contribution indicates the value each species group contributes to the dissimilarity between these two groups. SD indicates the standard deviation of each species group average contribution. Average before is the average abundance of fish species (\pm SD), before and average after is the average abundance of fish species after sea otter recolonization (\pm SD). P-value is the permutation p-value based on the probability of getting a larger or equal contribution of the fish species to the group based on randomizations of the groups.

<i>Fish species</i>	<i>Contribution (mean \pm SE)</i>	<i>Abundance Before (mean \pm SE)</i>	<i>Abundance After (mean \pm SE)</i>	<i>p-value</i>
<i>Bay Pipefish</i>	0.154 (\pm 0.213)	53.00 (\pm 115.72)	26.14 (\pm 56.92)	0.081
<i>Unknown rockfish</i>	0.037 (\pm 0.068)	0.00 (\pm 0.00)	7.86 (\pm 15.52)	0.095
<i>Cooper Rockfish</i>	0.036 (\pm 0.036)	11.0 (\pm 16.97)	5.71 (\pm 14.24)	0.035
<i>Unknown Greenling</i>	0.026 (\pm 0.036)	5.80 (\pm 6.22)	0.00 (\pm 0.00)	0.017
<i>Artemius spp</i>	0.017 (\pm 0.017)	0.00 (\pm 0.00)	5.14 (\pm 6.06)	0.055
<i>Northern Sculpin</i>	0.011 (\pm 0.012)	3.00 (\pm 3.53)	0.00 (\pm 0.00)	0.006
<i>Kelp greenling</i>	0.009 (\pm 0.013)	4.20 (\pm 7.75)	0.14 (\pm 0.38)	0.013
<i>Black Rockfish</i>	0.004 (\pm 0.006)	1.60 (\pm 3.57)	0.14 (\pm 0.38)	0.051
<i>Brown Rockfish</i>	0.004 (\pm 0.004)	1.20 (\pm 2.68)	0.57 (\pm 0.79)	0.014
<i>Red Irish Lord</i>	0.002 (\pm 0.002)	0.80 (\pm 0.83)	0.00 (\pm 0.00)	0.006
<i>Rock greenling</i>	0.001 (\pm 0.002)	0.00 (\pm 0.00)	0.29 (\pm 0.49)	0.066

Chapter 4: Seascape complexity and habitat heterogeneity influences Alaskan eelgrass fish assemblages³

4.1 Abstract

Nearshore marine ecosystems along heterogeneous coasts are composed of dynamic and complex habitats that provide important services including shelter and prey for juvenile, migratory, and residential species. Habitats are often intermixed, even though we often study them in isolation without considering surrounding influences. We examine how fish assemblages differ in Southeast Alaska eelgrass meadows when the surrounding seascape includes or does not include adjacent kelp habitat to test the role of spatial arrangement and composition of nearshore coastlines on associated fish assemblages. We characterize habitats using aerial imagery and field sampling and quantify eelgrass fish assemblages using beach seines. We find increased fish species richness and diversity in eelgrass when it includes adjacent kelp. The shift in the assemblage composition includes greater prevalence of Lingcod, Whitespotted Greenling, sculpins, Pacific Sand Lance, and Pink Salmon. Some species, however, are more abundant within eelgrass habitat without adjacent habitats, including Pacific Staghorn sculpin, Shiner Perch, and Threespine Stickleback. While both Threespine Sticklebacks and Shiner Perch were caught in both types of eelgrass habitats, juveniles were more abundant in eelgrass only seascapes highlighting its nursery importance. An appreciation of seascape complexity wherein nearshore habitats are contextualized is important for evaluating the role of these habitats when making trade-offs and decisions in nearshore habitat conservation and fisheries management.

³ Lia K. Domke, Jessica M. Whitney, Carter J. Johnson, Ginny L. Eckert. (2023). Seascape complexity and habitat heterogeneity influences Alaskan eelgrass fish assemblages. Prepared for submission to *Marine Ecology Progress Series*

4.2 Introduction

Seascapes are marine areas that, in the nearshore, are composed of heterogeneous coastlines formed from mosaics of habitat patches (Boström et al. 2011). These patches are connected through fluxes of energy, detritus, and organisms across patch boundaries. The movement of resources can be mediated by mobile organisms (i.e. fish and mobile invertebrates) and hydrodynamic forces and can be impacted by arrangement and distance to nearby habitats and quality of the habitats themselves (Loreau et al. 2003, Olson et al. 2019). As material and organisms flow from donor habitats to recipient habitats, this movement can change the recipient habitat's flora and faunal community diversity, species density, turnover, and potential nursery functions for specific species (Olson et al. 2019). Depending on the individual species' life history or physiological characteristics, certain composition of patches may constitute either a functionally connected seascape or a barrier to intra-habitat connectivity (Boström et al. 2011). Therefore, modifications in one nearshore patch, through fragmentation, disturbance, changes in quality and configuration, may impact processes in adjacent habitat patches and species' distribution (Loreau et al. 2003). Applying landscape ecology to the marine ecosystem provides an avenue to evaluate the role of spatial patterns and configuration of submerged habitats on their associated faunal assemblages.

Seascape structure can be characterized by spatial arrangement (edge effects, patch sizes, and habitat configuration across a seascape) and composition (type and quality of habitats present) (Pittman 2017, Staveley et al. 2017, Olson et al. 2019). Spatial arrangement of habitats can influence species through edge effects or boundaries that allow fluxes of nutrients and prey (Smith et al. 2011, Olson et al. 2019). The patch size of a specific habitat can increase foraging

area and shelter for species (Semmens 2008, Kennedy et al. 2018). The composition of habitats, including the number of distinct habitats patches and fine-scale variation in quality of habitats within a delineated area or seascape, can influence the number and type of species present through increased niche density compared to homogenous coastlines (MacArthur and MacArthur 1961, Proudfoot et al. 2023). Fish assemblages are influenced by seascape variability within focal habitats of seagrasses (Staveley et al. 2017, Proudfoot et al. 2023), coral reefs (Nagelkerken et al. 2000) and mangroves (Pittman et al. 2007).

Nearshore marine habitats, including eelgrass meadows (*Zostera marina*), are productive shallow water (< 6 m) ecosystems that provide valuable shelter and prey to juvenile and adults faunal communities for survival and growth (Robards et al. 1999, Dean et al. 2000). In concert with other nearshore habitats, they can help decrease coastal erosion, sequester carbon, and provide other ecosystem services. Despite their importance, nearshore ecosystems are susceptible to climatic and anthropogenic stressors, such as coastal development, dredging, eutrophication, pollution, disease, and habitat destruction (Lotze et al. 2006, Aoki et al. 2022). Eelgrass meadows co-occur with numerous vegetated and non-vegetated nearshore habitat patches including understory and canopy kelp forests, sand, gravel, and bedrock and thus the ecological benefit of eelgrass meadows depends not only on the quality of the habitat itself, but the context in which the eelgrass is situated. Understanding how habitat heterogeneity and spatial composition of the nearshore influences fish assemblage is crucial for integrating the role of habitat into species distribution modelling, conservation, and ecosystem-based fisheries management.

Contextualizing eelgrass assemblages within their surrounding environment informs species diversity, richness, and composition and emphasizes that these habitats do not function in

isolation. In eelgrass meadows in British Columbia, juvenile rockfish (*Sebastes* spp.) consumed higher quality prey and had better body condition when they occurred in eelgrass meadows adjacent to canopy kelp forests compared to when they occurred in eelgrass meadows adjacent to unvegetated sand habitats; thereby enhancing the nursery role of eelgrass for juvenile rockfish (Olson et al. 2019). Edge habitat heterogeneity and meadow area influenced species richness and diversity in eelgrass meadows in British Columbia, with increased edge habitat heterogeneity associated with declines in Threespine Stickleback (*Gasterosteus aculeatus*), Pacific Staghorn sculpins (*Leptocottus armatus*) and increased abundance of Black (*Sebastes melanops*) and Copper Rockfish (*Sebastes caurinus*) (Proudfoot et al. 2023). The benefits of adjacent habitats include food supplementation, as demonstrated by the evidence of canopy kelp (*Nereocystis luetkeana*) and epiphytic algae (*Smithora naiadum*) in fish and crab diets when these consumers were caught in eelgrass or kelp beds (Chittaro et al. unpubl. manuscript). The influence of surrounding environments of eelgrass meadows can impact epifaunal communities as well, with epifaunal communities varying within a meadow as much as variation between meadows separated by kilometers (Whippo et al. 2018). Processes influencing eelgrass meadows are likely occurring across seascapes rather than just within habitat patches, indicating linkages among mosaics of patches along the coastline.

The heterogeneous nature of Southeast Alaska's nearshore coasts provides an opportunity to test the role of spatial arrangement and composition of nearshore habitats on associated fish assemblages. Southeast Alaska has over 30,000 km of shoreline composed of dynamic and complex habitats that provide important services for a variety of species, including shelter and prey resources for migratory and residential species. In addition, Alaska and specifically the nearshore and estuarine regions are integral in supplying and supporting commercial fisheries

and seafood availability in the United States. Alaska contributes approximately 60% of the total volume of commercial seafood landed in the U.S. and 46% of U.S. commercial seafood landings by weight are from species that reside in or spend a portion of their life history in the estuary (Lellis-Dibble et al. 2008, National Marine Fisheries Service 2022). Despite their importance and the extensive coastline nearshore habitats occupy, limited research on the role of seascape composition and arrangement for fish assemblages has been conducted in Southeast Alaska. Applying a seascape ecology approach to understanding nearshore coastal environments requires shifting the focus from a single habitat to mosaics of multiple habitat types within the nearshore. This could be particularly beneficial for identifying and protecting essential fish habitat for various species especially for generalists and multi-habitat fish species that are prey (e.g. sandfish, sand lance or pricklebacks) or themselves are essential parts of Alaska's rich commercial, recreational, and subsistence fisheries (Boström et al. 2011).

We are interested in understanding how the nearshore seascape and its mosaic of habitats can influence the eelgrass associated fish assemblage. To understand how variation in nearshore seascapes in Southeast Alaska may impact eelgrass-associated fish assemblages, we sample fish assemblages using beach seines in a focal habitat (e.g. eelgrass) and compare how these fish assemblages differ as a function of the composition of neighboring habitat. The sampled eelgrass meadows occur along a gradient from expansive eelgrass meadows to eelgrass meadows with adjacent habitats (understory kelp, canopy kelp). We first investigate variation in fish species richness, diversity, abundance, and evenness between eelgrass meadows with adjacent habitats (heterogeneous seascapes) and without adjacent habitats (homogeneous seascapes). We hypothesize that closely arranged highly structured habitats (i.e. understory kelp, canopy kelp) adjacent to eelgrass meadows will enhance overall species richness and diversity in the eelgrass

meadow fish assemblage. Next, we explore variation in the overall fish assemblage composition between homogeneous and heterogeneous seascapes and identifies important seascape or habitat metrics that are driving fish species assemblages. We hypothesize that with increased diversity of habitats, even in smaller patch sizes, we will see an influence on fish assemblages and increased presence of nursery associated fishes (rockfishes (*Sebastes* spp.), Shiner Perch (*Cymatogaster aggregata*), Threespine Sticklebacks (*Gasterosteus aculeatus*)) due to increased nearshore complexity and niche diversity. However, we further hypothesize that juvenile fish species will be positively associated with larger mean patch size of the focal habitat due to increased refuge from larger predators (reduced edge effects).

4.3 Methods

4.3.1 Study area

Our sampling area encompassed southern Southeast Alaska (57°N, 131°W to 54°N, 134°W) in the Alexander Archipelago, a region composed of over 1,000 small and large islands with coastal mountains separated by deep channels and fjords (O'Clair et al. 1997). Sampling sites were located on Prince of Wales Island and surrounding smaller islands (Figure 4.1). These southern southeastern islands have a gradient of wave-exposure from very protected to exposed and have a diversity of habitats, ranging from highly exposed rocky habitats to low-energy soft-sediment estuaries and protected bays. In high-energy areas, understory kelps (*Laminaria* and *Saccharina* among others) and canopy kelps (*Nereocystis luetkeana* and *Macrocystis pyrifera*) occupy rocky shores. On the other end of the spectrum, very protected shorelines have both expansive and narrow, fringing seagrasses meadows (*Zostera marina* and *Phyllospadix* sp.) in low intertidal to subtidal zones.

4.3.2 Site selection

We sampled the fish assemblage within eelgrass meadows (*Zostera marina*) at all sites (n = 19); however, we selected eelgrass meadows on a gradient from expansive eelgrass meadows with homogeneous seascapes to heterogeneous seascapes of eelgrass meadows with adjacent habitats (understory kelp, canopy kelp). Candidate sites were identified using an historical and publicly-available aerial imagery and shoreline characterization dataset completed in 2004-2010 called ShoreZone (Harper and Morris 2014). We used this dataset to identify potential sites with eelgrass meadows with “patchy” or “continuous” distributions that were located within areas with “protected” wave exposure. Final site selection were confined to sites that contained eelgrass meadows that were large enough to be sampled using a large beach seine (minimum 40 m in length) with eelgrass that extended into the low-intertidal/subtidal. In addition, we selected eelgrass meadows from “Homogeneous seascapes” where eelgrass was the primary habitat patches or “Heterogeneous seascape” where eelgrass meadows contained adjacent habitats in proximity to the fish sampling location. Habitat characterization of a site extended in a 200 m radius from the focal eelgrass meadow where fish sampling took place and included the low intertidal to lower visible underwater edge of the habitat.

4.3.3 Fish assemblage composition

To compare the fish assemblage composition across nearshore coastlines, we sampled homogeneous seascapes (n = 9) and heterogeneous seascapes with adjacent habitats (n=10) using beach seine methods (as described in Johnson et al., 2012). Sites were sampled in June - July in 2021 and 2022 during the negative low-tide cycles (-0.003 to -0.8 m below mean lower low

water, MLLW) with a 37-m variable mesh net tapered in width from 10 m in the center to 5 m in the sides with variable mesh, 32 mm square mesh along sides, decreasing to 6 mm square mesh towards the center with a 3.2 mm square mesh in the middle. We set the net by boat in a round haul, brought the net to shore, and identified all fish to lowest possible taxonomic level, counted, and measured a subsample (n=30) to fork length or total length (depending on the species) to the nearest mm. The proportion of measured fish by site and species were used to assign lengths to the unmeasured fish. We then converted fish lengths to biomass using species-specific length to weight conversions (amended from Raymond et al. 2021b, Supplementary Table 4.1, eq. 1)

$$mass (g) = a * length (cm)^b \quad (1)$$

4.3.4 Habitat and seascape quantification

At each site we measured small-scale habitat metrics after fish sampling. We measured density by counting eelgrass (*Z. marina*) shoots (including flowering shoots) in five 0.5 x 0.5 m quadrats placed adjacent to where fish were sampled to represent the habitat where fish were located. We collected 15 shoots from each quadrat (n = 75), measured their total length (mm), and predicted eelgrass shoot biomass (kg m⁻²) from longest leaf length based on a developed log-log linear relationship between collected biomass and blade length data (from Raymond et al. 2021b, r² = 0.84). A few sites had a mixture of eelgrass (*Z. marina*) and surfgrass (*Phyllospadix serrulatus*), consistent with other observations in Southeast Alaska and Washington (Stephens et al. 2019). Where surfgrass were noted during sampling, we collected and identified minimum of 15 surfgrass plants and calculated the relative proportion of eelgrass or surfgrass present within the 0.5 x 0.5 m quadrat. Surfgrass longest leaf length to shoot biomass relationship was different than eelgrass, so a surfgrass specific relationship was developed from a subset of weighed plants

and used to convert the rest to biomass (kg m^{-2}). At heterogeneous seascape sites in addition to collecting eelgrass data (as outlined above), we quantified nearby habitat metrics in macroalgae patches adjacent to eelgrass patches where fish sampling took place using five 0.5×0.5 m quadrats. We placed quadrats in the nearest adjacent macroalgae patch at similar depth to the eelgrass quadrats. We recorded percent cover of major algae species within the quadrat and removed all attached vegetation from the quadrat. In the lab, macroalgae were weighed to determine total biomass per quadrat per species. This was then scaled to biomass per meter squared (kg m^{-2}). All algae and marine plant biomass were average to site level and species were retained in statistical analyses when the site had more than 0.01 kg m^{-2} . Additionally, if the species only occurred at one or two sites they were removed from analyses.

To quantify site-wide habitat patch composition and arrangement across the seascape, we used low flying (~ 60 m) Unoccupied Aerial Vehicles (UAVs or drones) collecting imagery within a 200 m radius from each fish sampling location (Yang et al. 2023). UAV imagery was collected with a DJI Phantom IV Pro v2 quadcopter with a RGB camera. Flights (following US FAA Part 107) occurred at the lowest point of the daytime low tide (-0.003 to -0.82 m below mean lower low water, MLLW). At each site, we used DJI Ground Station Pro (GS Pro) to set up flight transects with 70 - 80 % overlap between adjacent images and centered the mapping around the beach seine location within the eelgrass meadow and encompassing any adjacent habitats. We marked the underwater deeper edge of the eelgrass meadow with anchored buoys to aid in identifying the underwater edge of the meadow and to ease image alignment and stitching during post-processing. We completed flights with one battery (20 minutes flight time) creating image catalogs with 100 - 300 images depending on the orientation of the site.

Since this study focuses on the low intertidal habitat, we identified habitats in the drone imagery below the mid-intertidal zone and extending to the lower visible underwater edge. Post-processing of the drone imagery included orthorectifying and combining images using Agisoft Metashape (v. 2.0.2) to create orthomosaics. We first aligned photos using matching points between the photos, then built dense point clouds, and a digital elevation model before generating orthomosaics. Using qGIS (v. 3.10), we manually outlined the extent of all habitats, including continuous eelgrass meadow, patches of eelgrass, understory kelps, or canopy kelps present in a radius of 200 m from the beach seine location. Due to the shape and location of the beach, the total area (km²) quantified varied by site. From the orthomosaics with delineated habitat patches, we calculated the spatial arrangement of the seascape including total structured (i.e. vegetated) area (km²), number of structured habitats patches, proportion of each habitat type present in the seascape area (including non-vegetative habitats), and average ratio of area to perimeter length (m) for eelgrass patches (influence of edge). Additionally, we calculated the composition of the seascape including number of different habitats (habitat richness), patch size (km²) of the focal habitat (eelgrass meadow).

4.3.5 Data analyses

To investigate the influence of seascape variability through changes in habitat spatial arrangement and composition, we evaluated changes in the fish assemblage through univariate metrics and shifts in multivariate fish assemblage composition. We first examined univariate responses (total fish abundance, total fish biomass, richness, diversity, and evenness) in either homogeneous seascapes or heterogeneous seascapes (eelgrass with adjacent habitats). We calculated species richness (S) as the total number of species at each site not considering the

abundance of each species. We determined diversity from the Shannon-Wiener diversity index (H') (eq. 2) which incorporates species richness in a community and their relative evenness (Shannon and Weaver 1949). Shannon diversity is inflated by rare species and ranges from 0 representing a community with only one species to the log of species richness. We calculated H' by summing the product of the proportion of each species (p_i) and natural log of the proportion of i th species (p_i) from i to S (species richness).

$$H' = -\sum_{i=1}^S p_i \ln p_i \quad (2)$$

Pielou's evenness index (J') (eq. 3) ranges from 0 to 1, where J' close to zero represents a community strongly dominated by a single species and J' close to 1 is when all species are present in equal abundances in the community (Pielou 1966). J' incorporates the abundance of each species and we calculated it from the Shannon diversity index (H') divided by the natural logarithm of species richness.

$$J' = H' / \ln(S) \quad (3)$$

We tested if categorical habitat type (either homogeneous or heterogeneous seascapes) altered the univariate metrics of fish abundance (number seine⁻¹), fish biomass (kg seine⁻¹) richness, diversity, and evenness. To ensure we were relating sites of comparable sizes, we first evaluated if total habitat area surveyed per site differed between habitat type using one-way analysis of variance (ANOVA). We then proceeded with each measure of univariate response metrics and verified that they met assumptions of normality and constant variance. Species richness required no transformation. Based on the log-likelihood profile of power transformations, we transformed diversity by raising it to the power of the fourth, log transforming total fish abundance, and taking the reciprocal of fish biomass (Box and Cox 1964). Species evenness could not be transformed to constant residual variance, so we used a Mann-

Whitney U test which is robust violations of constant variance and normality (Mann and Whitney 1947). For fish abundance, fish biomass, richness, and diversity we tested for difference between habitat types using one-way ANOVA ($\alpha = 0.05$).

We tested the hypothesis that the fish assemblage composition differs between homogeneous and heterogeneous seascapes using a multivariate analytical approach. To address skew in species abundance data, we log transformed after adding one to abundance. We standardized fish catch to species maximum to downweight numerous species and calculated Bray-Curtis dissimilarity metrics for the scaled and transformed species abundance data (Bray and Curtis 1957, Jongman et al. 1995). We tested the assumption of homogeneity of dispersion using 'betadisper' function in the vegan package for subsequent permutation-based tests of differences with habitat type, either homogeneous seascape and heterogeneous seascape and year (McArdle and Anderson 2001, Anderson 2006, Oksanen et al. 2022). We evaluated differences in species composition between habitat types using the R 'adonis2' function in the vegan package, which performs permutation-based analysis of variance (PERMANOVA) (Oksanen et al. 2022). We visualized the species composition using non-metric multidimensional scaling (nMDS) and plotted the species vectors that significantly correlated with each axis.

To evaluate the relationship between the nearshore fish assemblage and habitat metrics, we examined correspondence in the variability in the fish assemblage with that of the habitat metrics and looked at patterns of different habitat metrics with the fish assemblage. All habitat metrics were standardized to mean of zero and standard deviation of one to account for measurements with different units and Euclidean distances between each site were calculated to determine how different or similar each site was in terms of habitat values. We tested overall

correspondence between fish assemblage and the habitat metrics with a Mantel test (Oksanen et al. 2022).

We identified which habitat metrics were significantly correlated with nMDS axes and presented those habitats with the vectors alongside the species composition, with the direction and length of the arrows indicating the direction and magnitude of steepest increase.

If nearshore fish assemblages were significantly different in each habitat as determined by the PERMANOVA above, we used similarity percentage (SIMPER) breakdown to determine which species may be driving the difference between habitats. SIMPER analysis compares the groups in pairwise fashion and identifies which species may be contributing most to the average between habitat dissimilarity based on the Bray-Curtis dissimilarity (Clarke 1993). The percent contribution of species is caused both by the within and between-fixed effect variation in species abundances. For the species that significantly contributed to dissimilarity in the fish assemblage, we visualized changes in their average abundance in each eelgrass meadow type. A subset of the fish species included highly abundant juveniles, so we repeated all the above multivariate methods using species biomass (g). All analyses were done in R v 4.1.2 (R Core Team 2021).

4.4 Results

4.4.1 Fish assemblage diversity metrics

Heterogeneous seascapes had significantly greater fish species richness (mean \pm SD, 20.6 ± 3.4) and diversity (1.8 ± 0.1) compared to homogeneous seascape richness (14.9 ± 4.3) and diversity (1.4 ± 0.2) (Figure 4.2c-d, Table 4.1). Species found in homogeneous seascapes, but not heterogeneous seascapes included Dolly Varden (*Salvelinus malma*), Coho Salmon (*Oncorhynchus kisutch*), Sockeye Salmon (*Oncorhynchus nerka*), Grunt Sculpin (*Rhamphocottus*

richardsonii), C-O Sole (*Pleuronichthys coenosus*), Yelloweye Sole (*Limanda aspera*), and Giant Wrymouth (*Cryptacanthodes giganteus*) (Supplementary Table 4.1). Greater species richness in heterogeneous seascapes was from the presence of several species of rockfishes (*Sebastes* spp), greenlings (*Hexagrammous* spp), Walleye Pollock (*Gadus chalcogrammus*), Cabezon (*Scorpaenichthys marmoratus*), Sturgeon Poacher (*Podothecus accipenserinus*), Pink Salmon (*Oncorhynchus gorbuscha*), Pacific Sandfish (*Trichodon trichodon*), Arctic Shanny (*Stichaeus punctatus*), Black-eyed Goby (*Rhinogobicops nicholsii*), and Speckled Sanddab (*Citharichthys stigmaeus*) (Supplementary Table 4.1). In contrast, we observed no difference between fish abundance (no. seine⁻¹), total fish biomass (kg seine⁻¹) or evenness between habitat types (Figure 4.2a, 4.2b, 4.2e; Table 4.1). Total fish count per seine was 1,244 (± 740) in homogeneous seascape and slightly lower in heterogeneous seascapes (729 \pm 380). Total fish biomass in homogeneous seascapes was greater (9.7 \pm 16.8) than in heterogeneous seascapes (6.0 \pm 4.3). Evenness was consistent between homogeneous (0.5 \pm 0.1) and heterogeneous seascapes (0.6 \pm 0.04).

The total area sampled using aerial imagery per habitat type did not differ between homogeneous seascapes (24.8 \pm 14.8 km²) compared to heterogeneous seascapes (32.4 \pm 11.8 km²) meadows (ANOVA, F-statistic = 1.58, P-value = 0.23). Descriptively homogeneous seascape sites had large numbers of eelgrass patches and a large proportion of eelgrass. Homogeneous seascapes had greater average eelgrass biomass (0.3 \pm 0.2 kg m⁻²) compared to heterogeneous (0.04 \pm 0.03 kg m⁻²) seascapes (ANOVA, F-statistic = 14.10, P-value = 0.002). We observed trends of greater algae and *Saccharina* spp. biomass in heterogeneous seascapes compared to homogeneous seascapes (Figure 4.3).

4.4.2 Fish assemblage composition

Nearshore fish assemblages were distinct between homogeneous and heterogeneous seascapes as illustrated by a significant effect of habitat type when using count-based species abundance by site (PERMANOVA, Marginal $R^2 = 0.20$, Pseudo F-statistic = 4.29, p-value = 0.001, Figure 4.4). We detected no difference in within-group dispersion, allowing us to attribute the difference in the assemblage solely to differences between habitats (F-statistic = 0.13, P-value = 0.72). The difference in assemblage composition was visualized with non-metric multidimensional scaling (nMDS) in two-dimensions (2D stress = 15.4%) with anything below 20% considered sufficient to represent the data (Kruskal 1964). Sites in different habitat types separated primarily along the first nMDS axis. Additionally, we included fish species abundances and environmental covariates that were significantly correlated with nMDS axes (p-value < 0.05), with the length of the vectors associated with the strength of the relationship.

The relationship among the nearshore fish assemblage composition and environmental co-variates indicated that only a few variables were influential. We did not detect overall correspondence between fish species composition variability and habitat metrics variability (Mantel stat = 0.10, P-value = 0.24). However, four habitat parameters out of 20 were significantly correlated with the nMDS axes (p-value < 0.05) including small-scale algae biomass of *Saccharina* spp, *Ulvaceae*, *Neorhodomela* spp, and one metric of seascape complexity, habitat richness (Figure 4.4, Table 4.2).

Ten fish species out of 56 significantly contributed to the shift in fish assemblage between homogeneous and heterogeneous seascapes. We observed greater counts of Threespine Sticklebacks (*Gasterosteus aculeatus*), Shiner Perch (*Cymatogaster aggregata*), and Pacific Staghorn Sculpin (*Leptocottus armatus*) in homogeneous seascapes compared to heterogenous

seascapes (Figure 4.5). Conversely, the remainder seven species, including Lingcod (*Cphiodon elongatus*), Whitespotted Greenling (*Hexagrammos stelleri*), juvenile Artedius (*Artedius* spp), Silverspotted Sculpin (*Blepsias cirrhosus*), Pacific Sand Lance (*Ammodytes personatus*), Copper Rockfish (*Sebastes caurinus*), and Pink Salmon (*Oncorhynchus gorbuscha*) were more abundant in heterogeneous seascapes compared to homogeneous seascapes. Collectively, these ten species contribute 19.3% of the difference in the fish assemblage composition between these two habitats, with the other 80.7% divided among the remaining 46 species caught.

When we compared fish sizes of the top three species contributing to the difference in the fish assemblage from each habitat type, we observed smaller or juvenile sized individuals present. Both Threespine Sticklebacks and Shiner Perch had bi-modal size distributions in homogeneous seascapes (Figure 4.6). The other top contributing species (Pacific Staghorn Sculpins, Lingcod, Whitespotted Greenlings, and juvenile *Artedius* spp.) did not exhibit strong size distribution shifts between habitat type, however, the majority of the individuals caught appeared to be small (<150 mm fork length) (Figure 4.6).

Biomass-based species composition exhibited similar species and environmental patterns including distinct fish assemblage between homogeneous and heterogeneous seascapes (PERMANOVA, Pseudo F-statistic = 4.31, P-value = 0.001, Figure 4.7) and no within-group dispersion (F-statistic = 1.40, P-value = 0.25). Two habitat metrics, *Saccharina* spp. biomass and *Neorhodomela* spp., were significantly correlated with the nMDS axes (p-value < 0.05) (Figure 4.7, Table 4.2). Species vectors included seven species that were the same as the count-based analysis and four that were not present in the count-based analysis (Figure 4.8, Supplementary Table 4.1). Percent similarity analysis (SIMPER) indicated that the same species as the abundance-based SIMPER analysis were responsible for the difference in fish assemblage

composition between homogeneous and heterogeneous seascapes, aside from the absence of Silverspotted Sculpins and Threespine Sticklebacks (Figure 4.8).

4.5 Discussion

Habitat heterogeneity and seascape attributes influenced metrics of nearshore eelgrass associated fish assemblages. Distinct assemblages exist in heterogeneous seascapes that are situated within a matrix of functionally interconnected habitat patches with fish assemblages characterized by increased species richness and greater diversity compared to large expansive eelgrass meadows in homogeneous seascapes. We observed species-specific responses to the composition of the seascape, with certain species more successful in homogeneous seascapes and others more prominent in heterogeneous seascapes. The distribution of a species across coastal regions is reliant on individual species' relationship to the habitat and its resources, with specialist species adapted to specific habitat, prey, or environmental conditions and generalist species more resilient to changes to those conditions. However, because of these differences in life-history strategies, we see species-specific responses to variation in marine seascapes.

Species that were more abundant in heterogeneous seascapes included Lingcod (*Cphiodon elongatus*), Whitespotted Greenling (*Hexagrammos stelleri*), juvenile Artedius (*Artedius* spp), Silverspotted Sculpin (*Blepsias cirrhosus*), Pacific Sand Lance (*Ammodytes personatus*), Copper Rockfish (*Sebastes caurinus*), and Pink Salmon (*Oncorhynchus gorbuscha*). These seven species contributed to the difference in the fish assemblage composition between homogeneous and heterogeneous seascapes.

The prevalence of Lingcod in heterogeneous eelgrass is particularly interesting because of how infrequently (<20 individuals) this species was caught in the same region in previous

years (2017 - 2020) in other studies conducted in this geographic area (Raymond et al. 2021b, 2021a, Chapter 2, Chapter 3). Studies in British Columbia and Oregon suggest that juvenile Lingcod prefer structurally complex habitats (Cass et al. 1990, Petrie and Ryer 2006). In our current study (2021-2022) they were nearly exclusively caught in heterogeneous seascapes except for one instance (Guktu Bay) in a homogeneous seascape. The majority of the Lingcod in our study were young of the year or young juveniles (fork length 55 - 148 mm), when they began to be piscivorous and hunt in eelgrass or kelp beds, likely relying on abundant prey resources in the nearshore habitats (Cass et al. 1990). Likely, not only the structural complexity of nearshore habitat matter to juvenile Lingcod, but also the context of the surrounding habitats within the seascape as seen in other systems for different species (Bradley et al. 2019). Adjacent habitats likely confer an additional benefit for juvenile Lingcod and these heterogeneous seascapes represent an important nearshore nursery for Lingcod that have been potential underestimated. Ecologically, Lingcod serve as prey and predator being consumed by marine mammals and is a top predator in nearshore rocky habitats targeting other commercially important species including *Sebastes* spp and Pacific Herring (*Clupea pallasii*) (Cass et al. 1990, Beaudreau and Essington 2007). Due to the susceptibility of Lingcod to overfishing (Cass et al. 1990), their ecological, economical, and cultural importance, it is worthwhile to carefully consider the context of the identified essential or critical habitat for their conservation and management.

While our observation of greater abundance of Lingcod in heterogeneous seascapes is novel, other species, such as juvenile rockfishes are known to benefit from adjacent habitats. We observed greater abundance of Copper Rockfishes in heterogeneous seascapes consistent with other research that linked improved copper rockfish body condition in eelgrass meadows adjacent to canopy kelp forests (Olson et al. 2019). Access to better prey resources, could benefit

other species as well, as resources subsidies from bull kelp forests to fish and invertebrates has been documented in eelgrass meadows (Chittaro et al. unpubl. manuscript) and could be connected to increased abundances of sculpins, Whitespotted Greenlings, and Pink Salmon. In particular, in heterogeneous seascapes, a few large (>200 mm) Whitespotted Greenlings indicated that they may be present to predate on the abundance of smaller and /or juvenile species in the meadows. Additionally while not investigated here, it is worth noting that resources subsidies can be bidirectional with eelgrass and associated epiphytic algae constituting a subsidy from eelgrass to other adjacent habitats (Olson et al. 2019, Chittaro et al. unpubl. manuscript).

Conversely, in homogeneous seascapes, we observed greater number of Threespine Sticklebacks, Shiner Perch, and Pacific Staghorn Sculpins, which may be related to the availability of expansive eelgrass meadows. The nursery role of eelgrass meadows, for some of these and other species, is well-described (Beck et al. 2006, Lefcheck et al. 2019, Olson et al. 2019, Proudfoot et al. 2023). In June and July when our sampling took place, both Threespine Sticklebacks and Shiner Perch form large schools of juvenile and adults within eelgrass meadows as indicated by the bi-modal size distribution, potentially relying on the resources and shelter present there. Interestingly, in our biomass-based analyses, Threespine Sticklebacks did not contribute to the difference in species composition between habitat types, which was perhaps connected to the number of highly abundant, but small juvenile individuals that drove the patterns in abundance-based analyses. In our study we did not see the same abundant schools of Threespine Sticklebacks and Shiner Perch within eelgrass meadows surrounded by different habitats, indicating perhaps that large continuous eelgrass meadows are preferred nursery habitats for these species. The increased abundance of Pacific Staghorn Sculpins in

homogeneous seascapes, could be related to their preference for muddy or sandy bottoms. Eelgrass enhances wave attenuation and sediment stabilization (Eckman 1983, Meysick et al. 2022), with more expansive eelgrass meadows potentially more associated with these soft-sediment habitats. Likewise, in British Columbia as edge habitat heterogeneity increased, Threespine Sticklebacks and Pacific Staghorn Sculpins declined (Proudfoot et al. 2023) further indicating a potential preference for continuous eelgrass meadows in homogeneous seascapes.

We found that one seascape variable, site habitat richness, was significantly correlated with the division of the fish assemblage composition we observed between homogeneous and heterogeneous seascapes; however, we did not see that correlation with the other seascape variables. We initially included habitat as a categorical variable (either homogeneous or heterogeneous eelgrass) when realistically these meadows are not discrete habitats, but rather patches in a larger mosaic of interconnected habitats composing nearshore seascapes. Identifying which aspects of the seascape were important for certain species becomes difficult since many of the seascape composition and arrangement variables were correlated. Despite this, certain seascape variables appeared to vary between the two types of sites. While the total proportion of area surveyed that had structured habitat was similar between the two habitat types, we observed a smaller proportion of eelgrass habitat and more understory and canopy kelp forest and lower eelgrass biomass in heterogeneous seascapes. These sites represent similar availability of structured habitat but differ in the types of structured habitats indicating that the habitat heterogeneity and increased niche diversity is likely connected to the observed differences in fish species richness, diversity, and shifts in assemblage composition.

4.5.1 Conclusion

In our research we identified species-specific responses to varying habitat heterogeneity in nearshore seascapes. Across nearshore coastlines the surrounding environment or context of habitats influences which species are more successful. Increased heterogeneity led to greater species richness and diversity and benefited a select few species whereas, more expansive eelgrass meadows in homogeneous seascapes were important for schooling juveniles. This highlights that not only does the context of the habitat matter, but that the diversity of seascape configurations supports different fish species. Increasingly, more studies are using a seascape approach to identify crucial habitats and contributing our understanding of which habitat patches and what configuration are most important for different species. Thus, we can enhance our ability to incorporate habitat metrics in how we plan, manage species, and habitats that are important for growth, and rearing.

This work reinforces other work highlighting that the greater seascape influences faunal assemblages. In nearshore coastal regions the context, connectivity, configuration, and scale of interest should all be considered when identifying critical or essential habitat for fish species (Pittman 2017). Species-distribution models and other management approaches to identify what habitats should be prioritized, may need to consider other processes impacting the nearshore and linking seemingly disparate habitat patches through species dispersal, nutrient subsidies, and species phenology.

4.6 Author contributions

Lia K. Domke, Jessica Whitney, and Ginny L. Eckert conceived the ideas and designed the methodology. Lia K. Domke collected data, performed the formal analyses and visualization, and wrote the original draft. Jessica Whitney collected data and reviewed and edited the manuscript. Carter J. Johnson collected data and reviewed and edited the manuscript. Ginny L. Eckert acquired funding, administered and supervised the project, collected data, and reviewed and edited the manuscript.

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4.9 Figures

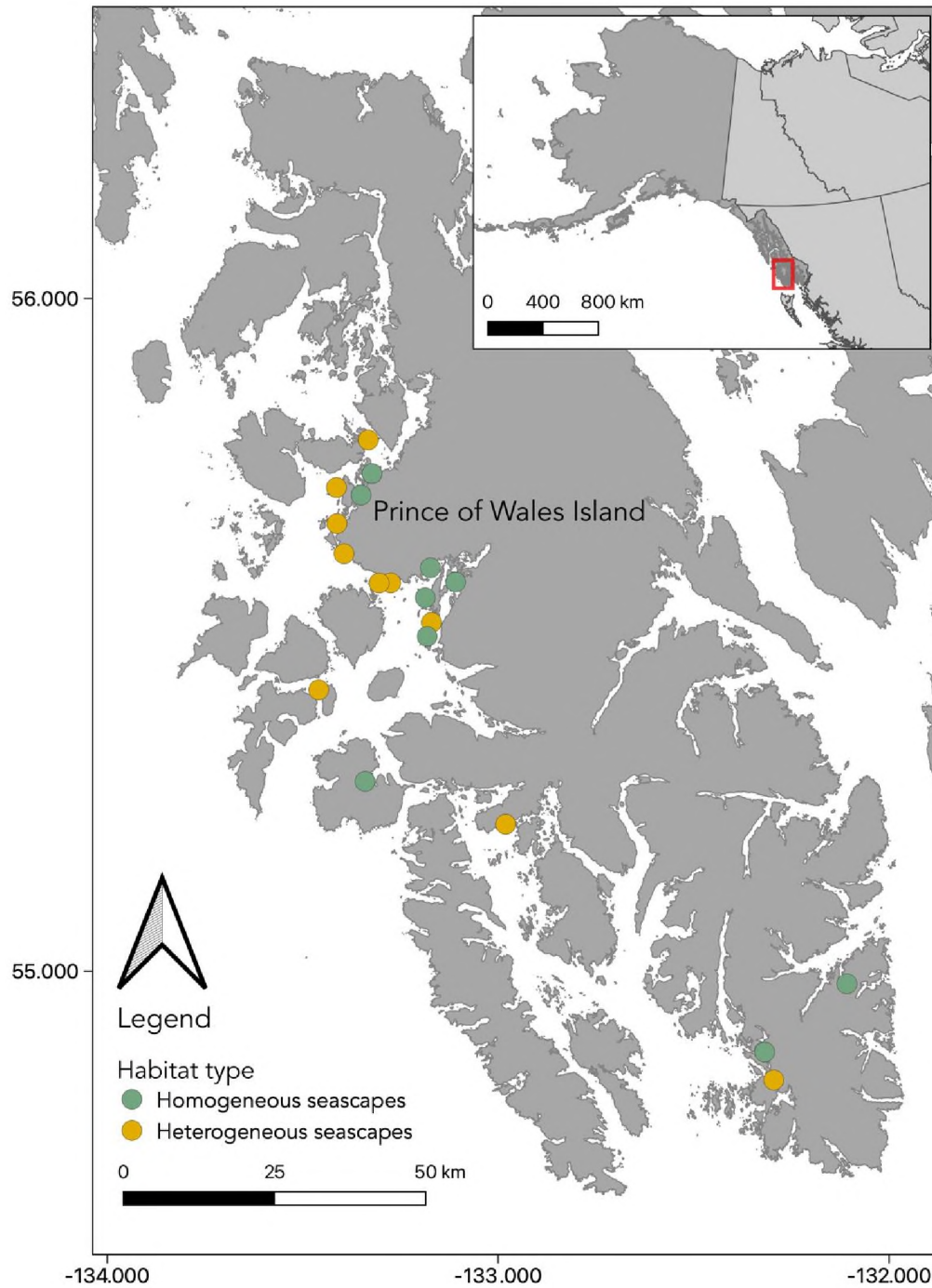


Figure 4.1. Map of southern Southeast Alaska centered on Prince of Wales Island where we conducted aerial imagery and seines in homogeneous seascapes (green) and heterogeneous seascapes (yellow).

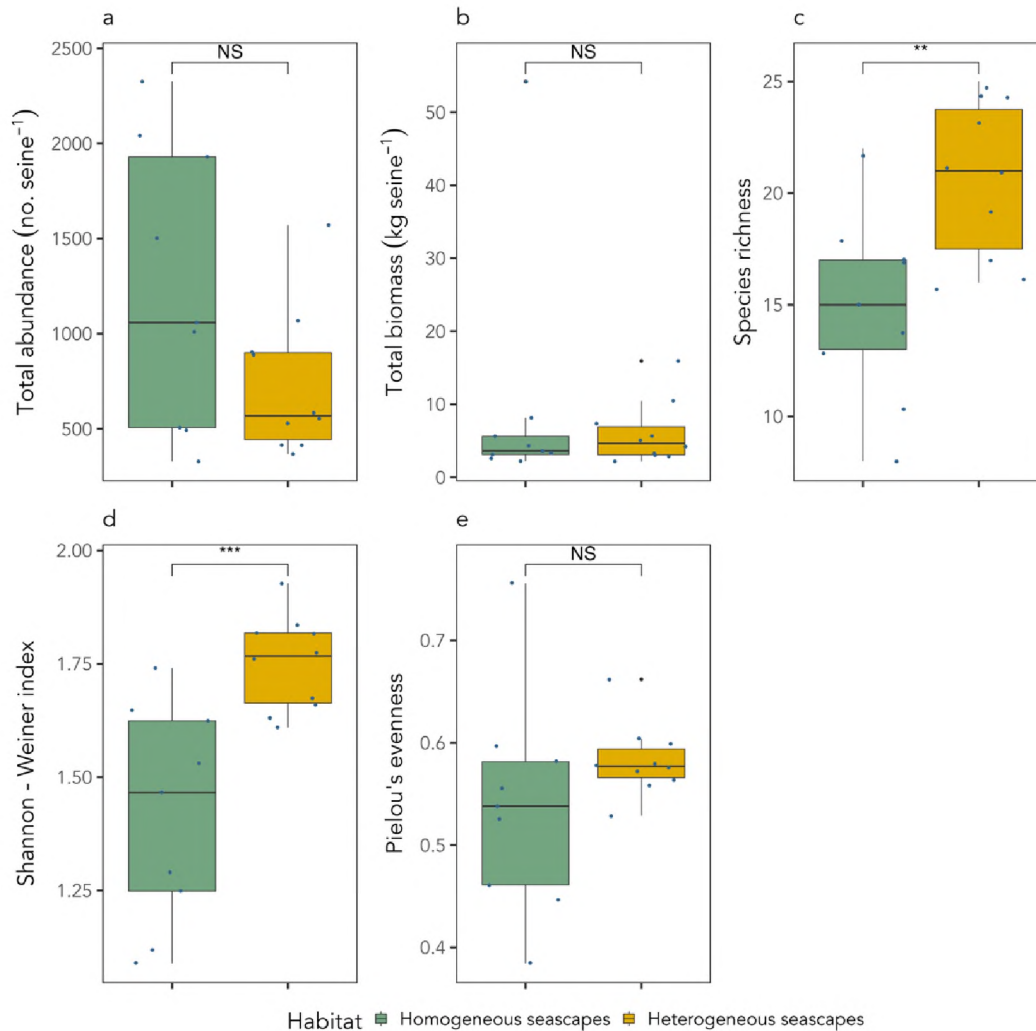


Figure 4.2. (a) Total abundance (number of fish seine⁻¹), (b) total biomass (kg seine⁻¹) (c) species richness, (d) Shannon-Weiner diversity index, and (e) Pielou's evenness index between homogeneous (green) and heterogeneous seascapes (yellow). Center of boxplot represents the mean of the data with the lower and upper extent of the box representing the 25th and 75th percentiles. Boxplot whiskers extend from the first and third quartile no more than 1.5 times the interquartile range below and above the box. Outliers are black points outside of the interquartile range. Blue points represent the value for each seine location. Significance of habitat values are represented by NS (no significant difference), * (0.01 < p-value < 0.05), ** (0.001 < p-value < 0.01), *** (p-value < 0.001).

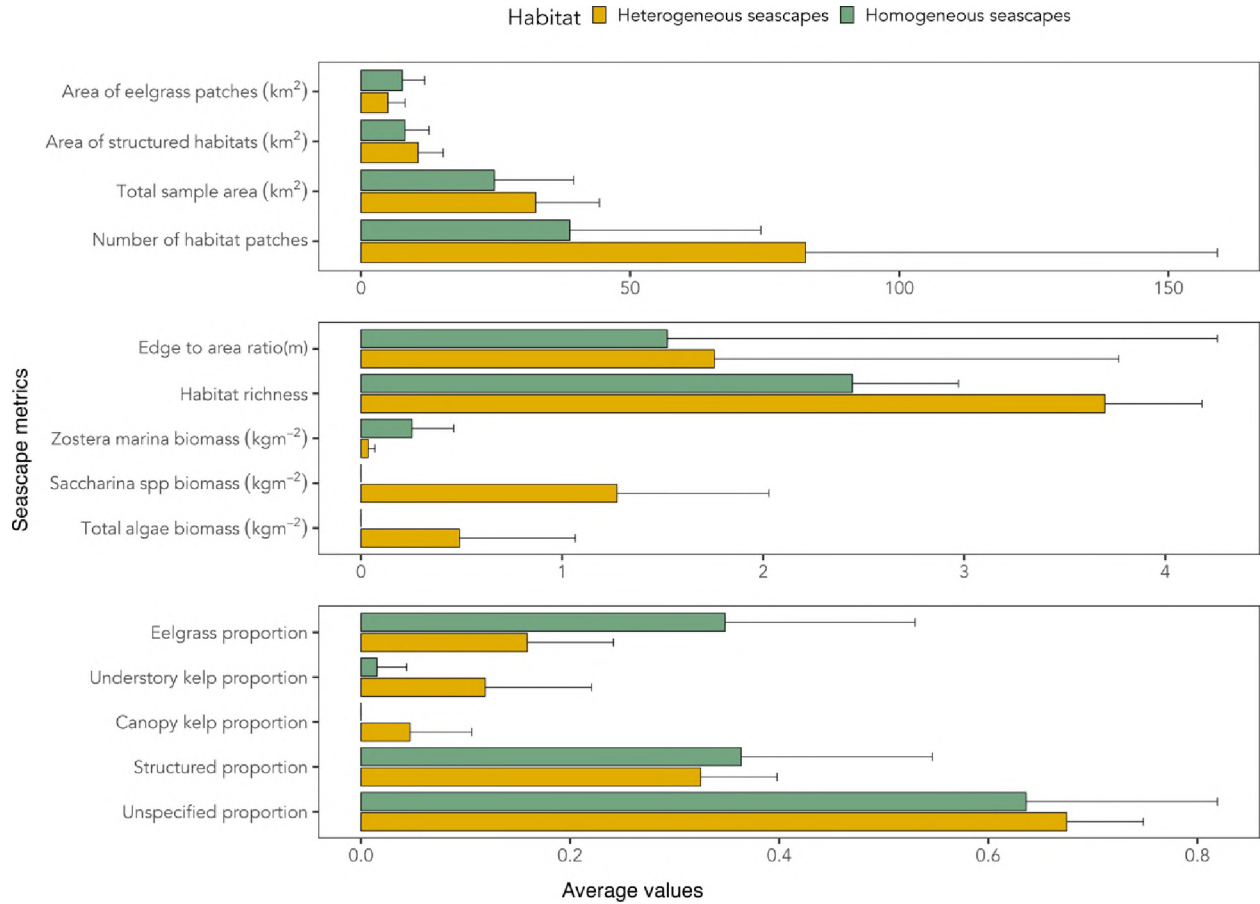


Figure 4.3. Seascap metrics used to describe the differences between homogeneous (green) and heterogeneous seascapes (yellow). Note differences in scale between each panel. Bars represent the average value for each metric (\pm standard deviation). Total algae biomass includes all algae caught per site aside from *Saccharina* spp.

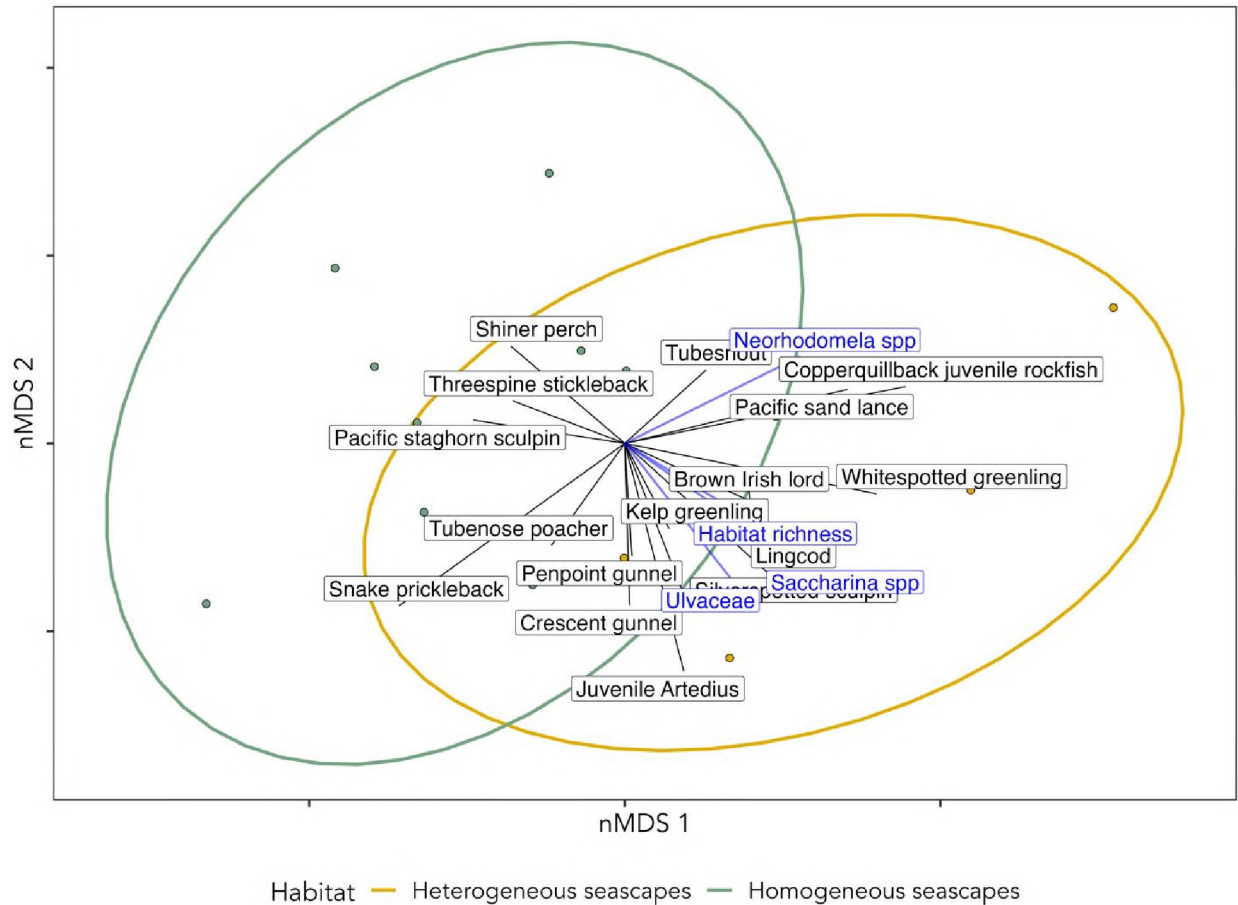


Figure 4.4. Non-metric multidimensional (nMDS) scaling plot of fish abundance species composition in at sites (represented by points) with homogeneous (green) and heterogeneous seascapes (yellow) with ellipses representing the 95% confidence region for each group of sites (2D stress = 15.4%). Black vectors indicate fish species that are significantly correlated with the axes (p -value < 0.05) and the length of the line indicates the strength of that correlation. Blue vectors are the environmental covariates that are significantly correlated with nMDS axes (p -value < 0.05).

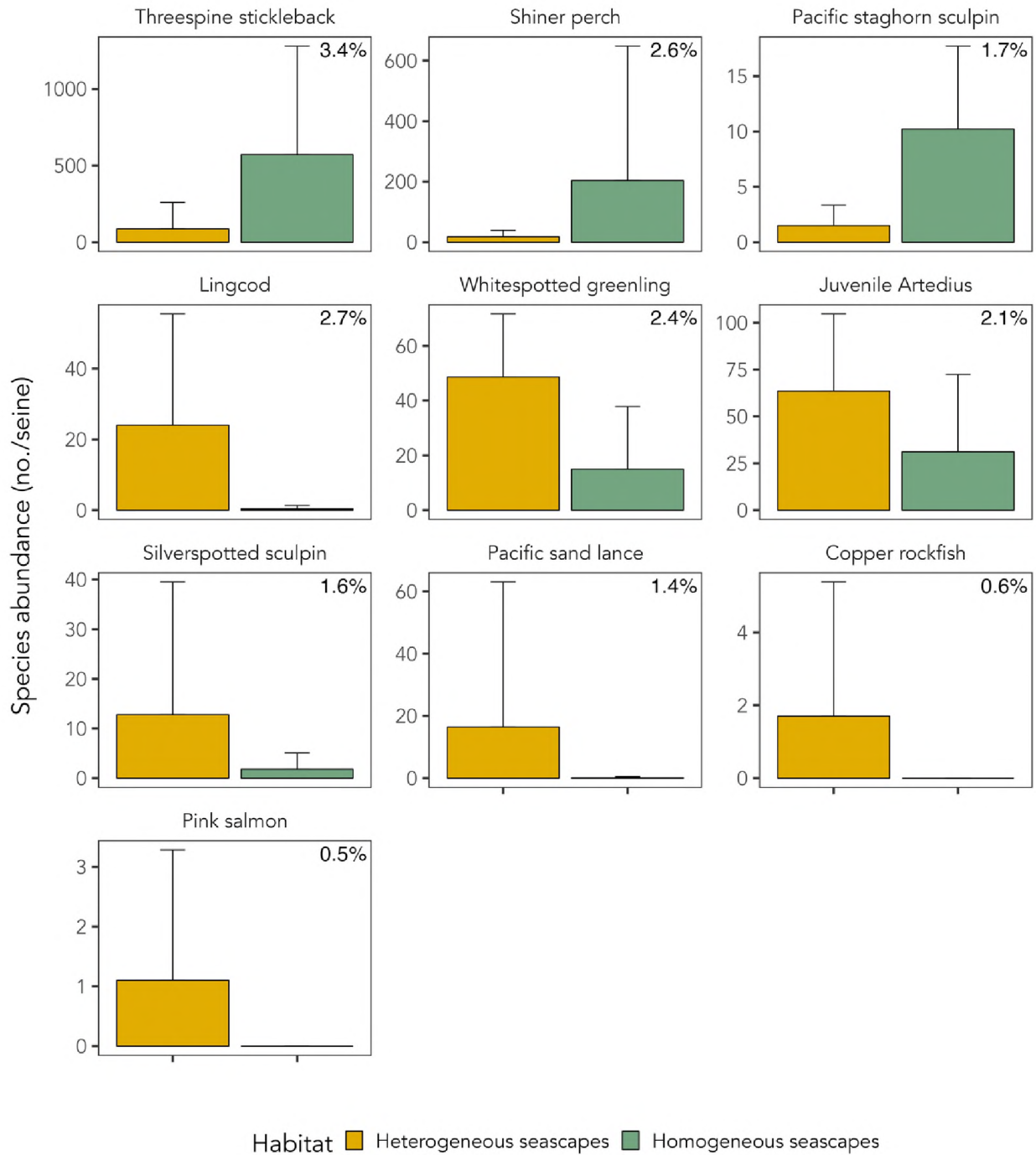


Figure 4.5. Average abundance (\pm SD) of fish species that significantly contribute to the difference in the fish assemblage composition between homogeneous seascapes (green) and heterogeneous seascapes (yellow). Percent values represent the contribution of each species to that difference between habitats.

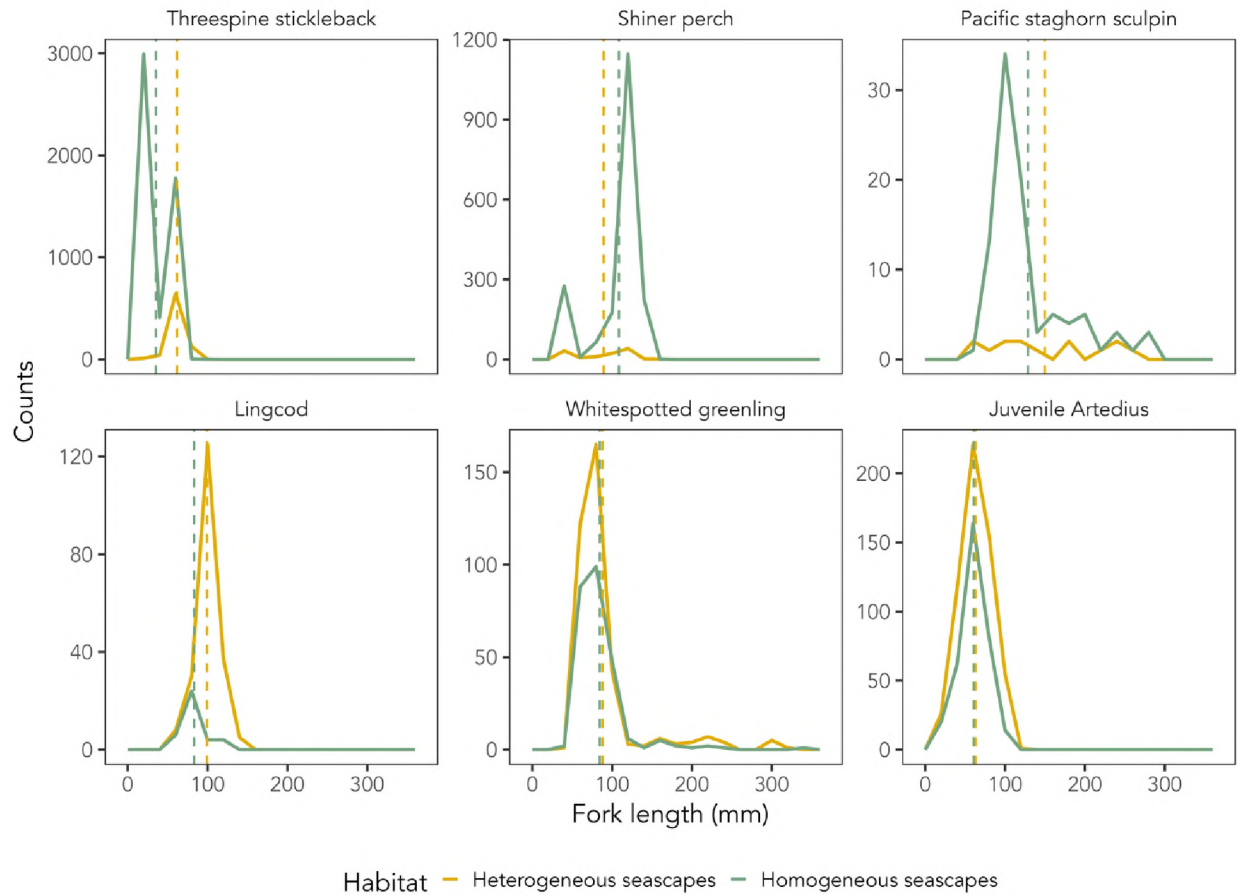


Figure 4.6. Fish sizes (fork length (mm)) for the top three species contributing to the difference between abundance-based fish assemblage composition in homogeneous seascapes (green) and heterogeneous seascapes (yellow) meadows. Dashed lines represent the average fork length for each species in each type of eelgrass site. Note the y-axis scale change.

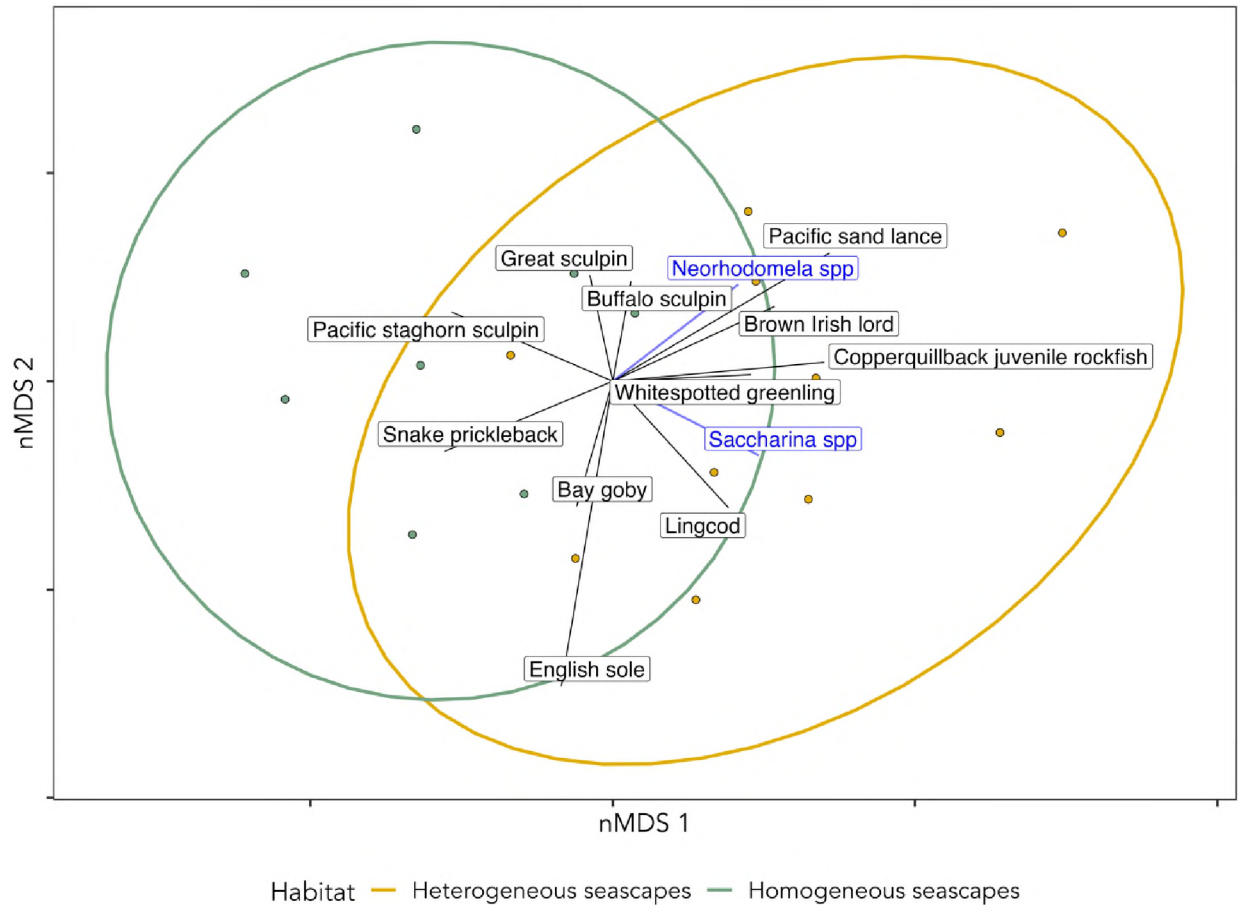


Figure 4.7. Non-metric multidimensional scaling plot of fish species biomass composition in at sites (represented by point) with homogeneous (green) and heterogeneous seascapes (yellow) with ellipses representing the 95% confidence region for each group of sites (2D stress = 16.7%). Black vectors indicate the fish species that are significantly correlated with the axes (p-value < 0.05) and the length of the line indicates the strength of that correlation. Blue vectors are the environmental covariates that are significantly correlated with nMDS axes (p-value < 0.05).

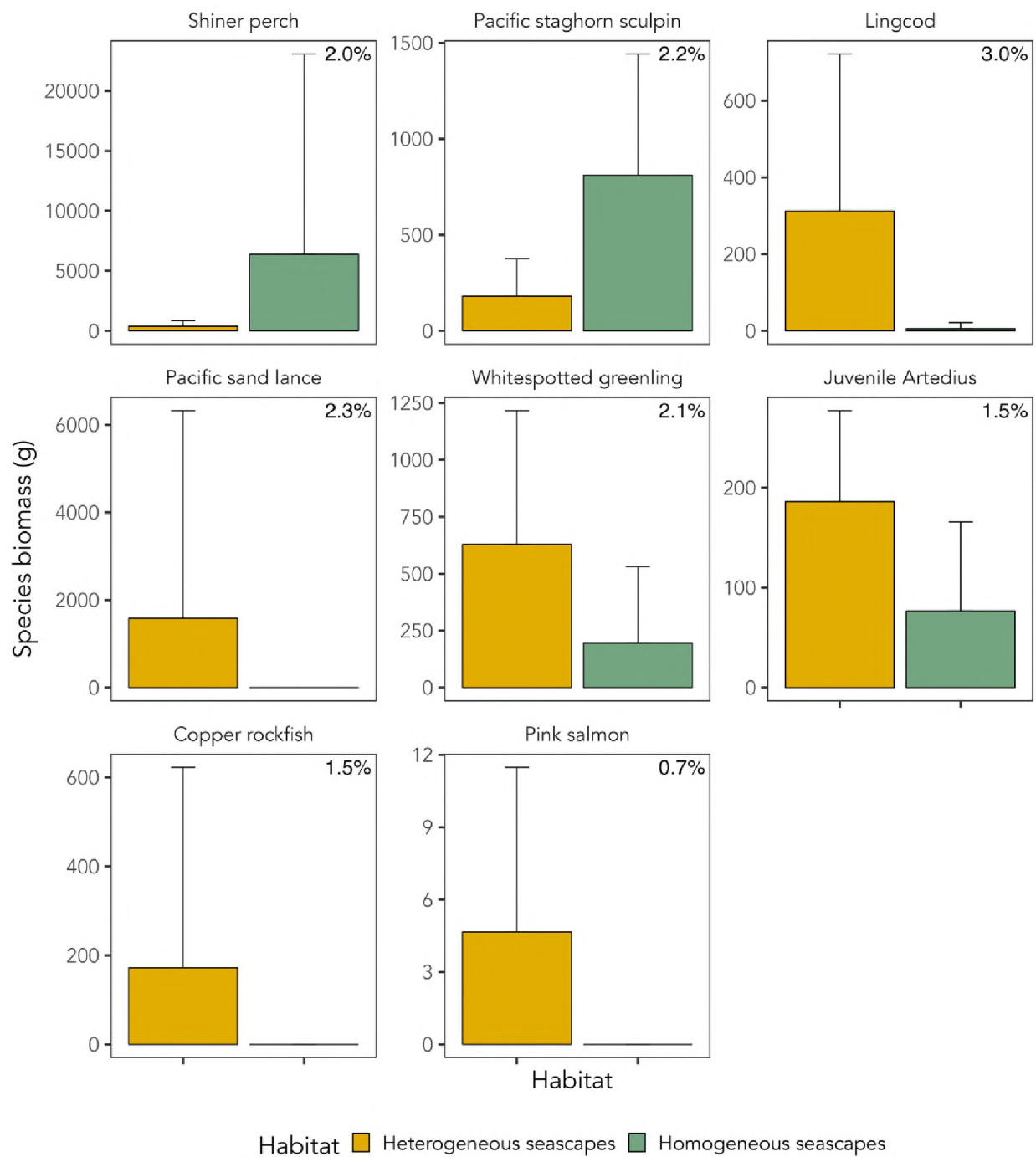


Figure 4.8. Average biomass (\pm SD) of fish species that significantly contribute to the difference in the fish biomass assemblage between homogeneous (green) and heterogeneous (yellow) seascapes. Percent values represent the contribution of each species to the difference between habitats.

4.10 Tables

Table 4.1. One-way analysis of variance (ANOVA) of total abundance, total biomass, species richness, and diversity and Mann Whitney U test by habitat type (either homogeneous seascape or heterogenous seascapes). Includes sum of squares (SS), degrees of freedom (df) for the ANOVA tests and test statistic (F-stat or W-stat), and p-value for each metric. Bolded p-values indicate a significant difference of a metric between habitat types ($\alpha = 0.05$).

		Habitat type	Residuals
Total abundance (no. seine ⁻¹)	SS	0.94	6.06
	df	1	17
	F-stat	2.62	
	P-Value	0.12	
Total biomass (kg seine ⁻¹)	SS	0.002	0.285
	df	1	17
	F-stat	0.103	
	P-Value	0.753	
Species Richness	SS	154.5	251.29
	df	1	17
	F-stat	10.45	
	P-Value	0.005	
Shannon-Weiner Index	SS	115.07	108.59
	df	1	17
	F-stat	18.02	
	P-Value	0.001	
Pielou's Evenness	W-stat	26	
	P-value	0.133	

Table 4.2. Habitat metrics used as to describe seascape context of sites, their units (m, m², km² number, and kg m⁻²), whether the metrics contribute to describing seascape arrangement or composition, their scale, and the method they were sampled. Bolded metrics are significantly correlated with the count-based nMDS axes ($\alpha = 0.05$, see Figure 4.4) and underlined metrics are correlated with the biomass-based nMDS axes ($\alpha = 0.05$, see Supplementary Table 4.1).

Habitat metric	Description	Units	Count P-value	Biomass P-value
Total area surveyed	Total area surveyed include vegetated and non-vegetated habitats	km ²	0.18	0.38
Total area with structured habitat	Total area with structured habitat including eelgrass, understory algae, and canopy kelp	m ²	0.12	0.19
Number of eelgrass patches	Number of eelgrass patches per site	no.	0.35	0.07
Average edge to perimeter ratio by site	Across the entire site average ratio of structured patches to perimeter of patch	m	0.94	0.85
Proportion of eelgrass habitat	Proportion of total site occupied by eelgrass	NA	0.25	0.54
Proportion of canopy habitat	Proportion of total site occupied by canopy kelp	NA	0.09	0.06
Proportion of understory habitat	Proportion of total site occupied by understory algae	NA	0.31	0.06
Proportion of unspecified habitat	Proportion of total site occupied by unspecified habitat (either un-vegetated or un-identifiable)	NA	0.91	0.36
Habitat richness	Number of habitats at a site	no.	0.01	0.07
Total area of patches	Total area of eelgrass patches	m ²	1.0	0.81
<i>Zostera marina</i>	Average biomass of species per site	kg m ⁻²	0.36	0.60
<i>Dictyosiphon foeniculaceus</i>	Average biomass of species per site	kg m ⁻²	0.92	0.98
<i>Farlowia mollis</i>	Average biomass of species per site	kg m ⁻²	0.17	0.25
<i>Mazzaella spp</i>	Average biomass of species per site	kg m ⁻²	0.11	0.13
<u><i>Saccharina spp</i></u>	<u>Average biomass of species per site</u>	<u>kg m⁻²</u>	<u>0.01</u>	<u>0.01</u>
<u><i>Neorhodomela spp</i></u>	<u>Average biomass of species per site</u>	<u>kg m⁻²</u>	<u>0.02</u>	<u>0.01</u>
Ulvaceae	Average biomass of species per site	kg m⁻²	0.01	0.12
<i>Stephanocystis geminata</i>	Average biomass of species per site	kg m ⁻²	0.06	0.08
<i>Ceramium pacificum</i>	Average biomass of species per site	kg m ⁻²	0.64	0.62
<i>Corallina c.jficinalis</i>	Average biomass of species per site	kg m ⁻²	0.54	0.63

4.11 Supplementary information

4.11.1 Supplementary tables

Supplementary Table 4.1. Species specific catch and biomass including the minimum, maximum counts, average counts \pm standard deviation (SD) in homogeneous seascape, average count \pm standard deviation (SD) in heterogeneous seascape, significance of relationship between species vector and count-based nMDS axes (Count p-value), minimum and maximum biomass caught (g), average biomass \pm standard deviation (SD) caught in homogeneous seascape, average biomass \pm standard deviation (SD) in heterogeneous seascape, and significance of relationship between species vector and biomass-based nMDS axes (Biomass p-value). Bolded species are significantly correlated with the count-based nMDS axes. Underlined species are significantly correlated with the biomass-based nMDS axes. Species are ordered by greatest count average in homogeneous seascape sites.

Scientific species name	Min count	Max counts	Mean count (SD) in homogeneous seascape	Mean count (SD) in heterogeneous seascape	Count P-values	Min mass	Max mass	Mean mass (SD) in homogeneous seascape	Mean mass (SD) in heterogeneous seascape	Biomass P-values
Gasterosteus aculeatus	0	1932	571.56 (708.36)	86.5 (173.09)	0.034	<u>0</u>	<u>3152.0</u> <u>2</u>	<u>638.82 (1006.7)</u>	<u>298.55 (621.83)</u>	<u>0.047</u>
Cymatogaster aggregata	0	1373	203.56 (444.34)	17.7 (21.46)	0.017	0	50905.31 (16704.33)	6374.02 (471.03)	388.85 (371.51)	0.124
Lumpenus sagitta	1	692	203 (211.49)	124.6 (208.87)	0.001	<u>10.05</u>	<u>2256.1</u> <u>3</u>	<u>732.33 (641.11)</u>	<u>352.73 (360.95)</u>	<u>0.003</u>
Pholis laeta	0	244	91.33 (70.95)	113.4 (76.33)	0.004	0	1244.0 7 (297.07)	386.07 (85.99)	615.41 (139.34)	0.051
Syngnathus leptorhynchus	17	213	65.56 (48.52)	104.5 (57.2)	0.067	29.06	478.35	109.87 (85.99)	177.05 (139.34)	0.705
Artedius spp.	0	138	31.22 (41.19)	63.5 (41.16)	0.002	0	306.81	76.88 (88.81)	186.06 (90.87)	0.117
Hexagrammos stelleri	0	87	15 (22.86)	48.6 (23.04)	0.002	<u>0</u>	<u>1866.6</u> <u>3</u>	<u>194.82 (335.73)</u>	<u>628.55 (587.49)</u>	<u>0.017</u>
Aulorhynchus flavidus	0	50	12.67 (15.7)	20.1 (18.3)	0.046	0	101.74	9.84 (23.32)	14.43 (30.99)	0.131
Pallasina barbata	0	92	12.22 (30.24)	0.4 (0.97)	0.02	0	119.05	26.94 (51.03)	0.51 (1.09)	0.16
Leptocottus armatus	0	22	10.22 (7.5)	1.5 (1.84)	0.019	<u>0</u>	<u>1892.1</u> <u>4</u>	<u>811.03 (631.22)</u>	<u>180.66 (194.98)</u>	<u>0.005</u>
Lepidogobius lepidus	0	30	4 (9.81)	1.2 (3.46)	0.444	<u>0</u>	<u>83.12</u>	<u>11.85 (27.29)</u>	<u>6.94 (19.73)</u>	<u>0.014</u>
Parophrys vetulus	0	17	4 (6.04)	2.7 (4.57)	0.17	<u>0</u>	<u>92.76</u>	<u>21.84 (32.43)</u>	<u>15.72 (20.65)</u>	<u>0.001</u>
Oncorhynchus kisutch	0	26	2.89 (8.67)	0 (0)	0.103	0	44.51	4.95 (14.84)	0 (0)	0.147
Myoxocephalus polyacanthocephalus	0	13	2 (3.16)	1.8 (4.02)	0.809	<u>0</u>	<u>241.68</u>	<u>34.55 (78.89)</u>	<u>32.14 (59.87)</u>	<u>0.018</u>
Hemilepidotus spinosus	0	17	1.89 (2.89)	6.4 (6.06)	0.02	<u>0</u>	<u>276.09</u>	<u>41.41 (83.53)</u>	<u>102 (104.99)</u>	<u>0.007</u>

Supplementary Table 4.1 (contd)

Sebastes auriculatus	0	33	1.78 (3.83)	4.4 (10.44)	0.508	0	88.69	7.24 (15.84)	12.71 (28.67)	0.503
Blepsias cirrhosus	0	88	1.78 (3.27)	12.8 (26.72)	0.007	0	216.34	7.67 (13.66)	30.78 (65.94)	0.204
Enophrys bison	0	23	1.22 (2.73)	3.4 (7.01)	0.342	0	<u>100.46</u>	<u>12.49 (33.23)</u>	<u>13.69 (27.2)</u>	<u>0.028</u>
Mallotus villosus	0	75	1 (3)	7.5 (23.72)	0.249	0	253.28	4.08 (12.25)	25.33 (80.1)	0.406
Gadus macrocephalus	0	37	1 (2.35)	7.4 (13.15)	0.299	0	159.42	1.13 (2.31)	30.06 (56.56)	0.105
Hexagrammos octogrammus	0	19	1 (1.5)	3.7 (6.07)	0.065	0	79.12	17.93 (30.1)	11.42 (18.41)	0.643
Apodichthys flavidus	0	7	0.89 (1.83)	1.8 (2.57)	0.02	0	54.2	0.3 (0.67)	5.93 (17.01)	0.731
Lepidopsetta spp.	0	4	0.67 (1.41)	0.1 (0.32)	0.672	0	79.77	16.83 (33.43)	7.98 (25.23)	0.467
Sebastes spp Copperquillback	0	16	0.56 (1.33)	3.5 (4.97)	0.001	0	<u>95.64</u>	<u>5.3 (11.49)</u>	<u>22.85 (29.56)</u>	<u>0.003</u>
Anoplarchus insignis	0	3	0.44 (1.01)	0.6 (0.7)	0.169	0	19.72	0.78 (2.31)	3.64 (7.19)	0.274
Ophiodon elongatus	0	107	0.33 (1)	24 (31.44)	0.004	0	<u>1389.0</u>	<u>5.38 (16.15)</u>	<u>312.22 (409.4)</u>	<u>0.006</u>
Hemilepidotus hemilepidotus	0	2	0.33 (0.71)	0.2 (0.42)	0.772	0	102.65	17.55 (36.78)	7.79 (18.57)	0.817
Salvelinus malma	0	2	0.22 (0.67)	0 (0)	0.624	0	109.73	12.19 (36.58)	0 (0)	0.791
Brachyistius frenatus	0	4	0.22 (0.67)	0.5 (1.27)	0.434	0	46.38	5.15 (15.46)	6.29 (14.25)	0.2
Synchirus gilli	0	24	0.22 (0.67)	2.7 (7.54)	0.247	0	28.74	0.06 (0.17)	3.54 (9.1)	0.354
Citharichthys sordidus	0	1	0.22 (0.44)	0.2 (0.42)	0.859	0	17.72	2.18 (4.61)	2.04 (5.57)	0.971
Cryptacanthodes giganteus	0	2	0.22 (0.67)	0 (0)	0.604	0	609.28	67.7 (203.09)	0 (0)	0.74
Platichthys stellatus	0	2	0.11 (0.33)	0.4 (0.7)	0.826	0	298.89	11.32 (33.96)	45.53 (94.78)	0.882
Clupea pallasii	0	364	0.11 (0.33)	37.1 (114.88)	0.721	0	5713.3	1.64 (4.93)	579.72 (1803.96)	0.792
Oncorhynchus nerka	0	1	0.11 (0.33)	0 (0)	0.103	0	2.51	0.28 (0.84)	0 (0)	0.147
Ammodytes personatus	0	149	0.11 (0.33)	16.4 (46.63)	0.003	0	<u>15066.</u>	<u>0.71 (2.14)</u>	<u>1582.04 (4739.07)</u>	<u>0.001</u>
Rhamphocottus richardsonii	0	1	0.11 (0.33)	0 (0)	0.484	0	0.07	0.01 (0.02)	0 (0)	0.616
Pleuronichthys coenosus	0	1	0.11 (0.33)	0 (0)	0.904	0	82.87	9.21 (27.62)	0 (0)	0.956
Limanda aspera	0	1	0.11 (0.33)	0 (0)	0.42	0	11.91	1.32 (3.97)	0 (0)	0.306
Hemilepidotus sp.	0	1	0.11 (0.33)	0.1 (0.32)	0.773	0	2.06	0.23 (0.69)	0.21 (0.65)	0.993
Scorpaenichthys marmoratus	0	2	0 (0)	0.2 (0.63)	1	0	122.05	0 (0)	12.2 (38.6)	0.433
Rhinogobiops nicholsii	0	2	0 (0)	0.3 (0.67)	0.254	0	9.06	0 (0)	1.05 (2.85)	0.393
Hexagrammos decagrammus	0	29	0 (0)	3.6 (9.02)	0.046	0	409.77	0 (0)	61.92 (137.4)	0.238
Oxylebius pictus	0	1	0 (0)	0.1 (0.32)	0.946	0	42.2	0 (0)	4.22 (13.34)	1
Hexagrammos lagocephalus	0	6	0 (0)	0.7 (1.89)	0.331	0	12.07	0 (0)	1.51 (3.83)	0.105
Podothecus accipenserinus	0	1	0 (0)	0.1 (0.32)	0.53	0	3.2	0 (0)	0.32 (1.01)	0.677
Gadus chalcogrammus	0	1	0 (0)	0.1 (0.32)	0.271	0	4.25	0 (0)	0.43 (1.34)	0.881
Sebastes caurinus	0	12	0 (0)	1.7 (3.68)	0.188	0	1447.0	0 (0)	172.47 (450.09)	0.109
Sebastes maliger	0	1	0 (0)	0.1 (0.32)	1	0	237.28	0 (0)	23.73 (75.03)	0.433
Sebastes spp YellowtailBlack	0	3	0 (0)	0.4 (0.97)	0.47	0	70.79	0 (0)	9.89 (23.15)	0.35
Oncorhynchus gorbuscha	0	7	0 (0)	1.1 (2.18)	0.146	0	17.14	0 (0)	4.66 (6.82)	0.165

Supplementary Table 4.1 (contd)

Trichodon trichodon	0	3	0 (0)	0.3 (0.95)	0.674	0	10.55	0 (0)	1.05 (3.34)	0.46
Nautichthys oculofasciatus	0	1	0 (0)	0.1 (0.32)	0.946	0	0.22	0 (0)	0.02 (0.07)	1
Citharichthys stigmaeus	0	1	0 (0)	0.1 (0.32)	0.946	0	4.76	0 (0)	0.48 (1.51)	1
Stichaeus punctatus	0	1	0 (0)	0.1 (0.32)	0.328	0	0.34	0 (0)	0.03 (0.11)	0.223
Scorpaenidae	0	7	0 (0)	0.7 (2.21)	0.328	0	32.06	0 (0)	3.21 (10.14)	0.223

Chapter 5: General conclusion

Nearshore ecosystems support tremendous biodiversity, including submerged vegetation, which forms shelter for fish and invertebrates and maintains complex food webs leading to dynamic predator-prey interactions. The commercial importance of nearshore ecosystems is often highlighted, with 46% by weight of commercially caught species spending at least a portion of their life history in nearshore estuaries (Lellis-Dibble et al. 2008). Ecologically, the nearshore sustains prey for higher trophic levels, forming an integral part of resilient and robust marine ecosystems. This coastal zone is characterized by immense environmental variability due to the influence of various abiotic and biotic forces from extreme tidal shifts, its location at the land-sea boundary, and varying wave exposure, among others. In Southeast Alaska, the geographic extent of nearshore habitats is vast, with a coastline stretching nearly 30,000 km, and likely supports fisheries in ways that are not fully realized. However, despite the importance of nearshore ecosystems, their role still needs to be better understood. In this dissertation, I endeavored to disentangle the influence of nearshore ecosystems on fish assemblages. Specifically, I examined the role of habitat type and environmental drivers on juvenile salmon, the indirect impacts of apex predators on nearshore fish assemblages, and how seascape habitat heterogeneity alters the fish assemblage in eelgrass meadows.

In my analysis of environmental drivers of juvenile salmon and their use of nearshore habitats, I established differences in Chum and Pink Salmon responses to variability in the nearshore. Juvenile salmon, at times, were present in high abundance within nearshore habitats, with Chum Salmon being more abundant in understory kelp compared to eelgrass. Seasonality was overwhelmingly the most important factor explaining variability in juvenile salmon catch; however, juvenile Pink Salmon abundance was negatively associated with increased eelgrass

biomass and positively with sea otter density and distance from anadromous streams (Chapter 2). Nonetheless, the considerable uncertainty within these patterns indicates that other factors may influence juvenile salmon use of the nearshore. Despite the transient nature of juvenile salmon and variability in their use of nearshore habitats, their survival and later recruitment to fisheries is reliant on their ability to retain food stores and adequately out-grow predation during the early marine phase (Beamish and Mahnken 2001, Beamish et al. 2004). Their distribution and use of the nearshore may depend more on prey availability within these habitats. Epifaunal prey availability can be higher at eelgrass patch edges (Moore and Hovel 2010), indicating that, in terms of prey availability, certain configurations of eelgrass patches may be more beneficial for juvenile salmon. Salmon are an iconic and cultural keystone species in Alaska (Carothers et al. 2021). The continued persistence of salmon populations in Southeast Alaskan culture and commercial fisheries relies on adequate habitat and prey throughout their life histories. The early marine phase is one of many life history stages that deserve consideration and research, particularly as heatwaves become more prevalent and detrimental impact coastal regions (Oliver et al. 2018, Raymond et al. 2022). The complex interplay of environmental variability, the migratory nature of juvenile salmon, and the utilization of nearshore habitats all likely contribute to the patchiness observed in our research.

Sea otters as apex predators in nearshore ecosystems have been well-described in canopy kelp forests (Estes and Duggins 1995), in understory kelp beds (Duggins 1980), and more recently in seagrass meadows (Hughes et al. 2013, Raymond et al. 2021). Still, the full breadth of their direct and indirect impacts has yet to be explored fully. This research contributes to the growing knowledge of the indirect implications of sea otters on fish assemblages and contributes to our understanding of their structuring force as they continue to recolonize regions of Southeast

Alaska. We found increased fish species richness in eelgrass meadows and shifts in the fish assemblage in understory kelp beds characterized by species-specific changes in abundance, including declines in rockfishes (*Sebastes* spp.) and increases in Rock Greenlings (*Hexagrammos lagocephalus*) (Chapter 3). This research is contextualized by expanding sea otter populations (current population at 22,000 sea otters) well under the proposed carrying capacity of Southeast Alaska of 74,650 sea otters (CI = 36,778 - 136,506) (Tinker et al. 2019, Schuette et al. 2023) and documented competition between sea otters and commercial, subsistence, and personal shellfish fisheries (Larson et al. 2013, Hoyt 2015, Ibarra 2021, Cates 2022). Continued legal harvest of sea otters by coastal Alaska Native peoples can control small-scale expansion of sea otters but does not impact region-wide populations (Tinker et al. 2019). Therefore, the shifting distribution of sea otters throughout Southeast Alaska, paired with the legal take of sea otters, their competition for invertebrate resources with humans, and their effective modification of coastal regions, has created a nuanced and complex management scenario.

While apex predators can be a structuring force in nearshore ecosystems, the surrounding environment or context of a habitat patch within a seascape can influence fish species composition. We observed species-specific responses of eelgrass fish species to varying habitat heterogeneity in the nearshore, with certain species more successful in homogeneous expansive eelgrass meadows and others only found within heterogeneous seascapes (Chapter 4). As these habitats are crucial for growth, rearing, and survival, incorporating the greater seascape context can facilitate effective management of fisheries populations through accounting for the value of both expansive habitat patches and mosaics of multiple habitats.

Despite this immense variability in coastal habitats, this dissertation documented patterns attributed to habitat, apex predators, and seascape heterogeneity, indicating that these forces

elicit a strong structuring role in nearshore fish assemblages. Additionally, synergistically, apex predators and seascape heterogeneity are likely modulating coastal fish assemblages in concert with the myriad of other abiotic and biotic forces. Therefore, it is worthwhile to consider the complexity of nearshore ecosystems and the delicate food webs they support when evaluating trade-offs in habitat conservation and fisheries management and the potential for coastal development to impact fish assemblages and overall coastal productivity.

5.1 References

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Appendix A: UAF IACUC Approval 2017



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Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

July 10, 2017

To: Ginny Eckert
Principal Investigator
From: University of Alaska Fairbanks IACUC
Re: [892147-6] Eelgrass associated fish communities

The IACUC reviewed and approved the Amendment/Modification to the Personnel List referenced above by Administrative Review.

Received: July 5, 2017
Approval Date: July 10, 2017
Initial Approval Date: April 15, 2016
Expiration Date: April 15, 2018

This action is included on the July 13, 2017 IACUC Agenda.

PI responsibilities:

Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.

Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)

Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.

Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.

Ensure animal research personnel are aware of the reporting procedures on the following page.

Appendix B: UAF IACUC Approval 2019



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Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

April 12, 2019

To: Ginny Eckert
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [892147-11] Eelgrass associated fish communities

The IACUC reviewed and approved the Amendment/Modification to the Personnel List referenced above by Administrative Review.

Received:	April 12, 2019
Approval Date:	April 12, 2019
Initial Approval Date:	April 15, 2016
Expiration Date:	April 15, 2020

This action is included on the April 16, 2019 IACUC Agenda.

PI responsibilities:

Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.

Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)

Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.

Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.

Ensure animal research personnel are aware of the reporting procedures on the following page.

Appendix C: UAF IACUC Approval 2021



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Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

June 1, 2021

To: Ginny Eckert
Principal Investigator
From: University of Alaska Fairbanks IACUC
Re: [892147-21] Eelgrass associated fish communities

The IACUC reviewed and approved the personnel list referenced above by Administrative Review.

Received:	June 1, 2021
Approval Date:	June 1, 2021
Initial Approval Date:	April 15, 2016
Expiration Date:	April 15, 2022

This action is included on the June 10, 2021 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

Appendix D: UAF IACUC Approval 2022



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Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

April 11, 2022

To: Ginny Eckert
Principal Investigator
From: University of Alaska Fairbanks IACUC
Re: [892147-25] Eelgrass associated fish communities

The IACUC reviewed and approved the Amendment/Modification referenced above by Designated Member Review.

Received: April 4, 2022
Approval Date: April 11, 2022
Initial Approval Date: April 15, 2016
Expiration Date: April 15, 2023

This action is included on the April 14, 2022 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

Appendix E: Alaska Department of Fish & Game Permit 2017



STATE OF ALASKA
DEPARTMENT OF FISH AND GAME
P.O. Box 115526
JUNEAU, ALASKA 99811-5526

Permit No. **CF-17-050**

Expires: **12/31/2017**

FISH RESOURCE PERMIT
(For Scientific/Collection Purposes)

This permit authorizes:

Wendel Raymond

(whose signature is required on page 2 for permit validation)

of

University of Alaska Fairbanks

17101 Point Lena Loop Rd., Juneau, AK 99801

(503)539-6073

wraymond2@alaska.edu

to conduct the following activities from **April 24, 2017** to **December 31, 2017** in accordance with AS 16.05.930 and AS 16.05.340(b).

Purpose: To identify abundance, biomass, and community structure in eelgrass communities.

Location: Prince of Wales and surrounding islands

Species: See **Species List** on pages 3-4 for retained species.

Method of Collection: Beach seine and hand collection.

Disposition: Species listed will be preserved and disposed of as directed after analysis. All other species will be released live at the site of capture. See **Stipulations** section.

A COLLECTION REPORT IS DUE January 30, 2018 and a COMPLETION REPORT IS DUE June 30, 2018. See **Stipulations** section for more information. Data from such reports are considered public information. Reports must be submitted to the Alaska Department of Fish and Game, Division of Commercial Fisheries, PO Box 115526, Juneau, AK 99811-5526, attention Michelle Morris (907-465-4724; dfc.fmpd.permitcoordinator@alaska.gov). A report is required whether or not collecting activities were undertaken.

GENERAL CONDITIONS, EXCEPTIONS AND RESTRICTIONS

1. This permit must be carried by person(s) specified during approved activities who shall show it on request to persons authorized to enforce Alaska's fish and game laws. This permit is nontransferable and will be revoked or renewal denied by the Commissioner of Fish and Game if the permittee violates any of its conditions, exceptions or restrictions. No redelegation of authority may be allowed under this permit unless specifically noted.
2. No specimens taken under authority hereof may be sold, bartered, or consumed. All specimens must be deposited in a public museum or a public scientific or educational institution unless otherwise stated herein. Subpermittees shall not retain possession of live animals or other specimens.
3. The permittee shall keep records of all activities conducted under authority of this permit, available for inspection at all reasonable hours upon request of any authorized state enforcement officer.
4. Permits will not be renewed until detailed reports, as specified in the Stipulation section, have been received by the department.
5. UNLESS SPECIFICALLY STATED HEREIN, THIS PERMIT DOES NOT AUTHORIZE the exportation of specimens or the taking of specimens in areas otherwise closed to hunting and fishing; without appropriate licenses required by state regulations; during closed seasons; or in any manner, by any means, at any time not permitted by those regulations.

Peter Bangs 3/28/17

Deputy or Assistant Director
Division of Commercial Fisheries
Alaska Department of Fish and Game

CF-17-050 continued (page 2 of 3)

Authorized Personnel: The following personnel may participate in collecting activities under terms of this permit:

Wendel Raymond, Brent Hughes, Ginny Eckert, Ashley Bolwek, Sonia Ibarra, and Catherine Mattson.

Employees and volunteers under the direct supervision of, and in the presence of, one of the authorized personnel listed above may participate in collecting activities under terms of this permit.

Stipulations:

1. Permits will indicate the number of specimens that may be taken by species and life stage. Sampling or collecting activities must stop when the maximum allowable number of specimens is obtained. All live fish, shellfish, and aquatic plants collected in excess of the number specified on the permit must be released immediately and unharmed at the capture location, unless otherwise specified in the permit. All unintended mortalities must be recorded and returned to capture site waters.
2. Up to 2 individuals of each unknown species may be killed and saved for later identification.
3. Specimens collected under the authority of this permit are ONLY to be used for the purposes outlined in this permit.
4. All unattended collecting gear (including minnow, fyke, and hoop nets) must be labeled with the permittee's name, telephone number, and permit number. Pots must conform to 5 AAC 77.553(b) and 5 AAC 39.145, *Escape Mechanisms for Shellfish and Bottomfish Pots*.
5. Upon disposition, specimens must be double-bagged and placed in sanitary landfill.
6. A copy of this permit, including any amendments, must be made available at all field collection sites and project sites for inspection upon request by a representative of the department or a law enforcement officer.
7. Issuance of this permit does not absolve the permittee from compliance in full with any and all other applicable federal, state, or local laws regulations, or ordinances.
8. **A report of collecting activities, referencing this fish resource permit, must be submitted within 30 days after the expiration of this permit.** This report must summarize the number of all specimens, including bycatch, captured by date, location, species, size (weight and length where appropriate), age (where appropriate), numbers, and the fate of those specimens. A report is required whether or not collecting activities were undertaken.
9. **A report of research activities, referencing this fish resource permit, must be submitted within 6 months after the expiration of this permit.** This report should present the research conducted in a format similar to a scientific paper including the following: introduction (objective of the study plan and hypothesis), methods, and results. The report is ad-hoc and intended to show that the specimens were used in a scientific method and allows for the evaluation of potential cumulative effects from multiple projects in the same area, but is not intended to be a full peer-reviewed scientific paper. A report is required whether or not research activities were undertaken.
10. Failure to comply with the conditions of this permit will result in the loss of future permitting privileges.
11. PERMIT VALIDATION requires permittee's signature agreeing to abide by permit conditions before beginning collecting activities:

Signature of Permittee

ecc: Flip Pryor, Judy Lum, Craig Schwanke
CF Division Files
Alaska Wildlife Troopers–Craig

Species List

Common Name	Scientific Name	Total retained (size)
Eelgrass (blade only)	<i>Zostera marina</i>	3,000 (5-300cm)
Shiner perch	<i>Cymatogaster aggregata</i>	180 (10-15cm)
Pink salmon	<i>Oncorhynchus gorbuscha</i>	180 (~10cm)
Coho salmon	<i>Oncorhynchus kisutch</i>	180 (~10cm)
Sockeye salmon	<i>Oncorhynchus nerka</i>	180 (10-15cm)
Variiegated chink snail	<i>Lacuna variegata</i>	1,500 (5-15mm)
Pacific blue mussel	<i>Mytilus trossulus</i>	3,000 (5-30mm)
Amphipods	Suborders Gammaridae and Caprellidae	30,000 (3-25mm)
Isopod	<i>Idotea spp.</i>	3,000 (5-35mm)
Polychaete	<i>Eteone spp.</i>	300 (10-50mm)

CF-17-050 continued (page 3 of 3)

Common Name	Scientific Name	Total retained
Pile worm	<i>Nereis vexillosa</i>	300 (10-50mm)
False white sea cucumber	<i>Eupentacta pseudoquinquesemita</i>	300 (10-50mm)
Spot shrimp	<i>Pandalus platyceras</i>	300 (10-75mm)
Dock shrimp	<i>Pandalus danae</i>	300 (10-75mm)
Opossum mysid	<i>Neomysis mercedes</i>	300 (10-75mm)
Alaskan crangon	<i>Crangon alaskensis</i>	300 (10-75mm)
Long-clawed crangon	<i>Crangon franciscorum angustimana</i>	300 (10-75mm)
Hermit crab	<i>Pagurus spp.</i>	300 (10-50mm)
Tuskworm	<i>Pectinaria granulata</i>	1,500 (10-50mm)
Featherduster worm	<i>Schizobranchia insignis</i>	900 (10-75mm)
Burrowing green anemone	<i>Anthopleura artemisia</i>	30 (5-25mm)
Littleneck clam	<i>Protothaca staminea</i>	300 (5-15mm)
Heart cockle	<i>Clinocardium nuttallii</i>	900 (5-50mm)
Green sea urchin	<i>Strongylocentrotus droebachiensis</i>	450 (5-30mm)
Broken back shrimp	<i>Hippolytidae</i>	300 (10-75mm)
Dungeness crab	<i>Metacarcinus magister</i>	180 (18-25cm)
Eelgrass Limpet	<i>Lotia pelta</i>	1,000 (2-12mm)
Snail	<i>Margarites sp.</i>	1,000 (2-12mm)
Snail	<i>Littorina sp.</i>	1,000 (2-12mm)
Skeleton shrimp	<i>Caprella sp.</i>	1,000 (2-12mm)
Leptochellidae	<i>Leptochelia savignyi</i>	500 (2-12mm)
	<i>Ulva sp.</i>	3,000 (1-20cm)
	<i>Monostroma sp.</i>	3,000 (1-20cm)
	<i>Scytosiphon sp.</i>	3,000 (1-20cm)
Sea lettuce	<i>Cladophora sp.</i>	3,000 (1-20cm)
	<i>Enteromorpha sp. (Ulva sp.)</i>	3,000 (1-20cm)
	<i>Smithora sp.</i>	3,000 (1-20cm)
Diatoms		unknown

Appendix F: Alaska Department of Fish & Game Permit 2019



STATE OF ALASKA
DEPARTMENT OF FISH AND GAME
P.O. Box 115526
JUNEAU, ALASKA 99811-5526

Permit No. **CF-19-067**

Expires: **12/31/2019**

AQUATIC RESOURCE PERMIT
(For Scientific/Collection/Holding Purposes)

This permit authorizes:

Lia Domke

(whose signature is required on page 3 for permit validation)

of

University of Alaska Fairbanks

17101 Pt Lena Loop Rd., Juneau, AK 99801

(907)321-4461

lkdome@alaska.edu

to conduct the following activities from **April 15, 2019** to **December 31, 2019** in accordance with AS 16.05.930, AS 16.05.340(b) and 5 AAC 41.600.

Purpose: To quantify the community composition and ecosystem services of seagrass and associated invertebrates and fishes.

Location: Prince of Wales and surrounding islands, Revillagigedo Island and surround islands.

Species: See **Species List** on pages 3-5.

Method of Collection: Hand collection, shovel and beach seine.

Disposition: Species will be sacrificed or released live at the site of capture. Sacrificed species will be destroyed as directed. **Stipulations** section.

A **COLLECTION REPORT IS DUE January 30, 2020** and a **COMPLETION REPORT IS DUE June 30, 2020**. See **Stipulations** section for more information. Data from such reports are considered public information. Reports must be submitted to the Alaska Department of Fish and Game, Division of Commercial Fisheries, PO Box 115526, Juneau, AK 99811-5526, attention Michelle Morris (907-465-4724; dfg_fmfd_permitcoordinator@alaska.gov). A report is required whether or not collecting activities were undertaken.

GENERAL CONDITIONS, EXCEPTIONS AND RESTRICTIONS

1. This permit must be carried by person(s) specified during approved activities who shall show it on request to persons authorized to enforce Alaska's fish and game laws. This permit is nontransferable and will be revoked or renewal denied by the Commissioner of Fish and Game if the permittee violates any of its conditions, exceptions or restrictions. No redelegation of authority may be allowed under this permit unless specifically noted.
2. No specimens taken under authority hereof may be sold, bartered, or consumed. All specimens must be deposited in a public museum or a public scientific or educational institution unless otherwise stated herein. Subpermittees shall not retain possession of live animals or other specimens.
3. The permittee shall keep records of all activities conducted under authority of this permit, available for inspection at all reasonable hours upon request of any authorized state enforcement officer.
4. Permits will not be renewed until detailed reports, as specified in the Stipulation section, have been received by the department.
5. **UNLESS SPECIFICALLY STATED HEREIN, THIS PERMIT DOES NOT AUTHORIZE** the exportation of specimens or the taking of specimens in areas otherwise closed to hunting and fishing; without appropriate licenses required by state regulations; during closed seasons; or in any manner, by any means, at any time not permitted by those regulations.

Peter Bangs 4/12/19

Deputy or Assistant Director
Division of Commercial Fisheries

CF-19-067 continued (page 2 of 5)

Authorized Personnel: The following personnel may participate in collecting activities under terms of this permit:

Lia Domke, Tiffany Stephens, Ginny Eckert, Ashley Bolwerk, Wendel Raymond, and Brent Hughes.

Employees and volunteers under the direct supervision of, and in the presence of, one of the authorized personnel listed above may participate in collecting activities under terms of this permit.

Stipulations:

1. **Bo Meredith** (Division of Commercial Fisheries, Ketchikan, (907)225-5195, bo.meredith@alaska.gov) (must be notified **prior** to you engaging in collecting or release activities. Division of Commercial Fisheries management biologists have the authority to specify methods for collecting, as well as limiting the collections of any species, and the number of specimens collected by time and area.
2. Permits will indicate the number of specimens that may be taken by species and life stage. Sampling or collecting activities must stop when the maximum allowable number of specimens is obtained. All live fish, shellfish, and aquatic plants collected in excess of the number specified on the permit must be released immediately and unharmed at the capture location, unless otherwise specified in the permit. All unintended mortalities must be recorded and returned to capture site waters.
3. Specimens collected under the authority of this permit are **ONLY** to be used for the purposes outlined in this permit.
4. If evidence of chronic sea star wasting disease is encountered, please report the finding at the University of California, Santa Cruz website, <http://www.seastarwasting.org>. Please leave organisms undisturbed.
5. **Dungeness crab collections are limited to 10 per collection site.**
For any species to be collected or held that require a federal permit, the applicant must obtain a federal permit and submit a copy of it with the application for an aquatic resource permit. Please contact the International Pacific Halibut Commission at (206) 634-1838, P.O. Box 95009, Seattle, WA 98145-2009 to obtain permission for halibut collection.
6. Destroyed specimens must be double-bagged and placed in a sanitary landfill.
7. A copy of this permit, including any amendments, must be made available at all field collection sites and project sites for inspection upon request by a representative of the department or a law enforcement officer.
8. Issuance of this permit does not absolve the permittee from compliance in full with any and all other applicable federal, state, or local laws regulations, or ordinances.
9. **A report of collecting activities, referencing this aquatic resource permit, must be submitted 30 days after the expiration of this permit.** This report must summarize the number of all specimens, including bycatch, captured by date, location, depth of capture, species, size (weight and length where appropriate), age (where appropriate), sex, numbers, and the fate of those specimens. A report is required whether or not collecting activities were undertaken.
10. **A report of research activities, referencing this aquatic resource permit, must be submitted within 6 months after the expiration of this permit.** This report should present the research conducted in a format similar to a scientific paper including the following: introduction (objective of the study plan and hypothesis), methods, and results. The report is ad-hoc and intended to show that the specimens were used in a scientific method and allows for the evaluation of potential cumulative effects from multiple projects in the same area, but is not intended to be a full peer-reviewed scientific paper.
11. Failure to comply with the conditions of this permit will result in the loss of future permitting privileges.
12. PERMIT VALIDATION requires permittee's signature agreeing to abide by permit conditions before beginning collecting activities:

Signature of Permittee

ecc: Bo Meredith, Craig Schwanke, Kelly Reppert, Judy Lum
CF Division Files
Alaska Wildlife Troopers – Ketchikan, Craig

CF-19-067 continued (page 3 of 5)

Species List - Released

Common Name	Scientific Name	Length Range (cm)	Number collected	Total number retained
Threespine stickleback	<i>Gasterosteus aculeatus</i>	1-20cm	12,000	0
Pacific Herring	<i>Clupea pallasii</i>	1-20cm	9,000	0
Shiner perch	<i>Cymatogaster aggregata</i>	1-20cm	9,000	0
Pacific staghorn sculpin	<i>Leptocottus armatus</i>	1-20cm	7,200	0
Pink salmon	<i>Oncorhynchus gorbuscha</i>	1-20cm	7,200	0
Chum salmon	<i>Oncorhynchus keta</i>	1-20cm	7,200	0
Coho salmon	<i>Oncorhynchus kisutch</i>	1-20cm	7,200	0
walleye pollock	<i>Gadus chalcogrammus</i>	1-20cm	6,000	0
Great sculpin	<i>Myoxocephalus polyacanthocephalus</i>	1-20cm	4,200	0
Crecent gunnel	<i>Pholis laeta</i>	1-20cm	4,200	0
Bay pipefish	<i>Syngnathus leptorhynchus</i>	1-20cm	4,200	0
Pacific sand lance	<i>Ammodytes hexapteru/personatus</i>	1-20cm	3,600	0
Kelp greenling	<i>Hexagrammos decagrammus</i>	1-20cm	3,600	0
Whitespotted greenling	<i>Hexagrammos stelleri</i>	1-20cm	3,000	0
Rock greenling	<i>Hexagrammos lagocephalus</i>	1-20cm	2,400	0
Masked greenling	<i>Hexagrammos octogrammus</i>	1-20cm	2,400	0
Smoothhead sculpin	<i>Artedius lateralis</i>	1-20cm	1,800	0
Tube-snout	<i>Aulorhynchus flavidus</i>	1-20cm	1,800	0
Silverspotted sculpin	<i>Blepsias cirrhosus</i>	1-20cm	1,800	0
Pacific cod	<i>Gadus macrocephalus</i>	1-20cm	1,800	0
Snake prickleback	<i>Lumpenus sagitta</i>	1-20cm	1,800	0
Sockeye salmon	<i>Oncorhynchus nerka</i>	1-20cm	1,800	0
Chinook salmon	<i>Oncorhynchus tshawytscha</i>	1-20cm	1,800	0
Painted greenling	<i>Oxylebius pictus</i>	1-20cm	1,800	0
Tubenose poacher	<i>Pallasina barbata aix</i>	1-20cm	1,800	0
Rock sole	<i>Pleuronectes bilineatus</i>	1-20cm	1,800	0
English sole	<i>Pleuronectes vetulus</i>	1-20cm	1,800	0
Dolly Varden	<i>Salvelinus malma</i>	1-20cm	1,800	0
Cabezon	<i>Scorpaenichthys marmoratus</i>	1-20cm	1,800	0
Padded sculpin	<i>Artedius fenestralis</i>	1-20cm	1,200	0
Kelp perch	<i>Brachyistius frenatus</i>	1-20cm	1,200	0
Pacific sanddab	<i>Citharichthys sordidus</i>	1-20cm	1,200	0
Speckled sanddab	<i>Citharichthys stigmæus</i>	1-20cm	1,200	0
Buffalo scupin	<i>Enophrys bison</i>	1-20cm	1,200	0
Red Irish lord	<i>Hemilepidotus hemilepidotus</i>	1-20cm	1,200	0
Brown Irish lord	<i>Hemilepidotus spinosus</i>	1-20cm	1,200	0
Surf smelt	<i>Hypomesus pretiosus</i>	1-20cm	1,200	0
Northern sculpin	<i>Icelinus borealis</i>	1-20cm	1,200	0
Butter sole	<i>Isopsetta isolepis</i>	1-20cm	1,200	0
Fluffy sculpin	<i>Oligocottus snyderi</i>	1-20cm	1,200	0
Starry flounder	<i>Platichthys stellatus</i>	1-20cm	1,200	0
Tadpole sculpin	<i>Psychrolutes paradoxus</i>	1-20cm	1,200	0
Copper rockfish	<i>Sebastes caurinus</i>	1-20cm	1,200	0
Yellowtail rockfish	<i>Sebastes flavidus</i>	1-20cm	1,200	0
Quillback rockfish	<i>Sebastes maliger</i>	1-20cm	1,200	0
Black rockfish	<i>Sebastes melanops</i>	1-20cm	1,200	0
Yellowfin sole	<i>Limanda asper</i>	1-20cm	900	0
Saifin sculpin	<i>Nautichthys oculofasciatus</i>	1-20cm	900	0
C-O sole	<i>Pleuronichthys coenosus</i>	1-20cm	900	0
Northern ronquil	<i>Ronquilus jordani</i>	1-20cm	900	0
Walleye pollock	<i>Theragra chalcogramma</i>	1-20cm	900	0
Northern spearnose poacher	<i>Agonopsis vulsa</i>	1-20cm	600	0
Penpoint gunnel	<i>Apodichthys flavidus</i>	1-20cm	600	0
Sculpin family	<i>Cottidae</i>	1-20cm	600	0
Black goby	<i>Coryphopterus nicholsi</i>	1-20cm	600	0
Leister sculpin	<i>Enophrys lucasi</i>	1-20cm	600	0
Pacific spiny lumpsucker	<i>Eumicrotremus orbis</i>	1-20cm	600	0

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Tidepool snailfish	<i>Liparis flavae</i>	1-20cm	600	0
capelin	<i>Mallotus villosus</i>	1-20cm	600	0
Steller's sculpin	<i>Myoxocephalus stelleri</i>	1-20cm	600	0
Cutthroat trout	<i>Oncorhynchus clarki</i>	1-20cm	600	0
Steelhead	<i>Oncorhynchus mykiss</i>	1-20cm	600	0
Lingcod	<i>Ophiodon elongatus</i>	1-20cm	600	0
sturgeon poacher	<i>Podothecus accipenserinus</i>	1-20cm	600	0
blackeye goby	<i>Rhinogobiops nicholsii</i>	1-20cm	600	0
Brown rockfish	<i>Sebastes auriculatus</i>	1-20cm	600	0
Dusky rockfish	<i>Sebastes ciliatus</i>	1-20cm	600	0
Arctic Shanny	<i>Stichaeus punctatus</i>	1-20cm	600	0
Manacled sculpin	<i>Synchirus gilii</i>	1-20cm	600	0
Pacific sandfish	<i>Trichodon trichodon</i>	1-20cm	600	0
Sablefish	<i>Anoplopoma fimbria</i>	1-20cm	300	0
Scalyhead sculpin	<i>Arctidius harringtoni</i>	1-20cm	300	0
Alaskan ronquil	<i>Bathymaster caeruleofasciatus</i>	1-20cm	300	0
Crested Sculpin	<i>Blepsias bilobus</i>	1-20cm	300	0
Sharpnose sculpin	<i>Clinocottus acuticeps</i>	1-20cm	300	0
Antlered sculpin	<i>Enophrys dicerca</i>	1-20cm	300	0
Armorhead Sculpin	<i>Gymnocanthus galeatus</i>	1-20cm	300	0
Pacific tomcod	<i>Microgadus proximus</i>	1-20cm	300	0
Shorthorn sculpin	<i>Myoxocephalus scorpius</i>	1-20cm	300	0
English sole	<i>Parophrys vetulus</i>	1-20cm	300	0
Puget Sound rockfish	<i>Sebastes emphaeus</i>	1-20cm	300	0
Bocaccio	<i>Sebastes paucispinis</i>	1-20cm	300	0
China rockfish	<i>Sebastes nebulosus</i>	1-20cm	300	0
ongfin smelt	<i>Spirinchus thaleichthys</i>	1-20cm	300	0
eulachon	<i>Thaleichthys pacificus</i>	1-20cm	300	0
Black prickleback	<i>Xiphister atropurpureus</i>	1-20cm	300	0

Species List - Retained

Common Name	Scientific Name	Number collected	Total number retained
Eelgrass	<i>Zostera marina</i>	5,000	5,000 (5-300cm)
Surfgrass	<i>Phylospadix spp.</i>	3,000	3,000 (5-300cm)
Variegated chink snail	<i>Lacuna variegata</i>	1,500	1,500 (5-15mm)
Pacific blue mussel	<i>Mytilus trossulus</i>	3,000	3,000 (5-30mm)
Amphipods	Family: Gammaridae	30,000	30,000 (3-25mm)
Isopod	<i>Idotea spp.</i>	30,000	3,000 (5-35mm)
Polychaete	<i>Eteone spp.</i>	300	300 (10-50mm)
Pile worm	<i>Nereis vexillosa</i>	300	300 (10-50mm)
False white sea cucumber	<i>Eupentacta pseudoquinquesemita</i>	300	300 (10-50mm)
Spot shrimp	<i>Pandalus platyceras</i>	300	300 (10-75mm)
Dock shrimp	<i>Pandalus danae</i>	300	300 (10-75mm)
Opossum mysid	<i>Neomysis mercedes</i>	300	300 (10-75mm)
Alaskan crangon	<i>Crangon alaskensis</i>	300	300 (10-75mm)
Long-clawed crangon	<i>Crangon franciscorum angustimana</i>	300	300 (10-75mm)
Hermit crab	<i>Pagurus spp.</i>	300	300 (10-50mm)
Tuskworm	<i>Pectinaria granulata</i>	1,500	1,500 (10-50mm)
Featherduster worm	<i>Schizobranchia insignis</i>	900	900 (10-75mm)
Burrowing green anemone	<i>Anthopleura artemisia</i>	30	30 (5-25mm)
Littleneck clam	<i>Protothaca staminea</i>	300	300 (5-15mm)
Heart cockle	<i>Clinocardium nuttallii</i>	900	900 (5-50mm)
Littleneck clam	<i>Protothaca staminea</i>	1,000	1,000 (5-15mm)
Heart cockle	<i>Clinocardium nuttallii</i>	1,500	1,500 (5-50mm)
Butter clam	<i>Saxidomus gigantea</i>	2,000	2,000 (5-1000mm)
Bentnose clam	<i>Macoma nasuta</i>	1,000	1,000 (5-70mm)
Green sea urchin	<i>Strongylocentrotus droebachiensis</i>	450	450 (5-30mm)
Broken back shrimp	Hippolytidae	300	300 (10-75mm)
Dungeness crab*	<i>Metacarcinus magister</i>	2,000	100 (14-25cm)
Helmet crab	<i>Telmessus cheiragonus</i>	500	100 (10-15cm)

CF-19-067 continued (page 5 of 5)

Graceful crab	<i>Metacarcinus gracilis</i>	500	100 (10-15cm)
Red rock crab	<i>Cancer productus</i>	500	100 (14-25cm)
Kelp Crab	<i>Pugettia producta</i>	500	100 (10-15cm)
Lyre Crab	<i>Hyas lyratus</i>	500	100 (5-15cm)
Decorator Crab	<i>Oregonia gracilis</i>	500	100 (5-15cm)
Eelgrass Limpet	<i>Lotia pelta</i>	1,000	1,000 (2-12mm)
Snail	<i>Margarites sp</i>	1,000	1,000 (2-12mm)
Skeleton shrimp	<i>Caprella sp</i>	1,000	1,000 (2-12mm)
Snail	<i>Littorina sp</i>	1,000	1,000 (2-12mm)
Leptocheiliidae	<i>Leptocheilia savignyi</i>	500	500 (2-12mm)
Sea lettuce	<i>Ulva sp.</i>	3,000	3,000 (1-20cm)
	<i>Monostroma sp.</i>	3,000	3,000 (1-20cm)
	<i>Scytosiphon sp.</i>	3,000	3,000 (1-20cm)
	<i>Cladophora sp.</i>	3,000	3,000 (1-20cm)
	<i>Enteromorpha sp. (Ulva sp)</i>	3,000	3,000 (1-20cm)
	<i>Smithora sp.</i>	3,000	3,000 (1-20cm)
	<i>Gracilaria spp.</i>	3,000	3,000 (1-20cm)
	<i>Saccharina latissima</i>	1,000	3,000 (1-20cm)
	<i>Cystoseira geminata</i>	3,000	3,000 (1-20cm)
	<i>Desmarestia sp.</i>	3,000	3,000 (1-20cm)
	<i>Ahnfeltia sp.</i>	3,000	3,000 (1-20cm)
	<i>Leathesia marina</i>	3,000	3,000 (1-20cm)
Giant kelp	<i>Macrocystis pyrifera</i>	3,000	3,000 (1-20cm)
Diatoms			

*See Stipulation 5 regarding number of Dungeness crab allowed per site.

Appendix G: Alaska Department of Fish & Game Permit 2021



**STATE OF ALASKA
DEPARTMENT OF FISH AND GAME**

P.O. Box 115526
JUNEAU, ALASKA 99811-5526

AQUATIC RESOURCE PERMIT
(For Scientific/Collection/Holding Purposes)

Permit No. **CF-21-062**

Expires: **12/31/2021**

This permit authorizes:

Lia Domke

(whose signature is required on page 3 for permit validation)

of

University of Alaska Fairbanks

17101 Pt Lena Loop Rd., Juneau, AK 99801

(907)321-4461

lkdomke@alaska.edu

to conduct the following activities from **May 1, 2021** to **December 31, 2021** in accordance with AS 16.05.930, AS 16.05.340(b) and 5 AAC 41.600.

Purpose: To quantify the community composition and ecosystem services of seagrass and kelp habitats and associated invertebrates and fishes.

Location: Prince of Wales and surrounding islands, Revillagigedo Island and surround islands

Species: See **Species List** on pages 3-6.

Method of Collection: Invertebrates - hand collection, shovel, pots, larval light traps; fish - beach seine; algae - hand collection. See **Stipulations** section.

Disposition: Species will be sacrificed or released live at the site of capture. Sacrificed species will be destroyed as directed. **Stipulations** section.

A COLLECTION REPORT IS DUE January 30, 2022 and a COMPLETION REPORT IS DUE June 30, 2022. See **Stipulations** section for more information. Data from such reports are considered public information. Reports must be submitted to the Alaska Department of Fish and Game, Division of Commercial Fisheries, PO Box 115526, Juneau, AK 99811-5526, attention Michelle Morris (907-465-4724; dfg.fmpd.permitcoordinator@alaska.gov). A report is required whether or not collecting activities were undertaken.

GENERAL CONDITIONS, EXCEPTIONS AND RESTRICTIONS

1. This permit must be carried by person(s) specified during approved activities who shall show it on request to persons authorized to enforce Alaska's fish and game laws. This permit is nontransferable and will be revoked or renewal denied by the Commissioner of Fish and Game if the permittee violates any of its conditions, exceptions or restrictions. No redelegation of authority may be allowed under this permit unless specifically noted.
2. No specimens taken under authority hereof may be sold, bartered, or consumed. All specimens must be deposited in a public museum or a public scientific or educational institution unless otherwise stated herein. Subpermittees shall not retain possession of live animals or other specimens.
3. The permittee shall keep records of all activities conducted under authority of this permit, available for inspection at all reasonable hours upon request of any authorized state enforcement officer.
4. Permits will not be renewed until detailed reports, as specified in the Stipulation section, have been received by the department.
5. **UNLESS SPECIFICALLY STATED HEREIN, THIS PERMIT DOES NOT AUTHORIZE** the exportation of specimens or the taking of specimens in areas otherwise closed to hunting and fishing; without appropriate licenses required by state regulations; during closed seasons; or in any manner, by any means, at any time not permitted by those regulations.

Peter Bangs 4/9/21

**Deputy or Assistant Director
Division of Commercial Fisheries**

CF-21-062 continued (page 2 of 6)

Authorized Personnel: The following personnel may participate in collecting activities under terms of this permit.

Lia Domke, Ginny Eckert, Rebecca Cates, Jessica Whitney, Carter Johnson and Emma Beaver.

Employees and volunteers under the direct supervision of, and in the presence of, one of the authorized personnel listed above may participate in collecting activities under terms of this permit.

Stipulations:

1. **Bo Meredith** (Division of Commercial Fisheries, Ketchikan, (907)225-5195, bo_meredith@alaska.gov) (must be notified prior to you engaging in collecting or release activities. Division of Commercial Fisheries management biologists have the authority to specify methods for collecting, as well as limiting the collections of any species, and the number of specimens collected by time and area.
2. Permits will indicate the number of specimens that may be taken by species and life stage. Sampling or collecting activities must stop when the maximum allowable number of specimens is obtained. All live fish, shellfish, and aquatic plants collected in excess of the number specified on the permit must be released immediately and unharmed at the capture location, unless otherwise specified in the permit. All unintended mortalities must be recorded and returned to capture site waters.
3. Specimens collected under the authority of this permit are ONLY to be used for the purposes outlined in this permit.
4. All unattended collecting gear (including minnow, fyke, and hoop nets) must be labeled with the permittee's name, telephone number, and permit number. Pots must conform to *Escape Mechanisms for Shellfish and Bottomfish Pots*.
5. If evidence of chronic sea star wasting disease is encountered, please report the finding at the University of California, Santa Cruz website, <http://www.seastarwasting.org>. Please leave organisms undisturbed.
6. **For any species to be collected or held that require a federal permit, the applicant must obtain a federal permit and submit a copy of it with the application for an aquatic resource permit.** Please contact the International Pacific Halibut Commission at (206) 634-1838, P.O. Box 95009, Seattle, WA 98145-2009 to obtain permission for halibut collection.
7. Destroyed specimens must be double-bagged and placed in a sanitary landfill.
8. A copy of this permit, including any amendments, must be made available at all field collection sites and project sites for inspection upon request by a representative of the department or a law enforcement officer.
9. Issuance of this permit does not absolve the permittee from compliance in full with any and all other applicable federal, state, or local laws regulations, or ordinances.
10. **A report of collecting activities, referencing this aquatic resource permit, must be submitted 30 days after the expiration of this permit.** This report must summarize the number of all specimens, including bycatch, captured by date, location, depth of capture, species, size (weight and length where appropriate), age (where appropriate), sex, numbers, and the fate of those specimens. A report is required whether or not collecting activities were undertaken.
11. **A report of research activities, referencing this aquatic resource permit, must be submitted within 6 months after the expiration of this permit.** This report should present the research conducted in a format similar to a scientific paper including the following: introduction (objective of the study plan and hypothesis), methods, and results. The report is ad-hoc and intended to show that the specimens were used in a scientific method and allows for the evaluation of potential cumulative effects from multiple projects in the same area, but is not intended to be a full peer-reviewed scientific paper.
12. Failure to comply with the conditions of this permit will result in the loss of future permitting privileges.
13. PERMIT VALIDATION requires permittee's signature agreeing to abide by permit conditions before beginning collecting activities:

Signature of Permittee

ecc: Bo Meredith, Whitney Crittenden, Kelly Reppert, Craig Schwanke, Matt Catterson
CF Division Files
Alaska Wildlife Troopers – Ketchikan, Craig

CF-21-062 continued (page 3 of 6)
Species List

Common Name	Scientific Name	Life stage	Maximum Project Total	Length Range (cm)	Total number retained
Threespine stickleback	<i>Gasterosteus aculeatus</i>	adult and non larval juveniles	12,000	1-20cm	0
Pacific sand lance	<i>Ammodytes hexapteru/personatus</i>		12,000	1-20cm	0
Pacific Herring	<i>Clupea pallasii</i>		9,000	1-20cm	0
Shiner perch	<i>Cymatogaster aggregata</i>		9,000	1-20cm	0
Snake prickleback	<i>Lumpenus sagitta</i>		9,000	1-20cm	0
Pacific staghorn sculpin	<i>Leptocottus armatus</i>		7,200	1-20cm	0
Pacific staghorn sculpin	<i>Leptocottus armatus</i>		7,200	1-20cm	0
Pink salmon	<i>Oncorhynchus gorbuscha</i>		7,200	1-20cm	0
Chum salmon	<i>Oncorhynchus keta</i>		7,200	1-20cm	0
Coho salmon	<i>Oncorhynchus kisutch</i>		7,200	1-20cm	0
Snake prickleback	<i>Lumpenus sagitta</i>		6,000	1-20cm	0
walleye pollock	<i>Gadus chalcogrammus</i>		6,000	1-20cm	0
Great sculpin	<i>Myoxocephalus polyacanthocephalus</i>		4,200	1-20cm	0
Crecent gunnel	<i>Pholis laeta</i>		4,200	1-20cm	0
Bay pipefish	<i>Syngnathus leptorhynchus</i>		4,200	1-20cm	0
Kelp greenling	<i>Hexagrammos decagrammus</i>		3,600	1-20cm	0
Whitespotted greenling	<i>Hexagrammos stelleri</i>		3,000	1-20cm	0
Rock greenling	<i>Hexagrammos lagocephalus</i>		2,400	1-20cm	0
Masked greenling	<i>Hexagrammos octogrammus</i>		2,400	1-20cm	0
Smoothhead sculpin	<i>Artedius lateralis</i>		1,800	1-20cm	0
Tube-snout	<i>Aulorhynchus flavidus</i>		1,800	1-20cm	0
Silverspotted sculpin	<i>Blepsias cirrhosus</i>		1,800	1-20cm	0
Pacific cod	<i>Gadus macrocephalus</i>		1,800	1-20cm	0
Sockeye salmon	<i>Oncorhynchus nerka</i>		1,800	1-20cm	0
Chinook salmon	<i>Oncorhynchus tshawytscha</i>		1,800	1-20cm	0
Painted greenling	<i>Oxylebius pictus</i>		1,800	1-20cm	0
Tube-nose poacher	<i>Pallasina barbata aix</i>		1,800	1-20cm	0
Rock sole	<i>Pleuronectes bilineatus</i>		1,800	1-20cm	0
English sole	<i>Pleuronectes vetulus</i>		1,800	1-20cm	0
Dolly Varden	<i>Salvelinus malma</i>		1,800	1-20cm	0
Cabezon	<i>Scorpaenichthys marmoratus</i>		1,800	1-20cm	0
Padded sculpin	<i>Artedius fenestralis</i>		1,200	1-20cm	0
Kelp perch	<i>Brachyistius frenatus</i>		1,200	1-20cm	140 (4- 22 cm)
Pacific sanddab	<i>Citharichthys sordidus</i>		1,200	1-20cm	0
Speckled sanddab	<i>Citharichthys stigmaeus</i>		1,200	1-20cm	0
Buffalo scuplin	<i>Enophrys bison</i>		1,200	1-20cm	0
Red Irish lord	<i>Hemilepidotus hemilepidotus</i>		1,200	1-20cm	0
Brown Irish lord	<i>Hemilepidotus spinosus</i>		1,200	1-20cm	0
Surf smet	<i>Hypomesus pretiosus</i>		1,200	1-20cm	0
Northern sculpin	<i>Icelinus borealis</i>		1,200	1-20cm	0
Butter sole	<i>Isopsetta isolepis</i>	1,200	1-20cm	0	
Fluffy sculpin	<i>Oligocottus snyderi</i>	1,200	1-20cm	0	
Starry flounder	<i>Platichthys stellatus</i>	1,200	1-20cm	0	
Tadpole sculpin	<i>Psychrolutes paradoxus</i>	1,200	1-20cm	0	
Copper rockfish	<i>Sebastes caurinus</i>	1,200	1-20cm	0	
Yellowtail rockfish	<i>Sebastes flavidus</i>	1,200	1-20cm	0	
Quillback rockfish	<i>Sebastes maliger</i>	1,200	1-20cm	0	
Black rockfish	<i>Sebastes melanops</i>	1,200	1-20cm	0	
Yellowfin sole	<i>Limanda asper</i>	900	1-20cm	0	
Sailfin sculpin	<i>Nautichthys oculofasciatus</i>	900	1-20cm	0	
Yellowfin sole	<i>Limanda asper</i>	900	1-20cm	0	

CF-21-062 continued (page 4 of 6)

Common Name	Scientific Name	Life stage	Maximum Project Total	Length Range (cm)	Total number retained
Sailfin sculpin	<i>Nautichthys oculoasciatus</i>	adult and non larval juveniles	900	1-20cm	0
C-O sole	<i>Pleuronichthys coenosus</i>		900	1-20cm	0
Northern ronquil	<i>Ronquilus jordani</i>		900	1-20cm	0
Walleye pollock	<i>Theragra chalcogramma</i>		900	1-20cm	0
Bay goby	<i>Lepidogobius lepidus</i>		600	1-20cm	0
Juvenile snailfish	<i>Liparidae</i>		600	1-20cm	0
Tidepool snailfish	<i>Liparis florae</i>		600	1-20cm	0
capelin	<i>Mallotus villosus</i>		600	1-20cm	0
Steller's sculpin	<i>Myoxocephalus stelleri</i>		600	1-20cm	0
Northern spearnose poacher	<i>Agonopsis vulsa</i>		600	1-20cm	0
Penpoint gunnel	<i>Apodichthys flavidus</i>		600	1-20cm	0
Sculpin family	<i>Cottidae</i>		600	1-20cm	0
Black goby	<i>Coryphopterus nicholsi</i>		600	1-20cm	0
Leister sculpin	<i>Enophrys lucasi</i>		600	1-20cm	0
Pacific spiny lumpsucker	<i>Eumicrotremus orbis</i>		600	1-20cm	0
Tidepool snailfish	<i>Liparis florae</i>		600	1-20cm	0
capelin	<i>Mallotus villosus</i>		600	1-20cm	0
Steller's sculpin	<i>Myoxocephalus stelleri</i>		600	1-20cm	0
Cutthroat trout	<i>Oncorhynchus clarki</i>		600	1-20cm	0
Steelhead	<i>Oncorhynchus mykiss</i>		600	1-20cm	0
Lingcod	<i>Ophiodon elongatus</i>		600	1-20cm	0
sturgeon poacher	<i>Podothecus accipenserinus</i>		600	1-20cm	0
blackeye goby	<i>Rhinogobius nicholsii</i>		600	1-20cm	0
Brown rockfish	<i>Sebastes auriculatus</i>		600	1-20cm	0
Dusky rockfish	<i>Sebastes ciliatus</i>		600	1-20cm	0
Arctic Shanny	<i>Stichaeus punctatus</i>		600	1-20cm	0
Manacled sculpin	<i>Synchirus gilli</i>		600	1-20cm	0
Pacific sandfish	<i>Trichodon trichodon</i>		600	1-20cm	0
Slender cockscomb	<i>Anoplarchus insignis</i>		300	1-20cm	0
Roughback sculpin	<i>Chitonotus pugetensis</i>		300	1-20cm	0
Slender eelblenny	<i>Lumpenus fabricii</i>		300	1-20cm	0
Pacific tomcod	<i>Microgadus proximus</i>		300	1-20cm	0
Shorthorn sculpin	<i>Myoxocephalus scorpius</i>		300	1-20cm	0
Tidepool sculpin	<i>Oligocottus maculosus</i>		300	1-20cm	0
Sablefish	<i>Anoplopoma fimbria</i>		300	1-20cm	0
Scalyhead sculpin	<i>Artemis harringtoni</i>		300	1-20cm	0
Alaskan ronquil	<i>Bathymaster caeruleofasciatus</i>		300	1-20cm	0
Crested Sculpin	<i>Blepsias bilobus</i>		300	1-20cm	0
Sharpnose sculpin	<i>Clinocottus acuticeps</i>		300	1-20cm	0
Antlered sculpin	<i>Enophrys diceraus</i>		300	1-20cm	0
Armorhead Sculpin	<i>Gymnocanthus galeatus</i>		300	1-20cm	0
Pacific tomcod	<i>Microgadus proximus</i>		300	1-20cm	0
Shorthorn sculpin	<i>Myoxocephalus scorpius</i>		300	1-20cm	0
English sole	<i>Parophrys vetulus</i>		300	1-20cm	0
Puget Sound rockfish	<i>Sebastes emphaeus</i>		300	1-20cm	0
Bocaccio	<i>Sebastes paucispinis</i>		300	1-20cm	0
China rockfish	<i>Sebastes nebulosus</i>		300	1-20cm	0
ongfin smelt	<i>Spirinchus thaleichthys</i>		300	1-20cm	0
eulachon	<i>Thaleichthys pacificus</i>		300	1-20cm	0
Black prickleback	<i>Xiphister atropurpureus</i>		300	1-20cm	0
Amphipods	Family: Gammaridae	30,000	3-25mm	30,000	
Isopod	<i>Idotea spp.</i>	30,000	5-35mm	3,000	

CF-21-062 continued (page 5 of 6)

Common Name	Scientific Name	Life stage	Maximum Project Total	Length Range (cm)	Total number retained
Pacific blue mussel	<i>Mytilus trossulus</i>	adults and non-larval juveniles	3,000	5-30mm	3,000
Butter clam	<i>Saxidomus gigantea</i>		2,000	5-100mm	2,000
Dungeness crab	<i>Metacarcinus magister</i>		2,000	10-25+cm	0
Graceful rock crab	<i>Metacarcinus gracilis</i>		2,000	10-15cm	0
Plankton sp.		larval juveniles	30 liters	1-20mm	0
Variagated chink snail	<i>Lacuna variegata</i>	adults and non-larval juveniles	1,500	5-15mm	1,500
Tuskworm	<i>Pectinaria granulata</i>		1,500	10-15mm	1,500
Heart cockle	<i>Clinocardium nuttallii</i>		1,500	5-70mm	1,500
Littleneck clam	<i>Protothaca staminea</i>		1,000	5-30mm	1,000
Bentnose clam	<i>Macoma nasuta</i>		1,000	5-70mm	1,000
Red rock crab	<i>Cancer productus</i>		1,000	10-20cm	0
Eelgrass Limpet	<i>Lotia pelta</i>		1,000	2-12mm	1,000
Snail	<i>Margarites sp</i>		1,000	2-12mm	1,000
Skeleton shrimp	<i>Caprella sp</i>		1,000	2-12mm	1,000
Snail	<i>Littorina sp</i>		1,000	2-12mm	1,000
Featherduster worm	<i>Schizobranhia insignis</i>		900	10-75mm	900
Heart cockle	<i>Clinocardium nuttallii</i>		900	5-50mm	900
Helmet crab	<i>Telmessus cheiragonus</i>		500	10-20cm	0
Kelp Crab	<i>Pugettia producta</i>		500	10-20cm	0
Lyre Crab	<i>Hyas lyratus</i>		500	10-20cm	0
Decorator Crab	<i>Oregonia gracilis</i>		500	10-20cm	0
Leptocheiliidae	<i>Leptocheilia savignyi</i>		500	2-12mm	500
Green sea urchin	<i>Strongylocentrotus droebachiensis</i>		450	5-30mm	450
Polychaete	<i>Eteone spp.</i>		300	10-50mm	300
Pile worm	<i>Nereis vexillosa</i>		300	10-50mm	300
False white sea cucumber	<i>Eupentacta pseudoquinquesemita</i>		300	10-50mm	300
Spot shrimp	<i>Pandalus platyceras</i>		300	10-75mm	300
Dock shrimp	<i>Pandalus danae</i>		300	10-75mm	300
Opossum mysid	<i>Neomysis mercedes</i>		300	10-75mm	300
Alaskan crangon	<i>Crangon alaskensis</i>		300	10-75mm	300
Long-clawed crangon	<i>Crangon franciscorum angustimana</i>		300	10-75mm	300
Hermit crab	<i>Paqurus spp.</i>		300	10-50mm	300
Littleneck clam	<i>Protothaca staminea</i>		300	5-15mm	300
Broken back shrimp	<i>Hippolytidae</i>	300	10-75mm	300	
Burrowing green anemone	<i>Anthopleura artemisia</i>	30	5-25mm	30	
Eelgrass	<i>Zostera marina</i>	adult	5,000	5-300cm	5,000
Surfgrass	<i>Phyllospadix spp.</i>		3,000	5-300cm	3,000
	<i>Phyllospadix spp</i>		1,000	5-300cm	1,000
Diatoms			microscopic	< 1mm	
	<i>Ulva spp</i>		7,000	5-300cm	7,000
	<i>Punctaria lobata</i>		5,000	5-300cm	500
	<i>Fucus distichus</i>		4,000	5-300cm	4,000
Sea lettuce	<i>Ulva spp</i>		3,000	1-20cm	3,000
	<i>Monostroma sp.</i>		3,000	1-20cm	3,000
	<i>Scytosiphon sp.</i>		3,000	1-20cm	3,000
	<i>Cladophora sp.</i>		3,000	1-20cm	3,000
	<i>Enteromorpha sp. (Ulva sp)</i>		3,000	1-20cm	3,000
	<i>Smithora sp.</i>		3,000	1-20cm	3,000
	<i>Gracilaria spp.</i>		3,000	1-20cm	3,000
	<i>Cystoseira geminata</i>		3,000	1-20cm	3,000
	<i>Desmarestia spp</i>		3,000	1-20cm	3,000
	<i>Ahnfeltia spp</i>		3,000	1-20cm	3,000
	<i>Leathesia marina</i>		3,000	1-20cm	3,000

CF-21-062 continued (page 6 of 6)

Common Name	Scientific Name	Life stage	Maximum Project Total	Length Range (cm)	Total number retained
Giant kelp	<i>Macrocystis pyrifera</i>	adult	3,000	1-20cm	3,000
	<i>Neorhodomela aculeata</i>		3,000	5-300cm	3,000
	<i>Saccharina spp</i>		1,000	1-20cm	3,000
	<i>Laminaria yezoensis</i>		500	5-300cm	500
	<i>Palmaria spp</i>		500	5-300cm	500
	<i>Sargassum spp</i>		500	5-300cm	500
	<i>Laminaria saccharina</i>		300	5-300cm	300
	<i>Odonthalia spp</i>		300	5-300cm	300
	<i>Polyneura latissima</i>		300	5-300cm	300
	<i>Sparangia pertula</i>		300	5-300cm	300
	<i>Cumantamion decipiens</i>		200	5-300cm	200
	<i>Cymathaere triplicata</i>		200	5-300cm	200
	<i>Dictyosiphon foeniculaceus</i>		200	5-300cm	200
	<i>Polysiphonia</i>		200	5-300cm	200
	<i>Acrosiphonia spp</i>		100	5-300cm	100
	<i>Blidingia minima</i>		100	5-300cm	100
	<i>Ectocarpus siliculosus</i>		100	5-300cm	100
	<i>Petalonia fascia</i>		100	5-300cm	100
	<i>Stephanocystis</i>		100	5-300cm	100
	<i>Analipus japonicus</i>		50	5-300cm	50
	<i>Chorda filum</i>		50	5-300cm	50
	<i>Chordaria flagelliformis</i>		50	5-300cm	50
	<i>Constantinia spp</i>		50	5-300cm	50
	<i>Corallina vancouveriensis</i>		50	5-300cm	50
	<i>Falonia mollis</i>		50	5-300cm	50
	<i>Fartomia mollis</i>		50	5-300cm	50

Appendix H: Alaska Department of Fish & Game Permit 2022



**STATE OF ALASKA
DEPARTMENT OF FISH AND GAME**

P.O. Box 115526
JUNEAU, ALASKA 99811-5526

AQUATIC RESOURCE PERMIT
(For Scientific/Collection/Holding Purposes)

Permit No. **CF-22-070**

Expires: **12/31/2022**

This permit authorizes:

Lia Domke

(whose signature is required on page 3 for permit validation)

of

University of Alaska Fairbanks

17101 Pt Lena Loop Rd., Juneau, AK 99801

(907)321-4461

lkdome@alaska.edu

to conduct the following activities from **May 1, 2022** to **December 31, 2022** in accordance with AS 16.05.930, AS 16.05.340(b) and 5 AAC 41.600.

Purpose: To quantify the community composition and ecosystem services of seagrass and kelp habitats and associated invertebrates and fishes.

Location: Prince of Wales and surrounding islands and Kupreanof Island
Crab sampling in Pybus Bay (Admiralty Island), Duncan Canal, Farragut Bay and Thomas Bay

Species: See **Species List** on pages 3-7.

Method of Collection: Invertebrates - hand collection, shovel, pots, larval light traps; fish - beach seine; algae – hand collection. See **Stipulations** section.

Disposition: Species will be sacrificed or released live at the site of capture. Sacrificed species will be destroyed as directed. **Stipulations** section.

A COLLECTION REPORT IS DUE January 30, 2023 and a COMPLETION REPORT IS DUE June 30, 2023. See **Stipulations** section for more information. Data from such reports are considered public information. Reports must be submitted to the Alaska Department of Fish and Game, Division of Commercial Fisheries, PO Box 115526, Juneau, AK 99811-5526, attention Permit Coordinator (907-465-4724; dfg.fmpd.permitcoordinator@alaska.gov). A report is required whether or not collecting activities were undertaken.

GENERAL CONDITIONS, EXCEPTIONS AND RESTRICTIONS

1. This permit must be carried by person(s) specified during approved activities who shall show it on request to persons authorized to enforce Alaska's fish and game laws. This permit is nontransferable and will be revoked or renewal denied by the Commissioner of Fish and Game if the permittee violates any of its conditions, exceptions or restrictions. No redelegation of authority may be allowed under this permit unless specifically noted.
2. No specimens taken under authority hereof may be sold, bartered, or consumed. All specimens must be deposited in a public museum or a public scientific or educational institution unless otherwise stated herein. Subpermittees shall not retain possession of live animals or other specimens.
3. The permittee shall keep records of all activities conducted under authority of this permit, available for inspection at all reasonable hours upon request of any authorized state enforcement officer.
4. Permits will not be renewed until detailed reports, as specified in the Stipulation section, have been received by the department.
5. UNLESS SPECIFICALLY STATED HEREIN, THIS PERMIT DOES NOT AUTHORIZE the exportation of specimens or the taking of specimens in areas otherwise closed to hunting and fishing; without appropriate licenses required by state regulations; during closed seasons; or in any manner, by any means, at any time not permitted by those regulations.

Peter Bangs 4/26/2022

**Deputy or Assistant Director
Division of Commercial Fisheries**

CF-22-070 continued (page 2 of 7)

Authorized Personnel: The following personnel may participate in collecting activities under terms of this permit:

Lia Domke, Elin Antaya, Ginny Eckert, Jessica Whitney and Carter Johnson.

Employees and volunteers under the direct supervision of, and in the presence of, one of the authorized personnel listed above may participate in collecting activities under terms of this permit.

Stipulations:

1. **Prior** to commencement of any field activity, the Division of Commercial Fisheries and/or Division of Sport Fish biologist of the appropriate area must be notified as to the location of operations, gear to be used, and number of specimens to be collected. Area management biologists have the authority to specify methods for collecting, as well as limiting the collections of any species, and the number of specimens collected by time and area. Please call the Permit Coordinator (970-465-4724) if there is a question about who to contact.

Petersburg – CF **Paul Salomone** (907) 465-2810 matt.catterson@alaska.gov

Ketchikan – CF **Bo Meredith** (907) 225-5195 bo.meredith@alaska.gov

2. Permits will indicate the number of specimens that may be taken by species and life stage. Sampling or collecting activities must stop when the maximum allowable number of specimens is obtained. All live fish, shellfish, and aquatic plants collected in excess of the number specified on the permit must be released immediately and unharmed at the capture location, unless otherwise specified in the permit. All unintended mortalities must be recorded and returned to capture site waters.
3. Specimens collected under the authority of this permit are **ONLY** to be used for the purposes outlined in this permit.
4. All unattended collecting gear (including minnow, fyke, and hoop nets) must be labeled with the permittee's name, telephone number, and permit number. Pots must conform to *Escape Mechanisms for Shellfish and Bottomfish Pots*.
5. If evidence of chronic sea star wasting disease is encountered, please report the finding at the University of California, Santa Cruz website, <http://www.seastarwasting.org>. Please leave organisms undisturbed.
6. **For any species to be collected or held that require a federal permit, the applicant must obtain a federal permit and submit a copy of it with the application for an aquatic resource permit.** Please contact the International Pacific Halibut Commission at (206) 634-1838, P.O. Box 95009, Seattle, WA 98145-2009 to obtain permission for halibut collection.
7. Destroyed specimens must be double-bagged and placed in a sanitary landfill.
8. A copy of this permit, including any amendments, must be made available at all field collection sites and project sites for inspection upon request by a representative of the department or a law enforcement officer.
9. Issuance of this permit does not absolve the permittee from compliance in full with any and all other applicable federal, state, or local laws regulations, or ordinances.
10. **A report of collecting activities, referencing this aquatic resource permit, must be submitted 30 days after the expiration of this permit.** This report must summarize the number of all specimens, including bycatch, captured by date, location, depth of capture, species, size (weight and length where appropriate), age (where appropriate), sex, numbers, and the fate of those specimens. A report is required whether or not collecting activities were undertaken.
11. **A report of research activities, referencing this aquatic resource permit, must be submitted within 6 months after the expiration of this permit.** This report should present the research conducted in a format similar to a scientific paper including the following: introduction (objective of the study plan and hypothesis), methods, and results. The report is ad-hoc and intended to show that the specimens were used in a scientific method and allows for the evaluation of potential cumulative effects from multiple projects in the same area, but is not intended to be a full peer-reviewed scientific paper.
12. Failure to comply with the conditions of this permit will result in the loss of future permitting privileges.
13. PERMIT VALIDATION requires permittee's signature agreeing to abide by permit conditions before beginning collecting activities:

Signature of Permittee

ecc: Bo Meredith, Whitney Crittenden, Kelly Reppert, Craig Schwanke, Matt Catterson, Paul Salomone, Dan Teske
CF Division Files
Alaska Wildlife Troopers – Ketchikan, Craig, Petersburg

CF-22-070 continued (page 3 of 7)

Species List

Common Name	Scientific Name	Life stage	Maximum Project Total	Length Range (cm)	Total number retained
Threespine stickleback	<i>Gasterosteus aculeatus</i>	Juvenile/Adult	12000	1-20cm	0
Pacific sand lance	<i>Ammodytes hexapteru/personatus</i>		12000	1-20cm	0
Pacific Herring	<i>Clupea pallasii</i>		9000	1-20cm	0
Shiner perch	<i>Cymatogaster aggregata</i>		9000	1-20cm	0
Snake prickleback	<i>Lumpenus sagitta</i>		9000	1-20cm	0
Pacific staghorn sculpin	<i>Leptocottus armatus</i>		7200	1-20cm	0
Pacific staghorn sculpin	<i>Leptocottus armatus</i>		7200	1-20cm	0
Pink salmon	<i>Oncorhynchus gorbuscha</i>		7200	1-20cm	0
Chum salmon	<i>Oncorhynchus keta</i>		7200	1-20cm	0
Coho salmon	<i>Oncorhynchus kisutch</i>		7200	1-20cm	0
Snake prickleback	<i>Lumpenus sagitta</i>		6000	1-20cm	0
walleye pollock	<i>Gadus chalcogrammus</i>		6000	1-20cm	0
Great sculpin	<i>Myoxocephalus polyacanthocephalus</i>		4200	1-20cm	0
Great sculpin	<i>Myoxocephalus polyacanthocephalus</i>		4200	1-20cm	0
Crecent gunnel	<i>Pholis laeta</i>		4200	1-20cm	0
Bay pipefish	<i>Syngnathus leptorhynchus</i>		4200	1-20cm	0
Kelp greenling	<i>Hexagrammos decagrammus</i>		3600	1-20cm	0
Whitespotted greenling	<i>Hexagrammos stelleri</i>		3000	1-20cm	0
Rock greenling	<i>Hexagrammos lagocephalus</i>		2400	1-20cm	0
Masked greenling	<i>Hexagrammos octogrammus</i>		2400	1-20cm	0
Smoothhead sculpin	<i>Artedius lateralis</i>		1800	1-20cm	0
Tube-snout	<i>Autorhynchus flavidus</i>		1800	1-20cm	0
Silverspotted sculpin	<i>Blepsias cirrhosus</i>		1800	1-20cm	0
Pacific cod	<i>Gadus macrocephalus</i>		1800	1-20cm	0
Sockeye salmon	<i>Oncorhynchus nerka</i>		1800	1-20cm	0
Chinook salmon	<i>Oncorhynchus tshawytscha</i>		1800	1-20cm	0
Painted greenling	<i>Oxylebius pictus</i>		1800	1-20cm	0
Tube-nose poacher	<i>Pallasina barbata</i>		1800	1-20cm	0
Rock sole	<i>Pleuronectes bilineatus</i>		1800	1-20cm	0
English sole	<i>Pleuronectes vetulus</i>		1800	1-20cm	0
Dolly Varden	<i>Salvelinus malma</i>		1800	1-20cm	0
Cabezon	<i>Scorpaenichthys marmoratus</i>		1800	1-20cm	0
Padded sculpin	<i>Artedius fenestralis</i>		1200	1-20cm	0
Kelp perch	<i>Brachyistius frenatus</i>		1200	1-20cm	0
Pacific sanddab	<i>Citharichthys sordidus</i>		1200	1-20cm	0
Speckled sanddab	<i>Citharichthys stigmaeus</i>		1200	1-20cm	0
Buffalo scuplin	<i>Enophrys bison</i>		1200	1-20cm	0
Red Irish lord	<i>Hemilepidotus hemilepidotus</i>		1200	1-20cm	0
Brown Irish lord	<i>Hemilepidotus spinosus</i>		1200	1-20cm	0
Surf smet	<i>Hypomesus pretiosus</i>		1200	1-20cm	0
Northern sculpin	<i>Icelinus borealis</i>	1200	1-20cm	0	
Butter sole	<i>Isopsetta isolepis</i>	1200	1-20cm	0	
Fluffy sculpin	<i>Oligocottus snyderi</i>	1200	1-20cm	0	
Starry flounder	<i>Platichthys stellatus</i>	1200	1-20cm	0	
Tadpole sculpin	<i>Psychrolutes paradoxus</i>	1200	1-20cm	0	
Copper rockfish	<i>Sebastes caurinus</i>	1200	1-20cm	0	
Yellowtail rockfish	<i>Sebastes flavidus</i>	1200	1-20cm	0	
Quillback rockfish	<i>Sebastes maliger</i>	1200	1-20cm	0	

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Black rockfish	<i>Sebastes melanops</i>	Juvenile/Adult	1200	1-20cm	0
Yellowfin sole	<i>Limanda asper</i>		900	1-20cm	0
Sailfin sculpin	<i>Nautichthys oculofasciatus</i>		900	1-20cm	0
Yellowfin sole	<i>Limanda asper</i>		900	1-20cm	0
Sailfin sculpin	<i>Nautichthys oculofasciatus</i>		900	1-20cm	0
C-O sole	<i>Pleuronichthys coenosus</i>		900	1-20cm	0
Northern ronquil	<i>Ronquilius jordani</i>		900	1-20cm	0
Walleye pollock	<i>Theragra chalcogramma</i>		900	1-20cm	0
Bay goby	<i>Lepidogobius lepidus</i>		600	1-20cm	0
Juvenile snailfish	<i>Liparidae</i>		600	1-20cm	0
Tidepool snailfish	<i>Liparis flarae</i>		600	1-20cm	0
capelin	<i>Mallotus villosus</i>		600	1-20cm	0
Steller's sculpin	<i>Myoxocephalus stelleri</i>		600	1-20cm	0
Northern spearnose poacher	<i>Agonopsis vulsa</i>		600	1-20cm	0
Penpoint gunnel	<i>Apodichthys flavidus</i>		600	1-20cm	0
Sculpin family	<i>Cottidae</i>		600	1-20cm	0
Black goby	<i>Coryphopterus nicholsi</i>		600	1-20cm	0
Leister sculpin	<i>Enophrys lucasi</i>		600	1-20cm	0
Pacific spiny lumpsucker	<i>Eumicrotremus orbis</i>		600	1-20cm	0
Tidepool snailfish	<i>Liparis flarae</i>		600	1-20cm	0
capelin	<i>Mallotus villosus</i>		600	1-20cm	0
Steller's sculpin	<i>Myoxocephalus stelleri</i>		600	1-20cm	0
Cutthroat trout	<i>Oncorhynchus clarki</i>		600	1-20cm	0
Steelhead	<i>Oncorhynchus mykiss</i>		600	1-20cm	0
Lingcod	<i>Ophiodon elongatus</i>		600	1-20cm	0
sturgeon poacher	<i>Podothecus accipenserinus</i>		600	1-20cm	0
blackeye goby	<i>Rhinogobiops nicholsii</i>		600	1-20cm	0
Brown rockfish	<i>Sebastes auriculatus</i>		600	1-20cm	0
Dusky rockfish	<i>Sebastes ciliatus</i>		600	1-20cm	0
Arctic Shanny	<i>Stichaeus punctatus</i>		600	1-20cm	0
Manacled sculpin	<i>Synchirus gilli</i>		600	1-20cm	0
Pacific sandfish	<i>Trichodon trichodon</i>		600	1-20cm	0
Slender cockscomb	<i>Anoplarchus insignis</i>		300	1-20cm	0
Roughback sculpin	<i>Chitonotus pugetensis</i>		300	1-20cm	0
Slender eelblenny	<i>Lumpenus fabricii</i>		300	1-20cm	0
Pacific tomcod	<i>Microgadus proximus</i>		300	1-20cm	0
Shorthorn sculpin	<i>Myoxocephalus scorpius</i>		300	1-20cm	0
Tidepool sculpin	<i>Oligocottus maculosus</i>		300	1-20cm	0
Sablefish	<i>Anoplopoma fimbria</i>		300	1-20cm	0
Scalyhead sculpin	<i>Artedius harringtoni</i>		300	1-20cm	0
Alaskan ronquil	<i>Bathymaster caeruleofasciatus</i>		300	1-20cm	0
Crested Sculpin	<i>Blepsias bilobus</i>		300	1-20cm	0
Sharnose sculpin	<i>Clinocottus acuticeps</i>		300	1-20cm	0
Antlered sculpin	<i>Enophrys diceraus</i>		300	1-20cm	0
Armorhead Sculpin	<i>Gymnocanthus galeatus</i>		300	1-20cm	0
Pacific tomcod	<i>Microgadus proximus</i>	300	1-20cm	0	
Shorthorn sculpin	<i>Myoxocephalus scorpius</i>	300	1-20cm	0	
English sole	<i>Parophrys vetulus</i>	300	1-20cm	0	
Puget Sound rockfish	<i>Sebastes emphaeus</i>	300	1-20cm	0	
Bocaccio	<i>Sebastes paucispinis</i>	300	1-20cm	0	
China rockfish	<i>Sebastes nebulosus</i>	300	1-20cm	0	
ongfin smelt	<i>Spirinchus thaleichthys</i>	300	1-20cm	0	
eulachon	<i>Thaleichthys pacificus</i>	300	1-20cm	0	
Black prickleback	<i>Xiphister atropurpureus</i>	300	1-20cm	0	

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Amphipods	<i>Family: Gammaridae</i>	Juvenile/Adult	30000	5-25mm	30000 (3-25mm)
Isopod	<i>Idotea spp.</i>		30000	5-35mm	3000 (5-35mm)
Pacific blue mussel	<i>Mytilus trossulus</i>		3000	5-30mm	3000 (5-30mm)
Butter clam	<i>Saxidomus gigantea</i>		2000	5-100mm	2000 (5-100mm)
Dungeness crab	<i>Metacarcinus magister</i>		6000	10-25+ cm	0
Graceful rock crab	<i>Metacarcinus gracilis</i>		6000	10-15cm	0
Plankton sp.			larval juveniles	30 liters	1-20mm
Variegated chink snail	<i>Lacuna variegata</i>	Juvenile/Adult	1500	5-15mm	1500 (5-15mm)
Tuskworm	<i>Pectinaria granulata</i>		1500	10-15mm	1500 (10-50mm)
Heart cockle	<i>Clinocardium nuttallii</i>		1500	5-70mm	1500 (5-50mm)
Littleneck clam	<i>Protothaca staminea</i>		1000	5-30mm	1000 (5-15mm)
Bentnose clam	<i>Macoma nasuta</i>		1000	5-70mm	1000 (5-70mm)
Red rock crab	<i>Cancer productus</i>		3000	10-20cm	0
Eelgrass Limpet	<i>Lotia pelta</i>		1000	2-12mm	1000 (2-12mm)
Snail	<i>Margarites sp</i>		1000	2-12mm	1000 (2-12mm)
Skeleton shrimp	<i>Caprella sp</i>		1000	2-12mm	1000 (2-12mm)
Snail	<i>Littorina sp</i>		1000	2-12mm	1000 (2-12mm)
Featherduster worm	<i>Schizobranchia insignis</i>		900	10-75mm	900 (10-75mm)
Heart cockle	<i>Clinocardium nuttallii</i>		900	5-50mm	900 (5-50mm)
Helmet crab	<i>Telmessus cheiragonus</i>		1500	10-20cm	0
Kelp Crab	<i>Pugettia producta</i>		1500	10-20cm	0
Lyre Crab	<i>Hyas lyratus</i>		1500	10-20cm	0
Decorator Crab	<i>Oregonia gracilis</i>		1500	10-20cm	0
Leptochelidae	<i>Leptochelia savignyi</i>		500	2-12mm	500 (2-12mm)
Green sea urchin	<i>Strongylocentrotus droebachiensis</i>		450	5-30mm	450 (5-30mm)
Polychaete	<i>Eteone spp.</i>		300	10-50mm	300 (10-50mm)
Pile worm	<i>Nereis vexillosa</i>		300	10-50mm	300 (10-50mm)
False white sea cucumber	<i>Eupentacta pseudoquinquesemita</i>		300	10-50mm	300 (10-50mm)
Spot shrimp	<i>Pandalus platyceras</i>		300	10-75mm	300 (10-75mm)
Dock shrimp	<i>Pandalus danae</i>		300	10-75mm	300 (10-75mm)
Opossum mysid	<i>Neomysis mercedes</i>		300	10-75mm	300 (10-75mm)
Alaskan crangon	<i>Crangon alaskensis</i>		300	10-75mm	300 (10-75mm)
Long-clawed crangon	<i>Crangon franciscorum angustimana</i>		300	10-75mm	300 (10-75mm)

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Hermit crab	<i>Pagurus spp.</i>	Juvenile/Adult	300	10-50mm	300 (10-50mm)
Littleneck clam	<i>Protothaca staminea</i>		300	5-15mm	300 (5-15mm)
Broken back shrimp	<i>Hippolytidae</i>		300	10-75mm	300 (10-75mm)
Burrowing green anemone	<i>Anthopleura artemisia</i>		30	5-25mm	30 (5-25mm)
Eelgrass	<i>Zostera marina</i>	Adult	5000	5-300cm	5000 (5-300cm)
Surfgrass	<i>Phyllospadix spp.</i>		3000	5-300cm	3000 (5-300cm)
	<i>Phyllospadix spp</i>		1000	5-300cm	1000 (5-300cm)
Diatoms			microscopic	<1mm	
	<i>Ulva spp</i>		7000	5-300cm	7000 (5-300cm)
	<i>Punctaria lobata</i>		5000	5-300cm	500 (5-300cm)
	<i>Fucus distichus</i>		4000	5-300cm	4000 (5-300cm)
Sea lettuce	<i>Ulva spp</i>		3000	1-20cm	3000 (1-20cm)
	<i>Monostroma sp.</i>		3000	1-20cm	3000 (1-20cm)
	<i>Scytosiphon sp.</i>		3000	1-20cm	3000 (1-20cm)
	<i>Cladophora sp.</i>		3000	1-20cm	3000 (1-20cm)
	<i>Enteromorpha sp. (Ulva sp)</i>		3000	1-20cm	3000 (1-20cm)
	<i>Smithora sp.</i>		3000	1-20cm	3000 (1-20cm)
	<i>Gracilaria spp.</i>		3000	1-20cm	3000 (1-20cm)
	<i>Cystoseira geminata</i>		3000	1-20cm	3000 (1-20cm)
	<i>Desmarestia spp</i>		3000	1-20cm	3000 (1-20cm)
	<i>Ahnfeltia spp</i>		3000	1-20cm	3000 (1-20cm)
	<i>Leathesia marina</i>		3000	1-20cm	3000 (1-20cm)
Giant kelp	<i>Macrocystis pyrifera</i>		3000	1-20cm	3000 (1-20cm)
	<i>Neorhodomela aculeata</i>		3000	5-300cm	3000 (5-300cm)
	<i>Saccharina spp</i>	1000	1-20cm	3000 (1-20cm)	
	<i>Laminaria yezoensis</i>	500	5-300cm	500 (5-300cm)	
	<i>Palmaria spp</i>	500	5-300cm	500 (5-300cm)	
	<i>Sargassum spp</i>	500	5-300cm	500 (5-300cm)	
	<i>Laminaria saccharina</i>	300	5-300cm	300 (5-300cm)	
	<i>Odonthalia spp</i>	300	5-300cm	300 (5-300cm)	

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	<i>Polyneura latissima</i>	Adult	300	5-300cm	300 (5-300cm)
	<i>Sparangia pertula</i>		300	5-300cm	300 (5-300cm)
	<i>Cumantamion decipiens</i>		200	5-300cm	200 (5-300cm)
	<i>Cymathaere triplicata</i>		200	5-300cm	200 (5-300cm)
	<i>Dictyosiphon foeniculaceus</i>		200	5-300cm	200 (5-300cm)
	<i>Polysiphonia</i>		200	5-300cm	200 (5-300cm)
	<i>Acrosiphonia spp</i>		100	5-300cm	100 (5-300cm)
	<i>Blidingia minima</i>		100	5-300cm	100 (5-300cm)
	<i>Ectocarpus siliculosus</i>		100	5-300cm	100 (5-300cm)
	<i>Petalonia fascia</i>		100	5-300cm	100 (5-300cm)
	<i>Stephanocystis</i>		100	5-300cm	100 (5-300cm)
	<i>Analipus japonicus</i>		50	5-300cm	50 (5-300cm)
	<i>Chorda filum</i>		50	5-300cm	50 (5-300cm)
	<i>Chordaria flagelliformis</i>		50	5-300cm	50 (5-300cm)
	<i>Constantinia spp</i>		50	5-300cm	50 (5-300cm)
	<i>Corallina vancouveriensis</i>		50	5-300cm	50 (5-300cm)
	<i>Falonia mollis</i>	50	5-300cm	50 (5-300cm)	
	<i>Farfomia mollis</i>	50	5-300cm	50 (5-300cm)	