SEA OTTERS IN SOUTHEAST ALASKA: SUBSISTENCE HARVEST AND ECOLOGICAL EFFECTS IN SEAGRASS COMMUNITIES

By

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Abstract

The recovery of sea otters (*Enhydra lutris*) to Southeast Alaska is a conservation success story, but their increasing population raises questions about sea otter population dynamics and the ecological role of this top-level predator. In Chapter 1, we addressed these questions by investigating patterns and population effects of subsistence sea otter harvest. Subsistence harvest reduced populations at a small scale, with potential to slow or stop population growth, but across Southeast Alaska the population continues to grow, even with an average 3% subsistence harvest rate. In Chapters 2 and 3 we investigated the ecological role of sea otters in seagrass (*Zostera marina*) communities. When we tested for generality in a sea otter - seagrass trophic cascade across a large spatial scale in Southeast Alaska, we found a positive relationship between sea otters and seagrass. However, we found no evidence of a relationship between crabs and epifauna, suggesting that the ecological mechanisms in Southeast Alaska may differ from other regions. Our comparison of carbon and nitrogen stable isotopes (SI) to assess the role of sea otters on trophic structure and energetic pathways of seagrass beds found little effect of sea otters in overall community trophic niche space, suggesting similar carbon sources and food chain length in seagrass meadows regardless of sea otters. Conversely, the FA profiles of diverse consumer suggest variation in dietary sources with and without sea otters. This result suggests that the trophic cascade may not be the only or primary energetic pathway in Southeast Alaska seagrass communities. In all, our studies have revealed that sea otters in Southeast Alaska are linked to both people and a common Southeast Alaska nearshore habitat, seagrass. These results describe the varied interactions of a recovering top predator and highlight a need to consider these diverse interactions in resource management, conservation, and ecological research.

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General Introduction

The recovery of sea otter populations throughout the coastal northeastern Pacific is one of the world's greatest conservation success stories. From the mid-1700s to the early 1900s, sea otters were commercially hunted as a part of the maritime fur trade, reducing their range-wide population from an estimated 150,000 - 300,000 to approximately 2,000 (Lensink 1962, Kenyon 1969, Johnson 1982). Through legal protections, reintroductions, and conservation, sea otters have recovered to a global population of approximately 125,000 (Doroff and Burdin 2015). However, sea otter recovery has been met with mixed responses. Early research on the recovering sea otter population documented the strong effects of sea otters in structuring ecosystems through predation. Termed trophic cascades, researchers found that sea otters confer indirect positive effects to kelp by removing their primary herbivores, sea urchins (Estes et al. 1978). However, this same appetite for shellfish has led to conflicts with commercial, recreational, and subsistence harvesters throughout their range (Carswell et al. 2015). A notable region of sea otter recovery is Southeast Alaska (SEAK), where 412 sea otters re-introduced in the late 1960s have grown to 25,584 at last estimate, representing approximately one fifth of the global population (Burris and McKnight 1973, USFWS 2014a, Doroff and Burdin 2015, Tinker et al. 2019). While some of the foundational ecological research on the benefits of sea otters was conducted in SEAK (Duggins 1980, Estes and Duggins 1995), sea otters have also had profound negative effects on commercial fisheries (Larson et al. 2013, Hoyt 2015). These opposing views of sea otters have placed research, conservation, fisheries, and management in the difficult situation of having to reconcile conservation of this iconic apex predator with honoring the commercial and cultural interests tied to the species.

Sea otters rely on their fur, high metabolic rate, and high body temperature to stay warm (Morrison et al. 1974, Costa and Kooyman 1984, Yeates et al. 2007). Maintaining this high metabolism requires a large amount of food and sea otters can consume up to 20% percent of their body weight per day (Costa 1982). Sea otter diets primarily consist of shellfish, which are also harvested in commercial, recreational, and subsistence fisheries. In SEAK from 2009 to 2012, 46% of sea otter diets consisted of commercially harvested shellfish, including Dungeness crabs (*Metacarcinus magister*), sea urchins (*Strongylocentrotus* spp., and *Mesocentrotus* sp.), and geoducks (*Panopea generosa*) (Hoyt 2015). In one case, commercially harvested sea cucumbers (*Parasticupus californicus*) declined by 100% in areas occupied by sea otters for seven years (Larson et al. 2013).While clams (excluding geoducks) are not commercially harvested, they are popular recreational and subsistence foods and compose approximately 23% of sea otter diets (Hoyt 2015). These negative effects on resources have raised concerns about the growing sea otter population in SEAK. This has led to attempts by the Alaska State Legislature to allow increased sea otter hunting, including a bounty (Carswell et al. 2015), and calls for co-management of sea otter between the federal government and the State of Alaska (Stedman et al. 2018). The growing concern over the negative effects of sea otters is at odds with the documented beneficial effects of sea otters in some nearshore ecosystems (Estes et al. 1978, Duggins et al. 1989, Estes and Duggins 1995), highlighting a need to further investigate the role of sea otters in SEAK.

The commercial harvest of sea otters led to their near extinction from 1750 – 1911; however, sea otters have been hunted by indigenous peoples for thousands of years, and continues to this day (Fedje et al. 2001, Erlandson and Rick 2010, Szpak et al. 2013). The U.S. Marine Mammal Protection Act (MMPA) permits coastal Alaska Natives to harvest sea otters for purposes of subsistence and creating and selling native handicrafts and clothing (50 CFR 18.23). Harvest data is reported to the United States Fish and Wildlife Service (USFWS) and has been collected in SEAK since 1988. Recent increases in subsistence harvest (USFWS 2014b) and concern over impacts to fisheries, have raised questions about the potential population effects of subsistence sea otter harvest in the region. Previous analyses of the SEAK sea otter population suggested that subsistence sea otter harvest could affect the population (Esslinger and Bodkin 2009), especially at small spatial scales (Bodkin and Ballachey 2010, Tinker et al. 2019). Furthermore, the SEAK sea otter population is formally surveyed infrequently (7 – 10 yr), making detection of subsistence harvest effects difficult. In Chapter 1, we examine these questions by analyzing 28 years of subsistence sea otter harvest data to identify spatial and temporal patterns of harvest and test for its effects on the sea otter population.

Predation by sea otters has not only generated conflict with humans but can also cause drastic changes in marine ecosystems. As the sea otter population began to recover in the 1970s and 1980s, numerous studies described their effects in kelp forest ecosystems. Before sea otters recovered to an area, shallow rocky substrates were dominated by sea urchins, whose intense grazing kept kelp densities in check (Estes et al. 1978, Estes and Duggins 1995). As sea otters returned, they greatly reduced sea urchin abundance, releasing kelps from herbivory resulting in large kelp forests (Estes et al. 1978). Termed ‘trophic cascades’, this dramatic pattern of alternating abundance and a positive indirect effect of sea otters on kelp has been described in SEAK (Duggins 1980) and is relatively generalizable across the Alaskan range of sea otters (Estes and Duggins 1995). The positive effect on kelp can enhance primary productivity and lead to greater fish abundance and an overall increase in ecological diversity (Duggins et al. 1989, Reisewitz et al. 2006). A majority of sea otter-ecosystem research has been focused in rocky habitats, where they have been historically concentrated; however, as sea otter populations have continued to grow they have moved into other nearshore habitats, including seagrasses.

Seagrasses are found in shallow soft-sediment habitats around the world and support dense, diverse, and productive faunal communities (Duffy et al. 2014). While widespread, seagrasses are in global decline at an estimated rate of 110 km^2 per year since 1980 (Orth et al. 2006, Waycott et al. 2009). This decline has been attributed to multiple factors, including sediment and nutrient runoff, physical disturbance, invasive species, disease, commercial fishing practices, aquaculture, overgrazing, algal blooms, and climate change (Orth et al. 2006). SEAK has over 10,000 km of the seagrass shoreline, nearly as much shoreline (of any type) as the entire west coast of the continental United States (Harper and Morris 2004, NOAA 2019). While vast, little is known about the ecology of SEAK seagrass habitats and their contribution to nearshore ecosystems. Research from other regions shows that seagrass meadows enhance biodiversity and productivity (Duffy et al. 2014), and provide critical ecosystem services, such as nutrient cycling, and provide habitat for a wide variety of species (Waycott et al. 2009). Seagrasses also serve as essential nursery habitat for fish and invertebrates (Heck et al. 2003, Bertelli and Unsworth 2014, Lefcheck et al. 2019). In SEAK, seagrasses support commercial, recreational, and subsistence harvested species including four Pacific salmon species (*Oncorhynchus* spp.), multiple rockfish species (*Sebastes* spp.), Walleye pollock (*Gadus chalcogrammus*), Pacific cod *(G. macrocephalus*), Lingcod (*Ophiodon elongatus*), and Pacific herring (*Clupea pallasii*) (Murphy et al. 2000, Johnson et al. 2003).

Much of the research on seagrass ecosystems has focused on top-down versus bottom-up control and has been extensively studied in small-scale experiments (reviewed by Hughes et al. 2004, Heck and Valentine 2006). Meta-analysis of experiments manipulating both invertebrate grazers and nutrients identified that increasing water column nutrients leads to increased seagrass epiphyte growth and negative effects on seagrasses, but the positive effect of grazers on seagrasses is on average stronger than the negative effects of nutrients (Hughes et al. 2004). This pattern was further confirmed in a world-wide coordinated manipulative experiment (Duffy et al. 2015). While this paradigm is well accepted, further research employing stable isotope (SI) and fatty acid (FA) analyses has revealed diverse food web structures in many seagrass ecosystems that are supported by multiple primary energy sources including macroalgae, diatoms, and bacteria (Kharlamenko et al. 2001, Alfaro et al. 2006, Douglass et al. 2011, Thormar et al. 2016, Jankowska et al. 2018). These results suggest that strong herbivore-epiphyte interactions are not the only trophic pathways in seagrass communities and may buffer these communities from perturbations.

More recently, the connection between seagrasses and apex predators has gained attention. The loss of predatory fishes in the Baltic Sea resulted in an increase in mesopredators, which resulted in reduced invertebrate epifauna abundance (Baden et al. 2010, 2012). When released from herbivory by these epifauna, filamentous algae can increase and outcompete eelgrass for light and nutrients (Moksnes et al. 2008, Baden et al. 2010, 2012). In California, the recovery of sea otters resulted in a decrease in crabs, a resultant increase in grazers, and a decrease in algal epiphytes; this trophic cascade resulted in an overall increase to seagrass, which was able to overcome pervasive eutrophication in the system (Hughes et al. 2013). While studies on the role of apex predators and trophic relationships in seagrass ecosystems provide a strong conceptual framework for hypothesis testing in Alaska, it remains to be seen if the cascading effects of apex predators in seagrass ecosystems are transferable to other regions and at large spatial scales (Borer et al. 2005).

Southeast Alaska provides a unique setting to study the trophic dynamics of apex predators in seagrass ecosystems. Sea otters and seagrass ecosystems overlap across a large area, allowing for application of the conceptual trophic cascade model across a large scale. Furthermore, the population recovery of sea otters has not been equal across space and time, creating a gradient of sea otter population density and occupation time (Tinker et al. 2019). Unlike many other seagrass ecosystems, the SEAK nearshore environment is relatively remote and free from intensive shoreline development and agricultural runoff. In Chapter 2, we utilize the overlap of sea otters and seagrass and a gradient of sea otter presence to test for apex predator - seagrass trophic cascades across a broad scale in SEAK. Building off these results, in Chapter 3 we further investigate the trophic relationships of seagrass communities using a combination of biomass, SI, and FA to test for differences in trophic structure between seagrass meadows with high and low sea otter densities.

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Chapter 1: Location specific factors influence patterns and effects of subsistence sea otter harvest in Southeast Alaska[1]

Abstract

To better understand the spatial context of population dynamics of sea otters (*Enhydra lutris*) in Southeast Alaska (SEAK), we investigated the spatial and temporal patterns of subsistence sea otter harvest and assessed the effect of harvest on population growth. United States federal law permits subsistence harvest of sea otters and sale of clothing and handicrafts made by coastal Alaska Natives. Hunters are required to self-report these harvests along with information on date, location, age class and sex. Using harvest data collected from 1988 to 2015, we developed a spatially-explicit, age-structured, density-dependent population simulation model to explore the potential impacts of harvest on sea otter population dynamics. We examined patterns of harvest and simulation model results at two spatial scales: the SEAK stock and three smaller subregions that vary in sea otter occupation time and carrying capacity: Sitka Sound, Keku Strait, and the Maurelle Islands. Annual sea otter harvest in SEAK increased from 55 animals in 1988 to a reported maximum of 1,449 animals in 2013. Estimated mean annual harvest rate was 2.8% at the SEAK stock scale, but ranged from 0 to 39.3% across the three focal subregions described above. Across all subregions (n = 55) annual sea otter harvest rate was strongly influenced by time since recolonization, sea otter population density, and proximity to communities with sea otter hunters. The simulation model predicted population trends and per-capita harvest rates similar to those estimated from aerial survey data, providing a reasonable

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approximation of population dynamics. Results of the simulation model suggested that current harvest levels can reduce population size at both the SEAK and subregional scales. Variation in harvest impacts was a function of subregion-specific factors, including time since recolonization and population status with respect to carrying capacity. We found that subsistence harvest and its population effects were scale and location dependent, indicating that higher spatial and temporal resolution of sea otter population and hunting data could help address emerging sea otter management and conservation concerns in this region.

1.1 Introduction

Variation in ecological and demographic processes across different scales can lead to spatial structure in populations (Turner 1989, Dunning et al. 1992). Therefore, effective management of populations requires information about population status and dynamics at spatial scales relevant to the species in question. For populations that are hunted for subsistence, harvest data can provide local scale information that can be used to evaluate population status, management actions, and harvest sustainability (e.g. Shaffer et al. 2017, Mahoney et al. 2018). Furthermore, subsistence harvest data can inform our understanding of population dynamics and highlight spatially-dependent factors that may influence the population and hunting itself (van Vliet et al. 2010). For example, bowhead whale (*Balaena mysticetus*) populations declined significantly as a result of commercial whaling in the 1800s. After commercial whaling ceased, populations recovered slowly (George et al. 2004, Minerals Management Service 2009, Phillips et al. 2013, North Slope 2018). Thus, the use of subsistence harvest data has great potential to improve population management of particular species, in part because of the investment of local hunters in maintaining a viable population for future harvest, provided that competing interests do not exist. Here we examine the spatial and temporal patterns of sea otter subsistence harvest and test for effects of harvest on population abundance and trends, to better understand the factors affecting population trends of sea otters in Southeast Alaska (SEAK).

Sea otters are apex predators that once inhabited much of the coastal North Pacific Ocean from Baja California to the northeastern coast of Asia including the Kamchatka Peninsula and northern Japan. Indigenous peoples have hunted sea otters primarily for their fur as an integral part of their culture for thousands of years (Fedje et al. 2001, Erlandson et al. 2005, Szpak et al. 2012). However, commercialization of sea otter harvest for fur beginning in the mid-1700s drove populations to near extinction (Kenyon 1969, Riedman and Estes 1990). Through legal protections, reintroductions, and other conservation efforts, sea otters have recovered to a global population of approximately 125,000 (Doroff and Burdin 2015). One area of notable recovery is SEAK, where sea otters were extirpated around the turn of the 20th century and then reintroduced to seven sites in the late 1960s (Burris and McKnight 1973) (Fig. 1). From the 1970s through 1990s the initial population of 413 sea otters grew rapidly in areas near reintroduction sites on the outer coast. By the 2000s, the distribution and numbers of sea otters increased greatly, and from 2003 to 2011 the population grew at an average rate of approximately 8.6% per year (Tinker et al. 2019a). The most recent abundance estimate (2011) for the SEAK stock was 25,584 individuals (Tinker et al. 2019a), which represents approximately one-quarter of the sea otters in the United States and one-fifth of the global population (Doroff and Burdin 2015). The SEAK population now extends across much of the outer coast of SEAK, from Icy Bay in the north to Dixon Entrance in the south, and into the inside waters of SEAK including Glacier Bay, Icy Strait, Kuiu Island, and Sumner Strait (Fig 1).

While commercial harvest of sea otters is illegal, the U.S. Marine Mammal Protection Act (MMPA) permits coastal Alaskan Natives to harvest sea otters, as long as the harvest is done for subsistence and "is done for purposes of creating and selling authentic native articles of handicrafts and clothing" (50 CFR 18.23). Anecdotal reports indicate that sea otters are eaten very rarely, and the primary motivation for harvest is to obtain pelts. The U.S. Fish and Wildlife Service (USFWS) is responsible for management and conservation of sea otters in the U.S. and collects data on subsistence sea otter harvest in Alaska (no harvest is permitted outside of Alaska). Harvest data are collected by USFWS designees, usually Alaska Natives who are sea otter hunters or artisans. These designees, called "taggers", record information on the harvest and other basic demographic information and physically tag the pelt, as required under the MMPA. Previous analyses of the SEAK sea otter population have postulated that subsistence harvest of sea otters may affect sea otter population growth (Esslinger and Bodkin 2009), especially at local scales (Bodkin and Ballachey 2010, Tinker et al. 2019a). USFWS conducts aerial surveys to estimate population size and trend, but owing to budget and logistical constraints, surveys occur infrequently (7–10 years). Tinker et al. (2019a) recently estimated population trends and carrying capacity at multiple spatial scales, but to date, SEAK sea otter harvest data have not been analyzed for spatial and temporal trends or for potential effects to the sea otter population.

While hailed as a conservation success story, the return of sea otters exemplifies the challenge of a predator returning to its native range, which raises ecological, conservation, and management questions (Roman et al. 2015, Silliman et al. 2018). In particular the recovery of sea otter populations resulted in conflicts with human interests for shellfish resources (Carswell et al. 2015). In SEAK from 2009 to 2012, commercially important marine species represented 46% of sea otter diets, and sea otter expansion contributed to declines in shellfish available for commercial harvest (Larson et al. 2013, Hoyt 2015). In response, legislation was introduced to the Alaska State Senate in 2013 that proposed a bounty for sea otters that would be given to Alaskan Native harvesters (Carswell et al. 2015). However, its passage would have put the State of Alaska in direct conflict with the federal government who has the legal authority to implement the MMPA and manage sea otter harvest. More recently, a resolution was introduced in the Alaska State Senate urging the federal government to amend the MMPA to allow for co-management of sea otters between Alaska Native organizations and the Alaska Department of Fish and Game (which has no management authority over sea otters), arguing that local organizations may be better able to manage the population (Stedman et al. 2018). Furthermore, recent summaries of sea otter harvest in SEAK indicate a marked increase since 2010 (USFWS 2014a). These legislative actions and recent harvest increases have caught the attention of conservation organizations that want to prevent changes to current law (Friends of the Sea Otter 2018). This situation highlights the need for information surrounding the patterns of sea otter harvest and the impacts of harvesting on the SEAK population.

A recent analysis of population trends and estimation of carry capacity for sea otters in SEAK (Tinker et al. 2019a), together with the existence of hunter-reported data on harvest numbers, provide a unique opportunity to evaluate harvest impacts for this species and assess the spatial structure of the population. To assess population effects, we developed a spatially-explicit, age-structured, density-dependent population simulation model for sea otters in SEAK using empirical demographic data and recently-derived carrying capacity values from Tinker et al. (2019a). We hypothesized that sea otter harvest and any effect of harvest on the population would vary as a function of geographic location. Sea otters have small home ranges compared to most marine mammals, ranging from 1.0 to 11.0 km^2 (Garshelis and Garshelis 1984, Tarjan and

Tinker 2016), aggregate in social groups (Jameson 1989, Laidre et al. 2009), show spatial variability in carrying capacity (Tinker et al. 2019a) and variability in the history of sea otter recolonization and expansion in SEAK (Burris and McKnight 1973, USFWS 2008, 2014b). These factors all suggest that sea otter population dynamics and therefore patterns of harvest and harvest effects are likely to vary at scales smaller than the current scale of management, which is all of SEAK. Our analysis provides a structure for quantifying and testing the relationship between subsistence harvest and sea otter population dynamics and resilience in SEAK and the rest of Alaska where this species is harvested for subsistence. Our analysis provides a structure for quantifying and testing the relationship between subsistence harvest and sea otter population dynamics and resilience in SEAK and serves as a framework for further analysis of the sea otter population in SEAK and other regions in Alaska where this species is harvested for subsistence purposes.

1.2 Methods

1.2.1 Study area

The SEAK stock of sea otters is spatially defined as all sea otters from Dixon Entrance to Cape Yakataga on the southeastern coast of Alaska, which stretches over 850 km in length and encompasses 17,790 km^2 of suitable sea otter habitat (Bodkin and Udevitz 1999) (Fig. 1). The region is comprised of large and small islands, fjords, exposed and protected shorelines, and a wide array of nearshore habitats including kelp forests, seagrass beds, rocky reefs, and mud flats. Harvest occurs throughout most of this region with the exception of Glacier Bay National Park, where U.S. National Park Service regulations prohibit it. While the USFWS manages sea otters at the stock level, a number of recent studies and reviews have highlighted that demographically-important processes in sea otter populations, including density-dependent resource limitation, occur at much smaller scales because of the low mobility and high site fidelity of mature sea otters (Bodkin 2015, Tinker 2015, Tinker et al. 2017, Gagne et al. 2018). Therefore, we examined harvest patterns and potential impacts of harvest at both the stock and subregional scale.

We adopted the same subregions used by Tinker et al. (2019a) to estimate carrying capacity of sea otters in SEAK. The authors delineated these subregions in order to track population trends in SEAK at an appropriate spatial scale based on sea otter life history and ecology and on recent findings of fine-scale demographic structuring of sea otter populations (Bodkin 2015, Tinker 2015, Gagne et al. 2018, Tinker et al. 2019b, Johnson et al. 2019). Specifically, each subregion encompassed an area of sea otter habitat approximately 100 times the size of a typical adult home range, which ranges from 1.0 to 11.0 km^2 (Garshelis and Garshelis 1984, Tarjan and Tinker 2016), bounded by the low tide line inshore and the 40 m depth contour offshore (Fig. 1.1). Subregion size was chosen to be small enough so that individuals within a subregion could be considered a well-mixed population experiencing similar environmental and density-dependent conditions, but large enough so that demographic processes (births and deaths) would have a greater influence on population trends than movement between subregions (Tinker et al. 2019a). Thus, the mean “swimmable distance” (calculations below) from the centroid of a given subregion to its nearest neighbor was 50 km (+/- 28 km SD), twice the mean annual net displacement distance for female sea otters (Tinker et al. 2008), and boundaries between subregions corresponded, whenever possible, to natural geographic features (e.g., prominent headlands) that were assumed to discourage movements. In our analysis, we used 21 subregions identified by Tinker et al. (2019a) (N01 – N10, S01 – S12, and YAK). To ensure size-consistency, we further sub-divided Glacier Bay (GBY) into 3 subregions (GBYA, GBYB, GBYC) and sub-divided the coastal area of SEAK not occupied by sea otters at the time of the most recent survey (referred to in Tinker et al. (2019a) as "un-surveyed") into 29 additional subregions (N11 – N27 and S13 – S24; Fig 1). Thus, in our analysis we used 55 subregions across SEAK.

We summarized spatial and temporal patterns of sea otter harvest and population effects at two spatial scales, the SEAK stock and at three focal subregions that represented a range of sea otter occupation time, estimated carrying capacity, proximity to human communities, and harvest history and trends: Sitka Sound, Keku Strait, and the Maurelle Islands (Table 1.1). The Sitka Sound subregion includes a sea otter introduction site, is adjacent to the community of Sitka with a human population of 8,881 (*United States Census* 2010), and has a long history of sea otter harvests (USFWS 2014a). Keku Strait was recently colonized by sea otters, and is adjacent to the community of Kake with a human population of 557 (*United States Census* 2010, USFWS 2014a, Hoyt 2015) and has reported variable sea otter harvest since sea otters colonized this subregion (USFWS 2014a). The Maurelle Islands includes another reintroduction site, is directly adjacent to the small communities of Edna Bay and Naukati Bay, with a combined population of 155, and is reasonably accessible from the communities of Craig and Klawock with a combined human population of 1,956 (*United States Census* 2010).The Maurelle Islands subregion has had on average relatively high numbers of sea otter harvests but high year-to-year variability (USFWS 2014a).

1.2.2 Subsistence sea otter harvest data

We analyzed sea otter harvest data for SEAK from the start of records in 1988 through 2015. These data were collected by USFWS taggers who record information provided by hunters for each harvested sea otter and tag each pelt with a unique identifying physical tag. Data include date of tagging, date of harvest, location of tagging (community), location of harvest (latitude and longitude and description), age class (adult, sub-adult or pup), and sex of the harvested sea otter. The tagger also records if tissue specimens were taken and any other relevant information. The physical tag remains with the pelt, as only tagged pelts can be tanned by commercial tanning operators.

Before analysis, we reviewed data for consistency and spatial ambiguity. After removing duplicate harvests and addressing typographic errors 13,151 harvest records remained. Of those, 12,546 (95%) included acceptable geographic information and were used for spatial and temporal analyses and simulation models. We used the latitude and longitude of harvest to assign a geographic subregion. If the geographic coordinates of a harvest location resulted in a land-based location, we used the reported geographic description to generate coordinates in the adjacent marine-based subregion. If the geographic description was not specific enough to assign new coordinates, and the harvest location was less than 1 km inland, we adjusted the harvest latitude and longitude to the nearest subregion. In all other instances of spatial ambiguity, we removed records from analysis. All analyses were conducted at the subregion scale, thus the specific coordinates were not used after this assignment.

For parameterization of the population simulation model, we converted hunter reported age and sex into four age/sex classes: adult male, adult female, juvenile male, and juvenile female. If age and/or sex were missing, we assigned the age/sex as unreported for purposes of harvest summaries. For the population simulation model, we assigned harvest records with unreported age and sex data were assigned age/sex classes corresponding to the proportion of reported age/sex classes for the appropriate subregion and year.

1.2.3 Patterns of sea otter harvest

For SEAK as a whole and the three focal subregions we summarized annual reported number of harvested sea otters, the age/sex class of harvested sea otters, and the annual harvest rate using the estimated pre-harvest population abundance for that year from Tinker et al. (2019a) (Equation 1.1).

$$\text{Harvest rate}_{y,i} = \frac{harvest_{y,i}}{population'_{y,i}} \tag{1.1}$$

Where $harvest_{y,i}$ is the number of sea otters harvest in subregion, i in year y and $population'_{y,i}$ is the estimated pre harvest sea otter population from Tinker et al. (2019a). We also calculated the mean annual percent contribution to total harvest for each subregion (Equation 1.2).

$$\text{Mean annual percent contribution}_i = \frac{\sum \left(\frac{harvest_{y,i}}{\sum_i harvest_y} \times 100 \right)}{\text{N years of reported harvest}_i} \tag{1.2}$$

To identify factors that may be driving variation in sea otter harvest rate at the subregional scale, we constructed a linear mixed effects model to test for effects of time since sea otter recolonization (*TimeOcc*), sea otter population density (*SODens*), proximity to human communities (*PopProx*), and proximity to sea otter hunters (*HunterProx*):

$$HR_{y,i} = TimeOcc_{y,i} + TimeOcc^2_{y,i} + SODens'_{y,i} + PopProx_{y,i} + HunterProx_{y,i} + SRerr_i \quad (1.3)$$

where $HR_{y,i}$ is the harvest rate for subregion i in year y, measured as the number of sea otters harvested divided by the estimated pre-harvest population abundance. Time since occupation for each subregion and year ($TimeOcc_{y,i}$) were measured as the interval (in years) between a harvest record and the year in which sea otters were known to have first recolonized a given subregion (or year of translocation in the case of subregions containing translocation sites). We allowed for both linear and quadratic effects of $TimeOcc_{y,i}$, based on the *a priori* hypothesis that duration of sea otter occupation could have a non-linear relationship with harvest rate. Sea otter population density for each subregion and year was calculated as estimated abundance divided by habitat area (km^2). To account for collinearity between years of occupation and sea otter density (Tinker et al. 2019a), we first fit a separate linear model of sea otter population density as a function of years of sea otter occupation (Table S1.1) and extracted the residuals from this model, thereby creating a de-trended metric of relative sea otter population density ($SODens'_{y,i}$). We used inverse distance weighting (IWD) to interpolate the cumulative effects of human population centers ($PopProx_{y,i}$) and sea otter hunters ($HunterProx_{y,i}$) at each subregion and year (Shepard 1968). This was calculated as the sum of the inverse Euclidian (straight-line) distances from each community to the center of each subregion, multiplied by the natural log of that community's population size (human population proximity) or the reported number of unique sea otter hunters that tagged a sea otter pelt (sea otter hunter proximity). Finally, to account for unexplained spatial variation in harvest rate we also included a random effect of subregion ($SRerr_i$). In the absence of reliable survey data, we assumed that sea otters colonized a subregion one year prior to the first reported harvest. While the true time from recolonization to first harvest is unknown in many subregions, our exploration of harvest trends indicated that in many subregions where the year of colonization is well documented through aerial surveys, reported harvest appears immediately. We restricted the linear mixed effects analysis to the period of 1990 to 2010 and to subregions with reported harvest to avoid biases associated with limited data availability. We performed a simultaneous forward and backward selection procedure with delta AIC discrimination to identify the best model from our initial full model. For the purpose of model fitting, sea otter harvest rate was arcsine-square root transformed, human population proximity was natural log transformed, and sea otter hunter proximity was square root transformed to reduce the effect of extreme values. Human population data were obtained from the U.S. Census Bureau (*United States Census* 2010). Anonymized sea otter hunter data were obtained from USFWS.

1.2.4 Population simulation model

We developed a spatially-structured matrix projection model (Caswell 2001) to simulate population dynamics of SEAK sea otters both with and without harvest mortality. Assuming that the model accurately captures the key processes underlying sea otter population dynamics through the subregions defined above, we aimed to use the difference between projected abundance under the two scenarios, at both subregional and stock scales, as a quantitative measure of harvest impacts. While other population models have assessed the effects of sea otter harvest mortality generally (Samuel and Foin 1983, Bodkin and Ballachey 2010), our model differs in key mays. (1) Our model incorporates spatial structure at a scale that is meaningful for tracking demographic processes in sea otter populations (Bodkin 2015, Tinker 2015, Tinker et al. 2019a). (2) The model allows for density dependence, demographic stochasticity and environmental stochasticity in age- and sex-specific vital rates. (3) The model incorporates annually-reported sea otter harvest data, including the spatial distribution, age and sex structure of harvest. (4) The model allows for realistic spatial dynamics, including range expansion and dispersal/movement among subregions. (5) The model uses empirically derived and spatially-explicit carrying capacity estimates. (6) The model is initiated in 1970 using the known location and abundance of translocated populations, and then iteratively run forward in time, allowing validation of model performance by comparison of predicted dynamics with observed dynamics between 1970 and 2015 based on a recent analysis of survey data in Tinker et al. (2019a).

The simulation model is constructed on a stage-based projection model, where life stages correspond to easily recognized and demographically relevant age/sex classes (Caswell 2001). Adult males sea otters become sexually mature at age 4–8 and adult females at age 2–, and have an annual reproductive cycle (Jameson and Johnson 1993, Riedman et al. 1994). After a gestation period of six months, females give birth to a single pup that enters the juvenile age class (if weaned successfully) after a dependency period of approximately six months (Jameson and Johnson 1993). Our matrix model therefore tracks demographic transitions for two age classes of each sex, pre-reproductive juveniles and sub-adults (weaning – 2.5 years of age) and reproductive adults (>2.5 years of age). This division corresponds to the female age of first reproduction, because population dynamics are determined primarily by female survival and reproduction. We used an annual time-step to track dynamics, and for each stage i we defined the following vital rates: annual survival rate (s_i), growth transition probability for juveniles (g), birth rates (b) and weaning success rates (w) for adult females. These demographic transitions were combined mathematically into a population projection matrix for subregion j at time t:

$$M_{j,t} = \begin{bmatrix} s_1(1-g) & \frac{b}{2}\cdot w\cdot s_2 & 0 & 0 \\ s_1\cdot g & s_2 & 0 & 0 \\ 0 & \frac{b}{2}\cdot w\cdot s_2 & s_3(1-g) & 0 \\ 0 & 0 & s_3\cdot g & s_4 \end{bmatrix} \qquad (1.4)$$

The reproductive contributions to the juvenile stage depend on birth rate (halved to reflect a 50:50 sex ratio at birth) and weaning success rate, and are conditional upon the mother's survival (s_2). The growth transition probability parameter (g) was calculated for each new parameterization of Equation 1.5 using the standard equation for fixed-duration age classes (Caswell 2001):

$$g = \left(\frac{(s_1/\lambda)^T - (s_1/\lambda)^{T-1}}{(s_1/\lambda)^T - 1} \right) \qquad (1.5)$$

where T represents the time from recruitment to maturity (2 years) and λ is the annual growth rate associated with a particular matrix parameterization. Equation 1.5 is solved iteratively, whereby λ is initially set to 1, Equation 1.5 and then Equation 1.4 are solved, λ is re-computed as the dominant eigenvalue of $M_{j,t}$, and then calculations repeated until the value of λ stabilizes to two decimal places.

The primary goal of our simulation model was to approximate realistically demographic processes within a sea otter population while avoiding over. We parameterized vital rates based on estimates from previously published studies of sea otter populations. Adult female birth rates for sea otters remain almost invariant at approximately one pup per year (Monson et al. 2000, Tinker et al. 2006, Riedman et al. 2019), while all other vital rates exhibit both stochasticity and density-dependent variation (Siniff and Ralls 1991, Eberhardt 1995, Monnett and Rotterman 2000, Monson et al. 2000, Gerber et al. 2004, Tinker et al. 2017). To account for this variation, we first generated a large number (A = 1000) of random but, biologically feasible sets of vital rates, $\mathrm{VR}_a = \{b,w,s_1,s_2,s_3,s_4\}$. Each random array VR_a was consistent with published sea otter life history schedules and implied an associated annual rate of growth (λ_a) that was calculated algebraically as the dominant eigenvalue of $M_{j,t}$. We first created two extreme VR arrays corresponding to published vital rates for a population growing rapidly near the theoretical r_{max} ($\lambda_a = 1.22$ for VR_{high}) and a declining population ($\lambda_a = 0.95$ for VR_{low}; Monson et al. 2000). We then generated random adjustment factors to interpolate between the extreme values for each vital rate:

$$VR_a = adj_a \cdot VR_{low} + \left(1 - adj_a\right) \cdot VR_{high} \tag{1.6}$$

where $0 < adj < 1$. To allow flexibility in stage-specific vital rates (representing the effects of demographic stochasticity), while maintaining appropriate life history schedules (e.g., $s_2 > s_1 > w$), we used Cholesky Decomposition to ensure that the random adjustment factors were correlated across vital rates (assuming a correlation coefficient of 0.95). Solving Equation 1.6 resulted in 1000 unique sets of correlated vital rates, each with an associated value of λ_a. These random vital rate arrays were then selected during population simulations so as to account for density dependence and stochastic variation (Fig S1.1). At each year and for each subregion within a given simulation, an expected growth rate ($\hat{\lambda}_{j,t}$) was calculated to reflect environmental stochasticity and density-dependence. Specifically, if $N_{j,t-1}$ represents the abundance for subregion j at time $t-1$, K_j is the estimated carrying capacity for subregion j and σ_e is the standard error of $\log(\lambda)$ across years (estimates of K_j and σ_e were based on Tinker et al. (2019a), we calculate $\hat{\lambda}_{j,t}$ as:

$$\hat{\lambda}_{j,t} = \exp\left(r_{\max}\left(1 - {N_{j,t-1}}\big/{K_j}\right) + \varepsilon_{j,t} \right), \quad where\ \varepsilon_{j,t} \sim Normal\left(0, \sigma_e\right) \tag{1.7}$$

An appropriate set of vital rates (VR_a) was then selected randomly after filtering by $\lambda_a = \hat{\lambda}_{j,t}$, and used to parametrize $M_{j,t}$. We then calculated demographic transitions for subregion j at year t using standard matrix multiplication:

$$n'_{i,j,t} = M_{j,t} \times n_{i,j,t-1} \tag{1.8}$$

where $n'_{i,j,t}$ represents the expected number of individuals of stage i in subregion j at year t, prior to the effects of harvest and re-distribution (dispersal) among subregions.

We next adjusted $n'_{i,j,t}$ to reflect harvest mortality (for simulation runs including harvest) and dispersal:

$$n_{i,j,t} = n'_{i,j,t} - H_{i,j,t} + I_{i,j,t} - E_{i,j,t} \tag{1.9}$$

where $H_{i,j,t}$ is the total recorded harvest mortality for a given year, subregion, and age/sex class, $I_{i,j,t}$ represents immigration to subregion j from other occupied subregions, and $E_{i,j,t}$ represents emigration of animals out of subregion j to other occupied subregions. Immigration and emigration were treated as stochastic Poisson processes, with stage-specific dispersal probabilities computed from dispersal kernels fit to empirical data on tagged sea otter movements (Tinker et al. 2008). Specifically, following previous analyses (Tinker et al. 2008, 2019b) we used maximum likelihood methods to fit Weibull probability distributions to stage-specific data on annual net linear displacement (NLD) measurements from radio-tagged sea otters (Hoyt 2015). We calculated NLD as the most direct, swimmable distance between an individual's recorded position at the start and end of one year. We used minimum cost path (MCP) analysis to prevent over-land movements when calculating distances between an otters' starting and ending locations. We also used MCP to compute pairwise swimmable distances between the geographic centroids of all subregions, resulting in a distance matrix D giving the pairwise movement distances between any two subregions. The probability that a sea otter of stage *i* does not disperse from subregion *j* is computed by evaluating the fitted Weibull cumulative density function at critical distance δ_j, defined as the average distance between the centroid of subregion *j* and the centroids of adjacent subregions that share a common boundary. The probability of emigration (P_E) is then calculated as one minus this value, and the actual number of animals of stage *i* emigrating from subregion *j* in year *t* is calculated as a stochastic variable:

$$E_{i,j,t} \sim Poisson\left(n_{i,j,t} \cdot P_{E,i}\right) \tag{1.10}$$

For those sea otters that emigrate from subregion *j*, we also must specify the recipient subregion. We did this by first restricting consideration to those subregions known to be colonized at time *t* (as explained in the next paragraph): for this sub-set of potential recipient subregions (z = 1,2... z), the relative probability of dispersal from *j* to *z* was computed by evaluating the Weibull density function at the pairwise distances in column *j* of matrix *D* (excluding the diagonal), and then re-scaling these probabilities to sum to 1 over all *z*. We distributed the emigrating otters stochastically among occupied subregions by drawing from a multinomial probability distribution with parameters $\alpha_{j,z}$ equal to these rescaled movement probabilities. The number of otters immigrating to subregion *j* ($I_{i,j,t}$) was computed as the sum of emigrants from all other occupied subregions for which *j* was randomly selected as the recipient subregion:

$$I_{i,j,t} = \sum_{z \neq j} E_{i,z,t} \rightarrow j \tag{1.11}$$

We augmented the stochastic movements between subregions with published data on two specific dispersal events: the colonization of Coronation Island by approximately 50 sea otters from the Maurelle Islands around 1975 (Pitcher 1989) and the colonization of Glacier Bay by approximately 500 sea otters from Icy Strait in 1995 (Esslinger and Bodkin 2009). The inclusion of these two well-documented dispersal events in the simulation model greatly improved overall performance; however, except for these two events, all modeled other dispersal between subregions was stochastic and determined by the simple probabilistic functions described above. Finally, after accounting for the dynamics of immigration, emigration and harvest mortality (Equation 1.9), we computed the expected population abundance for subregion j at time t as:

$$N_{j,t} = \sum_{i} n_{i,j,t} \tag{1.12}$$

The simulation model was initiated at $t_0 = 1970$, with the 413 sea otters reintroduced in the late 1960s distributed among seven subregions (Table S1.2, Burris and McKnight 1973). The year at which additional subregions became "colonized" (and thus eligible for receiving dispersers from other subregions) was set according to data from aerial and skiff surveys (Pitcher 1989, Esslinger and Bodkin 2009, Tinker et al. 2019a), and/or based on harvest records. As in our regression analysis of factors influencing harvest rate, in the absence of precise survey-based estimates of colonization year for a given subregion, we assumed colonization occurred the year before the first harvest records were recorded for that area. We ran simulations for each of two scenarios: (1) including known sea otter harvest and (2) without harvest (i.e. $H_{i,j,t}$ forced to 0). Each model was run for 46 years (1970 - 2015) with 10,000 iterations. Mean projected abundance was calculated for all of SEAK and for the three focal subregions. We generated 95% confidence intervals for annual expected abundance using a bootstrapping procedure with 10,000 samples. We calculated the simulation-based harvest rate as the ratio of harvested sea otters to the pre-hunted simulated population. Our simulation ran from 1970 through 2015, however scenarios with and without harvest did not differ from 1970 through 1987, before sea otter harvest data collection began, so we therefore present model results from 1988 through 2015. All simulation model parameters are summarized in Table 1.2.

1.2.5 Assessing model performance

To evaluate the ability of the simulation model to produce realistic dynamics, we compared model projections to observed abundance trends estimated from aerial survey data (Tinker et al. 2019a). Because the model consists of forward projections from the initial translocated population in 1970, and is not "fit" in any way to the survey data (although certain parameters such as local carrying capacity and environmental stochasticity are based on previous analysis of survey data), agreement between the simulations and observed trends would suggest that the model successfully captures the key factors driving sea otter population growth and range expansion. We visually compared the expected abundance from simulations to the most recent survey results (2010-2012) for the 21 subregions for which survey data were available.

1.2.6 Harvest effects on population

We measured the effect of harvest on sea otter population dynamics by comparing the projected trends with and without sea otter harvest mortality, using paired simulations. This meant that for a given random sequence of environmental stochastic effects, we ran a simulation with observed harvest numbers and a matching simulation with harvest mortality set to zero. We calculated the relative effect of harvest as the proportional difference in abundance at year t between paired simulations using all i bootstrap samples described above: $(N_{i,t,harvest} - N_{i,t,no\text{-}harvest})/\text{mean}(N_{,t,no\text{-}harvest})$. Thus, a negative value would indicate decreased abundance due to harvest. As with abundance estimates, we used bootstrap re-sampling with 10,000 replicate samples to calculate the mean difference and 95% CI for each year and area of interest. We considered years where the 95% CI did not include zero to be instances of significant differences between the two scenarios. We evaluated harvest effects by visually comparing temporal variation in the instantaneous growth rate of simulations with per-capita harvest rates.

All statistical analyses and population simulation runs and calculations were performed using R version 3.5.1 (R Core Team 2018). Data and analysis code can be viewed at https://doi.org/10.5281/zenodo.3378051. Sea otter harvest data is available from the USFWS Marking, Tagging, and Reporting Program.

1.3 Results

Patterns of sea otter harvest and population effects generally differed between the SEAK stock and the smaller subregions, and among subregions. Harvest records indicated an increase in harvested sea otters over time with stable harvest rates at the SEAK scale but variable harvest rates at the subregional scale. Furthermore, analysis indicated that harvest rate appears to be driven by factors that operate at the subregion scale. Sea otter population simulation results suggested that harvest can lead to reduced populations and in some cases population declines. Overall, our results indicate that variation in harvest itself and its effects on the sea otter population was dependent on the spatial location of interest, and that small-scale patterns did not necessarily appear at the SEAK scale.

1.3.1 Reported sea otter harvest

Reported sea otter harvest in the SEAK stock increased from 55 in 1988 to a maximum harvest of 1,449 animals in 2013 (Table S1.3, Fig. 1.2e; see Fig. 1.2a - d for sea otter population estimates from Tinker et al. (2019a)). Annual total harvest was low (range = 55 – 147) relative to the total sea otter population size in the late 1980s, but increased in the early 1990s from 313 to

833. Total annual harvest was low and stable (range = 120 – 432), from the mid-1990s through the late-2000s. From 2009 to 2013 total annual harvest increased from 597 to 1,449. Sea otter harvest remained greater than 1,000 per year through 2015. These fluctuations in harvest over time were largely mirrored in Sitka Sound, but at a lower magnitude (Table S1.3, Fig. 1.2f). Harvest patterns differed in the other two focal subregions. Harvest in Keku Strait began in 2000, a few years after sea otter colonization of this area in 1995. From 2000 to 2011 harvest was low, but then increased from 2012 to 2014 (Table S1.3, Fig. 1.2g). The Maurelle Islands experienced periodic pulsed harvest events that were consistently around 100 - 150 animals (Table S1.3, Fig. 1.2h). Sitka Sound and Maurelle Islands accounted for a similar and high contribution to average annual sea otter harvest in SEAK (18.6% +/- 10.10 SD, and 19.0% +/- 15.0 SD respectively). Keku Strait accounted for only 2.7% (+/- 4.40 SD) of annual harvest in SEAK (Table 1.3).

Annual reported sea otter harvest rate varied among the different geographic areas and spatial scales investigated (Table 1.3, Figs. 1.2i - l). Annual harvest rate over the whole region was low and stable through time (mean 2.9% +/- 1.9 SD), with the exception of the early 1990s, when a maximum harvest rate of 10.6% in 1993 was estimated (Table 1.3, Fig. 1.2i). Sitka Sound consistently showed a high annual harvest rate (mean 9.8% +/- 9.4 SD) that peaked in 1993 at 39.3% (Table 1.3, Fig. 1.2j). In contrast, Keku Strait had low harvest rates when sea otters first colonized the area in 1995. After 2000, the harvest rate increased and became more variable, fluctuating between 0% and 23%, with a mean annual harvest rate of 5.0% (+/- 6.4 SD) (Table 1.3, Fig. 1.2k). The Maurelle Islands showed periodic sharp increases in harvest rate (0.2% to 6.0%) followed by little to no harvest, with a mean harvest rate of 2.0% (+/- 1.4 SD) (Table 1.3, Fig. 1.2l).

Adult sea otters accounted for 82%, juveniles for 14%, and unidentified as 4% of all reported harvests (Table S1.4; Fig. S1.3). The male:female sex ratio of harvested animals was 70:30 for adults and 60:40 for juveniles. Age and sex ratios of harvested otters varied little across years and focal subregions, (Table S1.4; Fig. S1.3), regardless of total number of animals harvested (Table S1.3).

Our examination of factors potentially explaining variation in annual sea otter harvest rates found that inclusion of the random effect of subregion improved model performance (ΔAIC = 20.25). The best-supported mixed-effects model included linear and quadratic effects of years of sea otter occupation, a negative effect of sea otter population density (de-trended for occupation time) and a positive effect of proximity to sea otter hunters (Table 1.4). These results indicate that, on average, harvest rate increases after initial colonization, then stabilizes and eventually decreases. Furthermore, our results on the temporal patterns of sea otter harvest (above) indicate that even after sea otters colonize a subregion, like Keku Strait, hunting may not immediately increase. After controlling for years of sea otter occupation, subregions with higher sea otter densities had lower harvest rates. Finally, subregions with greater proximity to more hunters experienced higher harvest rates.

The spatial extent of sea otter harvest increased from 1988 to 2015, following the range expansion of sea otters. By 2015, harvest had occurred in nearly all subregions that sea otters occupied. Only the Glacier Bay subregions GBYB and GBYC and N01, and N10 had no reported sea otter harvest (Table S1.3).

1.3.2 Simulation model: estimating harvest effects on sea otter population dynamics

The simulation model produced estimated trends at both the SEAK stock and subregion scale that were consistent with observed trends based on survey data (compare Fig. 1.2a - d to Fig. 1.3a - d). Visual comparison between survey-based estimates of abundance and simulation-based estimates suggested good agreement for subregions all but GBY, where the simulation-based estimates were lower than survey-based estimates (Fig. 1.S2).

Comparison of simulations between harvest and no-harvest scenarios indicated that harvest of sea otters reduced sea otter growth for the SEAK stock and for the three focal subregions. However, the relative magnitude of this reduction varied among subregions (Fig. 1.3a - d). For the SEAK stock, the difference between harvest and no-harvest scenarios was evident in the early 1990s. Simulations including harvest showed 15 - 20% lower abundances relative to simulations without harvest in all years after 1990 (Fig. 1.3a, e). In the Sitka Sound subregion, the effect of harvest was more striking. From 1994 to 2010, simulations including harvest showed abundances that were approximately 20% lower relative to simulations without harvest. This difference increased sharply after 2010, when the simulations including harvest indicated population declines (Fig. 1.3b). By 2015, simulations including harvest predicted 50 - 70% lower sea otter abundance than simulations without harvest (Fig. 1.3f). In Keku Strait, the impacts of harvest did not precipitate a population decline, but harvest mortality was associated with a reduction in the rate of population increase after the area was colonized in the mid 2000s (Fig. 1.4c). Simulations including harvest showed a reduction in abundance of approximately 75% relative to simulations without harvest between 2011 and 2015 (Fig. 1.3g). Model results from the Maurelle Islands indicated a more limited effect of harvest than in Sitka Sound or Keku Strait subregions, with a slight reduction in the rate of growth associated with harvest mortality

(Fig 3d). Simulations including harvest showed a significant reduction in abundance relative to no-harvest simulations between 1990 and 1996 and between 2005 and 2015. Simulations including harvest predicted a population size approximately 15 - 20% lower than no-harvest simulations (Fig. 1.3h).

In summary, simulation models including sea otter harvest predicted a lower abundance of sea otters as compared to models without harvest. However, harvest was not necessarily associated with population declines at the SEAK or subregional level. The exception to this pattern was Sitka Sound, where the simulation estimated that the sea otter population declined from 575 (309 – 838 95% CI) in 1988 to 307 (81 – 546 95% CI) in 1998, presumably in response to high harvest rates (Fig. 1.3b).

1.4 Discussion

Our analysis of 27 years of sea otter harvest data, combined with the results of a spatially structured population simulation model built around these data, demonstrate that harvest mortality has strongly influenced population trends in SEAK. However, our results also highlight the importance of considering spatial scale and demographic context when evaluating harvest trends and effects on population dynamics. Patterns of harvest at the entire SEAK stock scale were comparatively muted to the patterns seen at the subregional scale, which showed much more year-to-year variability. The effects of harvest were most apparent at subregional scales and less evident at the scale of the entire SEAK stock, consistent with other recent findings indicating that demographic processes in sea otter populations are structured at relatively small scales (Garshelis and Garshelis 1984, Tarjan and Tinker 2016, Tinker et al. 2019a). Thus, concentrated local harvest mortality can have substantial impacts on trends at these scales, even causing local declines. However, sea otter population status with respect to carrying capacity appeared to mediate these effects. Moreover, the magnitude of harvest rate in a given area depended on both the social context (proximity to communities with hunters) as well as the number of years since that area was first colonized by sea otters.

A key insight gained from our simulation model was that the effects of harvest on population status were most relevant at spatial scales smaller than the SEAK stock scale at which management currently operates. At the SEAK stock scale, sea otter populations may be resilient to periods of high harvest, especially if they are followed by periods of low harvest. This resilience may be explained in part by the heterogeneity of sea otter population dynamics and carrying capacity across SEAK. For example, our analyses and other modeling efforts (Tinker et al. 2019a) showed that while some subregions may experience decline or reduced growth rate, they were usually compensated by other subregions experiencing high growth. Synchronous elevated mortality across the entire region, such as occurred in the early 1990s resulted in a brief cessation of population recovery at the stock scale, but this was the exception rather than the rule. In contrast, year to year patterns of population growth or decline at the subregional scale were more closely coupled to variation in harvest rate. The difference between stock and subregional patterns of harvest and population effects highlights the challenge of detecting impacts of localized perturbations at larger spatial scales. As seen in the range of environmental gradients across Hawaiian monk seal (*Monachus schauinslandi*) populations (Schmelzer 2000, Baker et al. 2007) and predatory control of coyotes (*Canis latrans*) (Mahoney et al. 2018) a clear understanding of the demographic impacts and context of a given perturbation is best achieved by monitoring dynamics at the appropriate spatial scale. For species which have high site fidelity and small home ranges localized disturbances can have outsized effects possibly leading to genetic bottlenecking, as seen in sea otters (Larson et al. 2002, 2012) and wolves (Moura et al. 2014).

Considering harvest in terms of a population's carrying capacity can be essential for evaluating critical population thresholds or tipping points (Lande et al. 1995). Samuel and Foin (1983) suggested that a sea otter harvest rate between 2% and 4% of an established population at or near carrying capacity may lead to a stable, albeit lower, sea otter population in approximately 25 years. Furthermore, Samuel and Foin (1983) and Tinker et al. (2019a) suggested that harvest rates greater than 8% to 10% may lead to population instability and decline. While these results do provide some guidelines for managers, they apply only to established populations at or near carrying capacity, and indeed they assume availability of reliable estimates of carrying capacity at appropriate scales. Equilibrium densities for sea otters in SEAK are estimated to range from 0.65 to 16.89 sea otters/km^2 with a mean of 4.20 sea otters/km^2 (+/- 1.58 SD) (Tinker et al. 2019a; Table S1.2). Variability across space in equilibrium densities, combined with differences in occupation time and current densities, imply that sustainable harvest levels also could vary widely. For example, Sitka Sound, a long-established subregion thought to be near carrying capacity by the mid-1990s (Tinker et al. 2019a), has declined in recent years, likely in response to high levels of harvest (annual average harvest rate of 9.8%; Fig. 1.2j). In contrast, Keku Strait is a recently-established and rapidly growing population, still well-below carrying capacity, where similar harvest rates (above 10% or more) slowed but did not stop growth. Thus, to predict and manage harvest levels sustainably, it is important to consider the subregional population history and status with respect to carrying capacity in addition to the ecology of the species.

Our analysis also provided important insights into some of the factors that determine the magnitude of sea otter harvest rates, including sea otter population status and proximity to human communities, both of which vary across subregions in SEAK (e.g. van Vliet et al. 2010). On average, sea otter harvests were greater in subregions that were in close proximity to sea otter hunters. However, the realized per-capita harvest rate also depended on how long sea otters had been in a subregion and the current density of the otter population in that location. The non-linear relationship between harvest rate and years of sea otter occupation suggests that when sea otters first occupy an area, there were several years of increased harvest effort, perhaps in part as communities respond to depletion of local subsistence shellfish resources (Carswell et al. 2015). Therefore, harvest rate increased initially, but then tended to decrease over time as the sea otter population continued to grow and as individual otters responded by moving away from higher-risk areas near communities (Hoyt 2015). Thus, some combination of avoidance behavior by sea otters and numerical saturation (i.e., a type-II functional response) ultimately led to a reduced per-capita harvest rate. Furthermore, demand for sea otter pelts may not be as high as hunters anticipated, leading to oversupply of pelts, reducing the need to harvest more sea otters.

In addition to considering subregional scale processes in management, it has been suggested that viewing sea otter population and the human communities that harvest them as a coupled social-ecological system may improve management overall (e.g. van Vliet et al. 2015). In SEAK the intensity of sea otter harvest has varied over time and space, with periods of elevated harvest associated with periods of increased information and outreach about sea otter hunting. The increase in hunting in the early 1990s may have been a result of increased awareness of the laws surrounding sea otter harvest. During that period, the USFWS led a series of meetings in SEAK communities to clarify the laws involving harvest of sea otters and other marine mammals under the MMPA (DeGange *pers comm* to V. Gill). The number of unique sea otter hunters in SEAK increased from 8 in 1992 before these meetings to 55 in 1994 after these meetings. Similarly, in the early 2000s, regional and local Alaska Native organizations supported classes focused on fur sewing (Sealaska 2013, Eddy 2015, Baxter 2018). Furthermore, increased discussion of commercial and subsistence fishery impacts and proposed sea otter legislation likely contributed to greater awareness (Carswell et al. 2015, Stedman 2018). Collectively, these events likely increased awareness of sea otter hunting in the regions and the number of unique hunters in SEAK has continued to increase, from 60 in 2009 to an overall high of 103 in 2014 (B. Benter *pers. comm.*). Furthermore, our analyses found that increased hunter participation was linked to increased reported harvest rate (Table 1.4). A comprehensive and effective management strategy should therefore recognize and incorporate these social factors.

Our simulation model predicted spatial and temporal trends in sea otter populations consistent with those estimated from aerial survey data, indicating that our model successfully captured the key processes influencing population dynamics in sea otters. However, data availability and quality likely influenced model prediction accuracy at both subregional and stock scales. For example, harvest mortality estimates in our analyses were based only on reported sea otter harvest numbers, even though unreported sources of hunting mortality undoubtedly exist. As seen in the subsistence harvest of beluga whales in Cook Inlet, Alaska, inaccuracies in reported harvest numbers may occur when hunters shoot an animal but are unable to recover the body, a phenomenon called “struck and loss” (Mahoney and Shelden 2000). Estimates of struck and loss from subsistence harvest marine mammals can be high. For example, struck and loss estimates of walrus (*Odobenus rosmarus*) in Alaska average 42% (Fay et al. 1994) and of harp seals (*Pagophilus groenlandicus*) in the northeastern Atlantic range from 0% to 50% (Sjare and Stenson 2002). Currently, USFWS does not have empirical estimates of struck and loss for sea otter harvests in SEAK. Inaccuracies in the sex composition of reported harvests also could have affected estimates of hunting impacts on the population. Following general population dynamic theory, removal of females reduces the reproductive capacity of the population while removal of males does not, except in extreme cases (Bodkin and Ballachey 2010). The sex of a harvested sea otter is hunter-reported and is not necessarily confirmed by the tagger or USWFS, potentially introducing further unaccounted noise to the data. Finally, our data filtering procedure removed 605 harvest records from the analyses. While this is a small proportion of the dataset (5%), it could have had a disproportionate effect on results. Low harvest numbers can result in high harvest rates for newly established populations and have a large effect on growth, as observed for Keku Strait.

Another limitation of our simulation model is that it did not explicitly account for variation in extrinsic mortality factors that are known to influence sea otter population growth (although we did indirectly account for such factors via inclusion of environmental stochasticity in the model). Extrinsic mortality can occur due to variation in food availability or habitat quality (Laidre et al. 2001, 2002, Gregr et al. 2008, Tinker et al. 2017), predation mortality from sharks (Estes and Hatfield 2003, Tinker et al. 2016), killer whale (*Orcinus orca*) (Estes et al. 1998), and bald eagles (*Haliaeetus leucocephalus*) (Sherrod et al. 1975), disease-associated mortality (DeGange and Vacca 1989, Kreuder et al. 2003) and mortality associated with fisheries, including gillnet and crab pot fisheries that have the potential to entangle sea otters (Wendell et al. 1986, Hatfield et al. 2011), though reports of entanglement of sea otters in Alaska are rare (Worton et al. 2016). Inclusion of any or all of these factors (data permitting) could improve precision and accuracy of future models.

As predator populations continue to recover worldwide, ecologists, conservation biologists, managers and other stakeholders are likely to face new questions regarding the management of these species (Silliman et al. 2018). In preparation for, or in response to recovering predator populations, it will be important to re-examine the spatial context of current management frameworks and their ability to effectively manage spatially heterogeneous populations (e.g. Mahoney et al. 2018). Our analyses showed that spatial scale, proximity to human settlements, and status and trends of the local population, are all important considerations when evaluating the effects of harvest on SEAK sea otter populations. Historically, observer-based aerial surveys have been the primary tool to monitor sea otter populations. While these surveys provide comprehensive data on abundance, they are expensive and time consuming and therefore have occurred infrequently, at intervals of 7 to 10 years (USFWS 2008, 2014b). In light of the growing conflicts between humans and recovering sea otter populations and the spatial heterogeneity of status, trends and equilibrium densities (Tinker et al. 2019a), a new approach may be necessary to help resolve some of these issues. To improve current management of sea otters in SEAK, we recommend (1) collecting sea otter population data at the subregional scale and at more regular intervals, perhaps through repeatedly sampling index sites; and (2) expanding harvest data collection to include information on struck and loss, hunter effort, and improve consistency of hunting location accuracy. These goals may be achieved, in-part, by changing the management paradigm to one of a social-ecological system rather than considering harvest, population dynamics, and human interests in isolation (e.g. van Vliet et al. 2015). If the spreading sea otter population in SEAK and other predator populations around the world are to coexist with human interests, more contemporary approaches to management and conservation are needed to ensure future sustainability of those populations.

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1.7 Figures

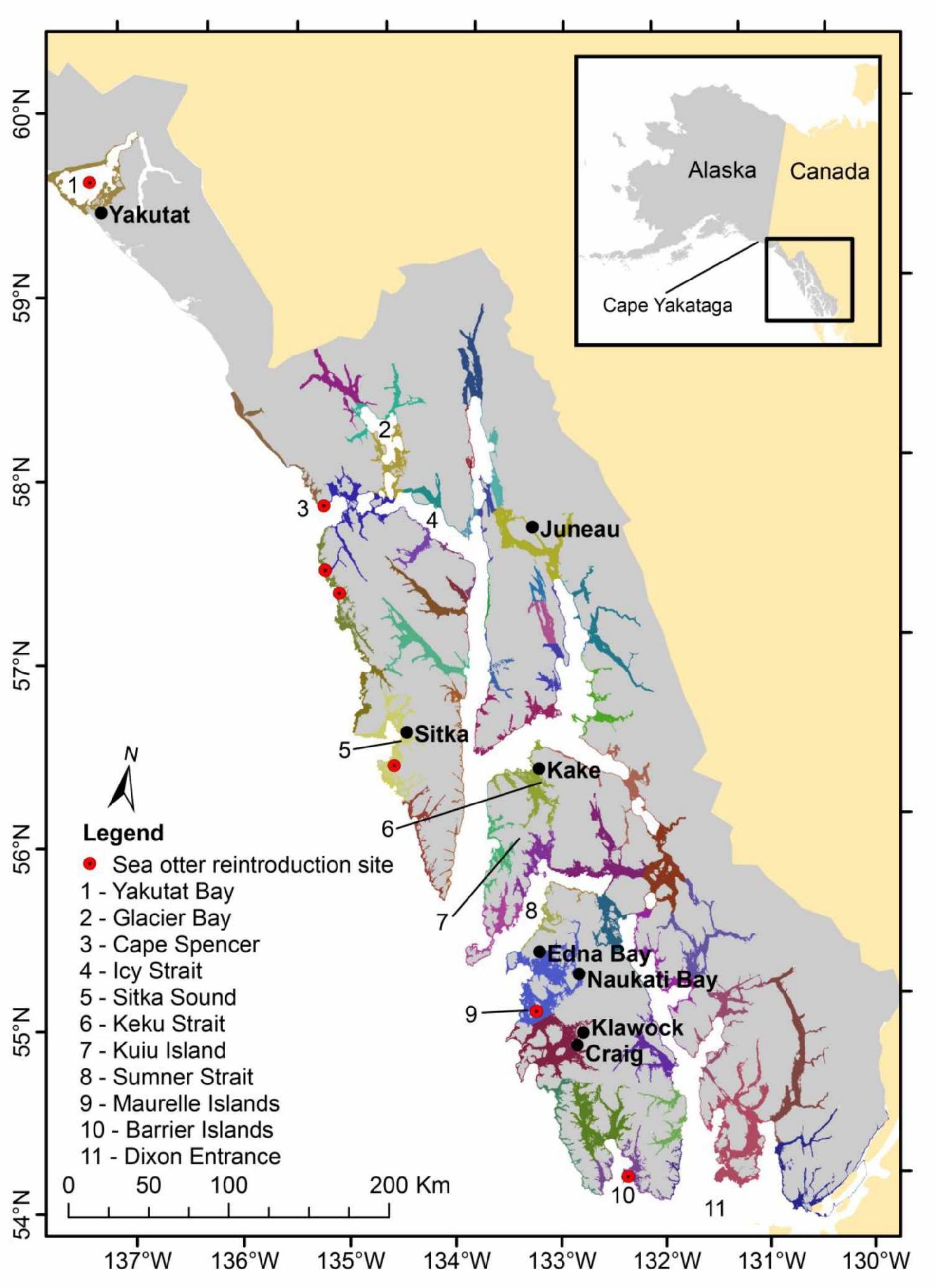

Fig. 1.1: Map of Southeast Alaska with sea otter reintroduction sites and sea otter population subregions (colors denote different subregions)

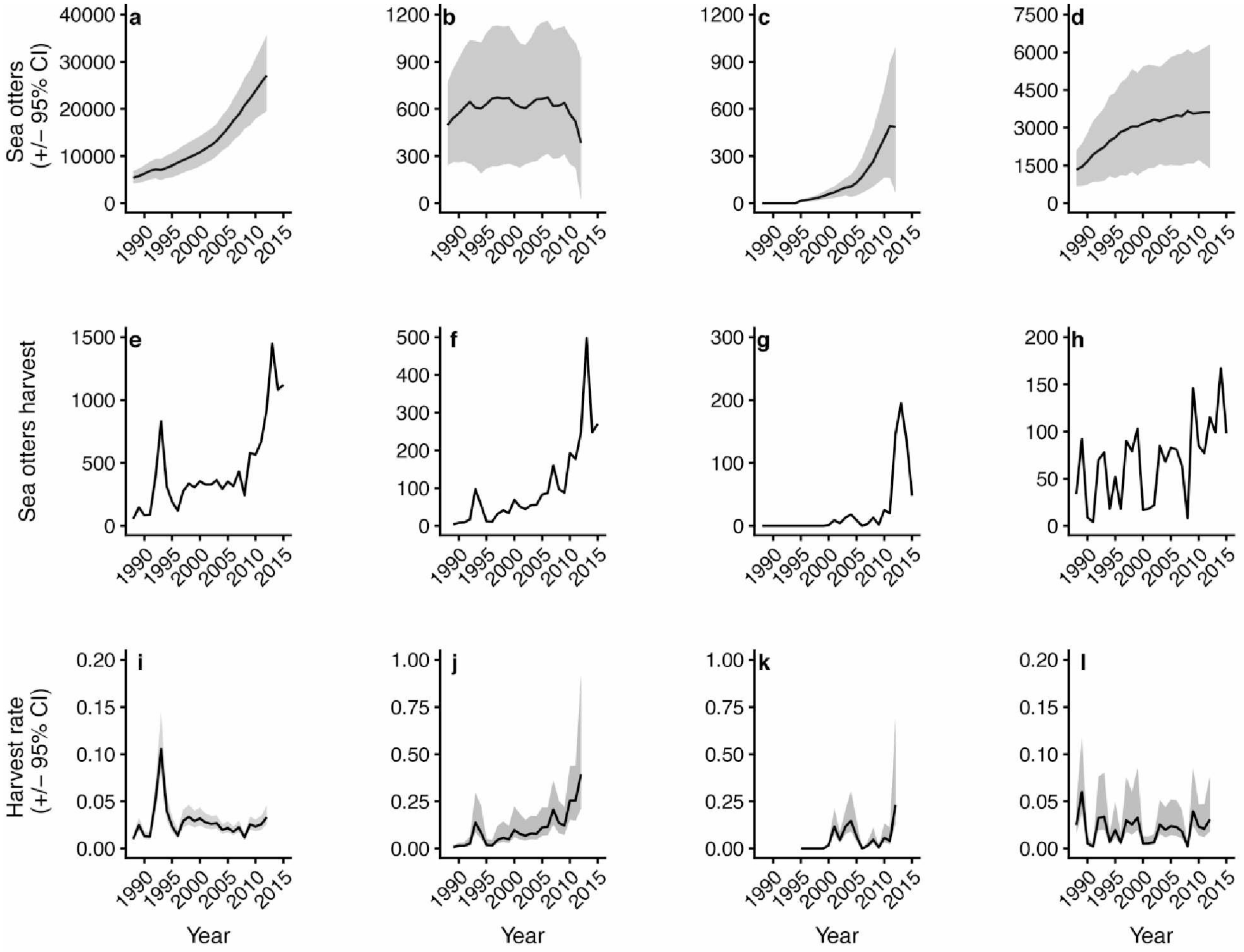

Fig. 1.2: Sea otter population estimates from Tinker et al. (2019a) (a–d), annual sea otter harvest (e–h), and annual sea otter harvest rate (i–l) from 1988 to 2015 for Southeast Alaska (a, e, i), Sitka Sound (b, f, j), Keku Strait (c, g, k), and the Maurelle Islands (d, h, l). Annual harvest rate was calculated as the proportion of harvested sea otters to the estimated pre-harvested sea otter abundance in a given year and location. Note the different y-axis scale on sea otter population estimates (a–d), annual sea otter harvest (e–h), and annual harvest rate (i-l).

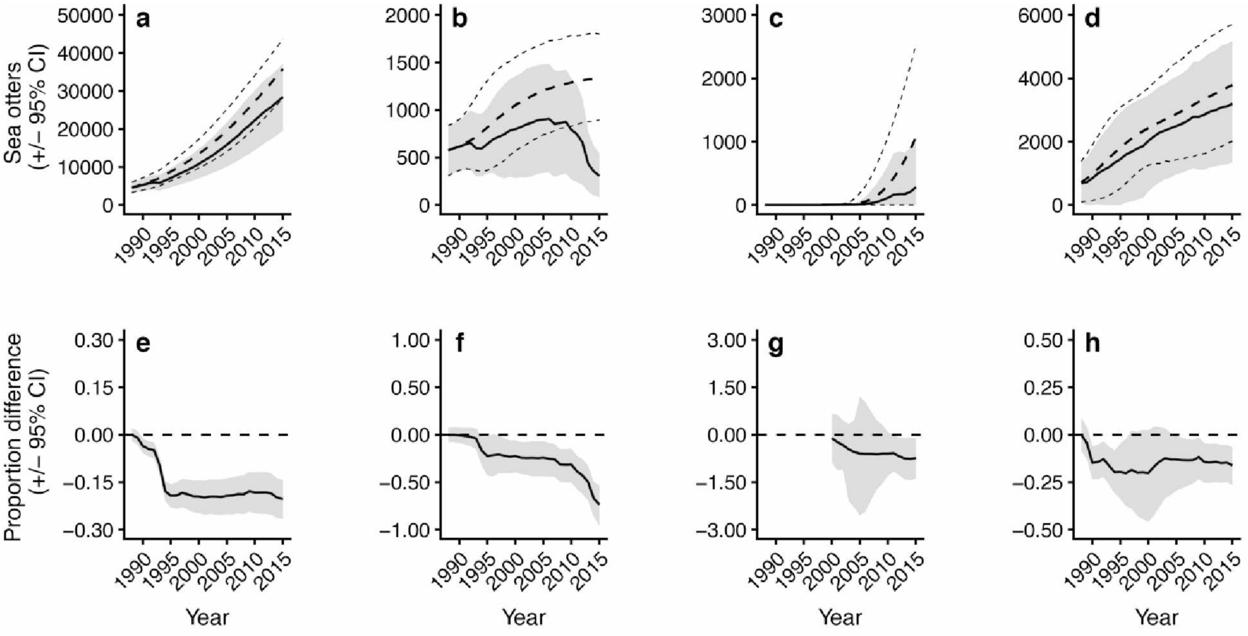

Fig. 1.3: Results from sea otter population simulation models (+/- 95% confidence intervals) without reported harvest (dashed lines) and with reported harvest (solid lines and shading) (a–d). Proportional difference (+/- 95% confidence intervals) between simulation model runs with and without reported sea otter harvest calculated from 10,000 bootstrap samples (e-h) from 1988 to 2015 from SEAK (a, e), Sitka Sound (b, f), Keku Strait (c, g), and the Maurelle Islands (d, h). Simulation model harvest rate was calculated as the proportion of reported harvest to modeled sea otter population pre-harvest. Note difference in y-axis scale of annual sea otter abundance plots (a – d), and proportional difference plots (e – h).

1.8 Tables

Table 1.1: Subregion data and reported sea otter harvest statistics from the Southeast Alaska population, Sitka Sound, Keku Strait, and the Maurelle Islands; including subregion area, estimated carrying capacity († Tinker et al. 2019a), percent Alaska Native population(‡*United States Census 2010*, §*Robinson* et al. 2017) minimum and maximum annual harvest, cumulative harvest, mean annual contribution to total harvest. ¶ Percent Alaskan Native population of the communities of Craig and Klawock AK, which are not directly adjacent to the Maurelle Islands subregion but are reasonably close to permit harvest.

Region	Area (km^2)	Carrying capacity (+/- SD)†	Percent Alaska Native‡	Mean annual hunters reporting (+/- SD)	Min annual harvest	Max annual harvest	Cumulative harvest (%)	Mean annual contribution to total harvest % (+/- SD)
Southeast Alaska	17,790	4.20 (1.58)	16.6§	53.5 (28.6)	55	1,449	12,546	-
Sitka Sound (N05)	615	1.76 (1.35)	24.6	18.9 (10.4)	4	498	2,744 (21.9)	18.6 (10.1)
Keku Strait (S08)	472	9.89 (9.61)	80.6	2.4 (1.4)	0	195	641 (5.1)	2.7 (4.4)
Maurelle Is. (S02)	976	4.09 (1.58)	4.5, 42.1¶	12.2 (7.6)	4	167	1,880 (15.0)	19.0 (15.0)

Table 1.2: Key to symbology used to denote model parameters.

Symbol	Description
s_i	annual survival of life stage *i*
g	juvenile growth transition probability
b	birth rate
w	adult female weaning success rate
$M_{j,t}$	projection matrix for subregion *j* and time *t*
T	time from recruitment to maternity
λ	annual growth rate associated with a particular $M_{j,t}$ parameterization
$\hat{\lambda}_{j,t}$	expected growth rate for subregion *j* and time *t*
$N_{j,t-1}$	sea otter abundance subregion *j* and time *t*
K_j	estimated carrying capacity for subregion *j*
σ_e	standard error of log(λ)
$n'_{i,j,t}$	expected number of individuals of stage *i* in subregion *j* at year *t*, prior to the effects of harvest and dispersal among subregions
$H_{i,j,t}$	total recorded harvest mortality of life stage *i*, subregion *j*, and year *t*
$I_{i,j,t}$	immigration to subregion *j* of life stage *i* in year *t* from other occupied subregions
$E_{i,j,t}$	emigration of animals out of subregion *j* of life stage *i* in year to other occupied sub-regions
$P_{E,\, i}$	probability of emigration of life stage *i*
δ_j	average distance between the centroid of subregion *j* and the centroids of adjacent subregions that share a common boundary
D	distance matrix

Table 1.3: Minimum, maximum and mean sea otter harvest rate calculated from survey data / population simulation data.

Region	Min	Max	Mean (+/- SD)
Southeast Alaska	1.0 / 1.2	10.6 / 12.6	2.9 (1.9) / 3.2 (2.2)
Sitka Sound (N05)	0.7 / 0.7	39.3 / 53.4	9.8 (9.4) / 12.4 (14.1)
Keku Strait (S08)	0.0 / 0.0	23.0 / 78.7	5.0 (6.4) / 35.0 (27.9)
Maurelle Is. (S02)	0.2 / 0.3	6.0 / 11.4	2.1 (1.4) / 3.3 (2.3)

Table 1.4: Regression output of the best fit model testing the effects of years of sea otter occupation, sea otter population density, human population effect and sea otter hunter effect on square-root transformed annual harvest rates.

Random effect of Subregion	Estimate	Lower	Upper	
Intercept	0.1166	0.0798	0.1703	
Residual	0.2018	0.1883	0.2164	
Fixed effects	Estimate	Std. Error	t-value	p-value
Intercept	0.0376	0.0430	0.8747	0.3823
Years sea otter occupation	0.0087	0.0038	2.3016	0.0219
Years sea otter occupation^2	-0.0002	0.0001	-2.1340	0.0212
Sea otter population density	-0.1565	0.0422	-3.7064	0.0002
Sea otter hunter	2.6655	1.2439	2.1429	0.0327

1.9 Supporting Information

1.9.1 Supporting Figures

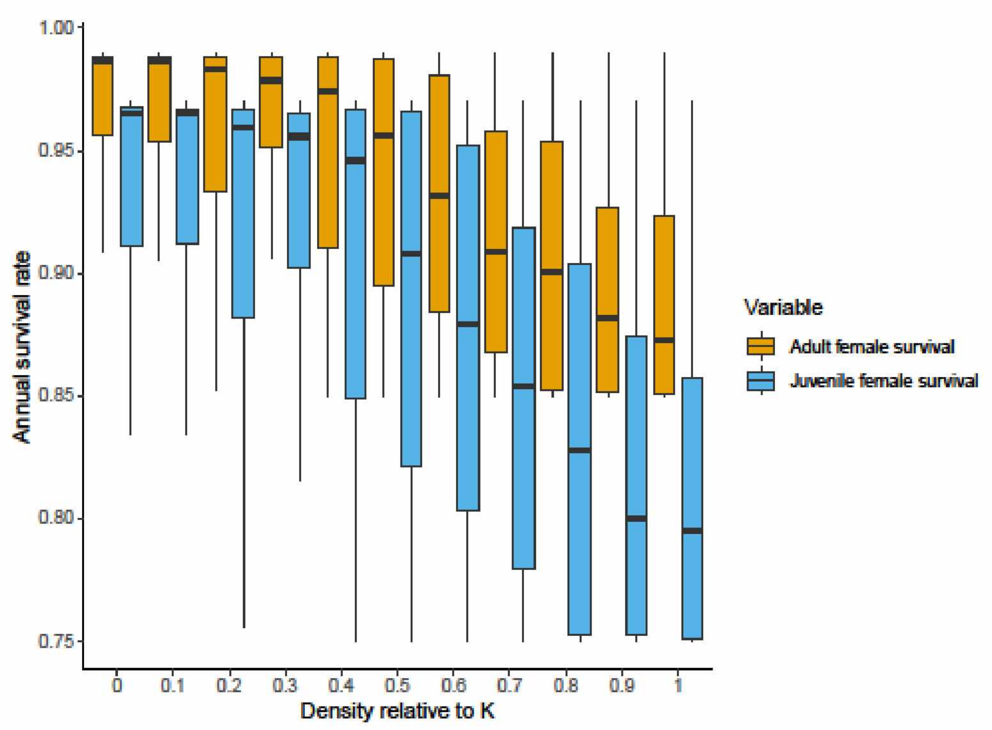

Fig. S1.1: Variation estimated annual survival rates as a function of population density relative to carrying capacity (K) for adult and juvenile females.

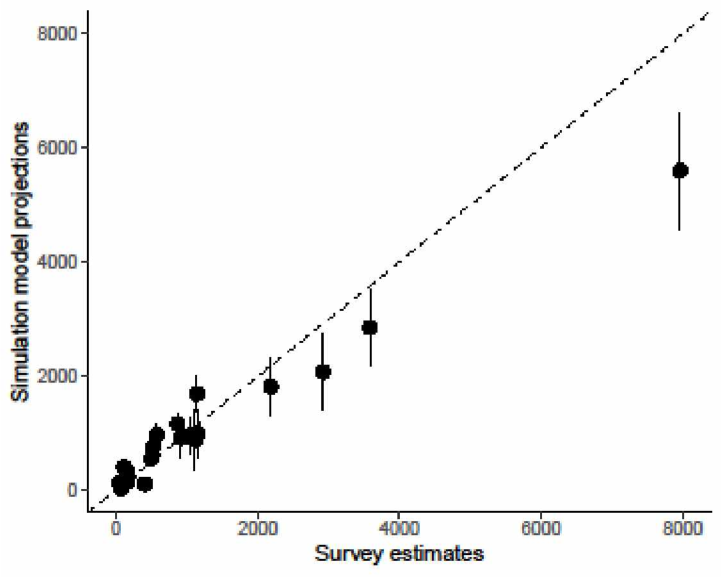

Fig. S1.2: Comparison of sea otter population simulation (solid line +/- 95% CI) to survey estimates from Tinker et al. 2019a. Dashed line represents 1:1 comparison. Points reflect actual sea otter abundance estimates from various surveys +/- 95% CI, see Tinker et al. 2019a.

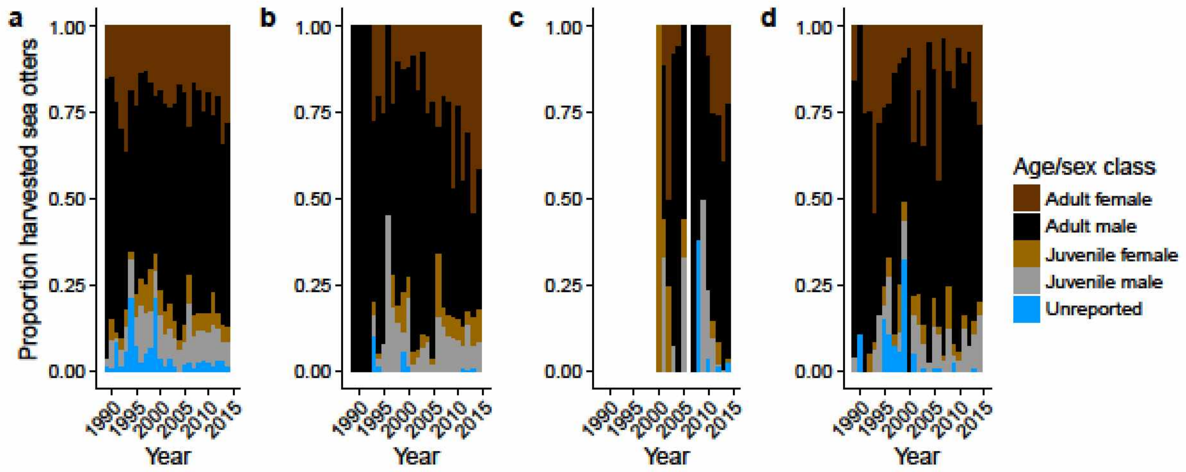

Fig. S1.3: Proportion of harvested sea otters in each age/sex class from 1988 to 2015 in Southeast Alaska (a), Sitka Sound (b), Keku Strait (c), and the Maurelle Islands (d).

1.9.2 Supplemental Tables

Table S1.1: Output from regression evaluating the linear relationships between sea otter population densities and years of sea otter occupation (fit as a quadratic term). Residuals from this analysis were used to de-trend sea otter population density values used in our analysis of factors influencing sea otter harvest rate (Table 3).

Fixed effects	Estimate	Std. Error	t-value	p-value
Intercept	0.0831	0.0465	1.7890	0.0743
Years sea otter occupation	0.0605	0.0060	10.0070	< 0.0001
Years sea otter occupation^2	-0.0009	0.0002	-5.9520	< 0.0001
$F_{2,417} = 131.3$ p-value <0.0001		Adjusted $R^2 = 0.38$		

Table S1.2: Initial sea otter abundance, mean carrying capacity (K) density, and standard deviation of K density in each subregion used in the sea otter population simulation model. Carrying capacity values taken from Tinker et al. 2019a

Subregion	Initial abundance	Mean K density (sea otters/km^2)	SD K density
GBYA	0	16.89	9.77
GBYB	0	16.89	9.77
GBYC	0	16.89	9.77
N01	24	0.65	0.29
N02	100	3.09	1.60
N03	125	2.84	0.95
N04	0	5.78	5.72
Sitka Sound (N05)	48	1.76	1.35
N06	0	2.25	2.29
N07	0	1.25	2.70
N08	0	1.20	8.89
N09	0	4.20	1.58
N10	0	8.17	9.68
N11	0	4.20	1.58
N12	0	4.20	1.58
N13	0	4.20	1.58
N14	0	4.20	1.58
N15	0	4.20	1.58
N16	0	4.20	1.58
N17	0	4.20	1.58
N18	0	4.20	1.58
N19	0	4.20	1.58
N20	0	4.20	1.58
N21	0	4.20	1.58
N22	0	4.20	1.58
N23	0	4.20	1.58

Table S1.2 continued

N24	0	4.20	1.58
N25	0	4.20	1.58
N26	0	4.20	1.58
N27	0	4.20	1.58
S01	25	3.56	1.21
Maurelle Is. (S02)	26	4.09	1.58
S03	0	4.10	8.87
S04	0	7.97	8.75
S05	55	1.61	0.60
S06	0	7.67	9.03
S07	0	16.65	9.83
Keku Strait (S08)	0	9.89	9.61
S09	0	11.98	8.59
S10	0	11.54	8.46
S11	0	4.20	1.58
S12	0	4.20	1.58
S13	0	4.20	1.58
S14	0	4.20	1.58
S15	0	4.20	1.58
S16	0	4.20	1.58
S17	0	4.20	1.58
S18	0	4.20	1.58
S19	0	4.20	1.58
S20	0	4.20	1.58
S21	0	4.20	1.58
S22	0	4.20	1.58
S23	0	4.20	1.58
S24	0	4.20	1.58
YAK	10	3.04	2.49

Table S1.3: Sea otter colonization year, occupation time, proximity to human communities and percent Alaskan native population, and annual sea otter harvests for subregions where sea otters are present. †Year of colonization was determined by population distribution from formal population surveys (Schneider 1975, Pitcher 1989, Gill and Burn 2007, USFWS 2008, 2014b) or from location from sea otter harvests, whichever year was earliest. ‡Percent Alaska Native in adjacent communities was calculated from U.S. 2010 census data except for GBYC and N08 where only 2000 census data was available (*United States Census* 2010). §Only two communities are directly adjacent to the Maurelle Islands (S02) subregion however they have a small (155) combined population. However, two additional communities are close to the subregion and represent most of the human population in the region. Further description in Methods.

Subregion	Year first colonized†	Years sea otter occupation	Number of communities directly adjacent	Percent Alaskan Native in adjacent communities‡	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	Total
GBYB	2002	13	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GBYC	1995	20	1	8.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
N01	1970	45	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
N02	1970	45	2	28.7	0	0	27	0	48	97	83	21	12	13	81	41	9	19	45	61	36	71	38	21	54	49	57	36	93	132	31	12	1,187
N03	1970	45	-	-	11	14	17	10	30	207	59	27	4	0	22	7	6	4	36	23	18	9	3	35	1	17	5	7	3	0	0	0	575
N04	1973	42	-	-	4	14	20	20	118	104	72	24	46	44	48	17	51	60	29	18	11	4	2	7	0	37	12	4	18	30	25	34	873
Sitka Sound (N05)	1970	45	1	24.6	0	4	8	9	17	97	55	12	11	32	41	34	69	51	44	55	56	83	87	160	97	88	193	177	248	498	248	270	2,744
N06	1987	28	-	-	0	0	0	0	0	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	0	0	0	10
N07	1987	28	1	66.1	2	0	0	0	0	16	0	0	0	0	1	1	0	0	1	4	0	4	1	6	0	0	0	0	1	2	0	75	114
N08	1992	23	1	8.2	0	0	0	0	0	15	0	0	0	0	4	0	1	1	2	15	27	3	2	5	18	13	40	9	41	48	76	202	522
N09	1987	28	-	-	2	0	2	1	1	1	1	0	0	4	2	3	8	4	1	4	1	0	4	3	9	0	0	0	4	15	19	9	98
N10	2007	8	1	3.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
N11	2007	8	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	3	0	5
N20	2002	13	1	19.2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	2	3	0	10
N21	2006	9	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	3
N23	2002	13	1	88.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2
S01	1975	40	-	-	0	5	1	25	101	24	0	0	5	0	0	41	10	6	17	0	0	0	0	0	0	0	0	0	0	0	0	0	235
Maurelle Is. (S02)	1970	45	2 (4)§	5.0 (42.1)§	34	92	9	4	70	78	18	52	18	90	79	103	17	18	22	85	68	83	81	64	8	146	85	77	115	99	167	98	1,880
S03	1994	21	2	42.1	0	0	0	0	0	0	0	5	1	7	20	11	40	45	30	26	1	10	31	32	11	94	40	78	49	102	114	107	854
S04	2000	15	-	-	0	0	0	0	0	0	0	0	0	0	0	0	3	42	1	0	0	0	0	0	0	0	0	0	0	19	0	4	69
S05	1970	45	-	-	2	17	0	0	0	47	7	3	16	43	4	15	89	1	8	2	23	0	0	4	0	0	2	22	30	5	1	55	396
S06	1987	28	1	86.2	0	0	0	0	0	0	0	0	0	0	0	0	11	7	4	19	0	0	0	0	0	0	0	0	3	1	15	3	63
S07	1987	28	-	-	0	0	0	0	0	49	2	32	3	20	0	0	12	8	0	0	2	11	0	45	14	0	0	0	2	0	0	0	200
Keku Strait (S08)	1999	16	1	80.6	0	0	0	0	0	0	0	0	0	0	0	0	1	9	4	13	18	9	0	3	13	2	25	20	145	195	136	48	641
S09	1996	19	-	-	0	0	0	0	0	0	0	0	0	0	0	0	1	0	9	0	0	0	0	0	0	0	0	0	0	35	0	6	51
S10	1987	28	2	23.8	0	0	0	19	5	79	2	0	0	11	3	31	0	44	23	3	11	3	7	6	8	15	8	4	11	11	0	5	309
S11	2002	13	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	82	49	43	32	33	251
S12	1993	22	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	2	0	1	0	0	5
S13	2009	6	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	0	5
S14	1993	22	2	27.9	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	4
YAK	1970	45	1	49.8	0	0	0	0	0	14	12	15	4	13	31	1	27	9	53	28	21	62	60	39	8	117	88	149	112	203	212	160	1,438
Total					55	147	84	88	390	833	313	191	120	277	336	305	355	328	329	363	293	352	316	432	243	579	567	670	925	1,449	1,083	1,121	12,544

Table S1.4: Percentage of age/sex classes of harvested sea otters in Southeast Alaska, Sitka Sound, Keku Strait, and the Maurelle Islands from 1988 to 2015.

	Mean annual harvest age-sex ratios % (+/- SD)				
Subregion	Adult male	Adult female	Juvenile male	Juvenile female	Unreported
Southeast Alaska	60 (9)	21 (6)	9 (4)	6 (2)	5 (5)
Sitka Sound (N05)	65 (20)	25 (13)	11 (9)	6 (4)	3 (3)
Keku Strait (S08)	64 (20)	24 (17)	19 (18)	20 (33)	12 (18)
Maurelle Is. (S02)	66 (17)	20 (13)	9 (5)	6 (4)	8 (9)

Chapter 2: Testing the generality of apex predator-mediated trophic cascades in seagrass meadows[2]

Abstract

In many ecosystems apex predators can play a critical role in promoting vegetated habitats, but generality in those roles has been debated for decades. The recovery of sea otters (*Enhydra lutris*) to seagrass (*Zostera marina*) meadows in California triggered cascading effects, leading to increased seagrass biomass and amelioration of eutrophication. The overlap of these species in Southeast Alaska provides a rare opportunity to test the generality of sea otter-mediated trophic cascades across a broad spatial scale. We found a greater proportion of sheltered shoreline with seagrass in regions where sea otters were present compared to where sea otters were absent. Further study across 21 seagrass meadows found evidence for trophic relationships predicted by the apex predator trophic cascade model, including a positive relationship between sea otters and seagrass and a negative relationship between sea otters and crabs. Expected relationships among nitrate, seagrass, epiphytes, and epifauna were present but weak. We also found no evidence of a relationship between mesopredatory crabs and epifauna, suggesting decoupling in the trophic system. These beneficial effects could have broad impacts, as seagrass provides valuable habitat for commercially important fisheries and carbon sequestration, both critical ecosystem services. Our results suggest generality in portions of apex predator-mediated trophic cascades across a large spatial scale; however, the trophic mechanisms leading to those results remain unclear. As apex predator populations recover, their effects should be assessed at various spatial scales as local patterns may not be completely transferable to larger scales of management and conservation.

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[2] Raymond, W.W., Hughes, B. B., Stephens, T. A., Mattson, C.R., Bolwerk, A. T., Eckert, G.L. Submitted to Proceedings of the National Academy of Sciences of United States of America.

Significance Statement

The loss of apex predators and shifting baselines in many ecosystems make it difficult to evaluate the ecological importance of these species. The recolonization of sea otters to Southeast Alaska provides a test of the trophic cascade hypothesis that top-down indirect effects result in a benefit of sea otters to seagrass across a broad geographic area. We demonstrate a positive relationship between sea otters and seagrass, indicating generality of the sea otter - seagrass relationship. However, all predicted relationships were not evident, and nitrate, seagrass, epiphytes, and epifauna were present at lower levels than in nutrient-polluted estuaries. Our results highlight how the recovery of apex predators can have large-scale effects in nearshore ecosystems, which can inform conservation and management.

2.1 Introduction

The loss of apex predators is one of humankind's greatest impacts on Earth (Estes et al. 2011, Ripple et al. 2014). Known as trophic downgrading (Estes et al. 2011), the functional decline of top predator populations can lead to drastic changes in many ecosystems including lakes, temperate and tropical reefs, terrestrial forests, and tundra (Terborgh and Estes 2010). Predators like sharks, fishes, sea otters, and alligators are linked to the health of vegetated coastal habitats by modulating the behavior or abundance of herbivores. The overfishing of predatory fishes and crabs, for example, resulted in an increase of epifauna that decimated salt marshes in the northwestern Atlantic Ocean (Altieri et al. 2012). The loss of seagrass meadows in Bermuda, Indonesia, and the Indian Ocean has been attributed to overgrazing by an abundance of sea turtles that resulted from a lack of shark predation (Fourqurean et al. 2010, Lal et al. 2010, Christianen et al. 2014). In the Baltic Sea, the decline of commercially valuable Atlantic cod increased mesopredatory fish abundance, leading to decreased epifauna abundance, and subsequent increased seagrass epiphyte load and decreased seagrass abundance (Jephson et al. 2008, Moksnes et al. 2008, Baden et al. 2010, 2012).

Examples of predator recovery suggest declines in vegetated or foundational habitats are reversible. The recovery of wolf (*Canis lupus*) populations in Yellowstone National Park led to increased riparian habitat by reducing elk (*Cervus elaphus*) foraging pressure (Ripple and Beschta 2003). In coral reef ecosystems, reefs with abundant predators, such as sharks and large-bodied fishes, had more reef-building corals, greater coral recruitment, and less coral disease than in reefs lacking these predators (Sandin et al. 2008). In the northeast Pacific Ocean, the recovery of sea otters (*Enhydra lutris*) to kelp forests resulted in increased kelp abundance, leading to enhanced primary productivity, greater fish abundance, and an overall increase in ecosystem diversity (Estes et al. 1978, Duggins 1980, Duggins et al. 1989, Estes and Duggins 1995, Reisewitz et al. 2006). The recovery of sea otters to seagrass (*Zostera marina*) habitats in California led to increased seagrass biomass by releasing invertebrate epifauna from predation by crabs. In turn these epifauna reduced epiphytic algae loads, preventing them from smothering the seagrass (Hughes et al. 2013). These cascading effects were strong enough to ameliorate eutrophication in the region, which provides a strong ‘bottom-up’ force that favors the production of epiphytes (Burkholder et al. 2007, Waycott et al. 2009). While dramatic, whether or not this beneficial effect of sea otters to seagrass occurs independent of eutrophic conditions, or in other regions, is an open question.

Sea otters inhabit an expansive and remote stretch of seagrass habitats in Southeast Alaska (Fig. 1), which provides a unique opportunity to assess the generality of apex predator-mediated effects without the bottom-up stress of nutrient over-enrichment. While seagrass is in global decline, Southeast Alaska supports over 10,000 km of seagrass shoreline (Harper and Morris 2004, Orth et al. 2006, Waycott et al. 2009, NOAA 2019), nearly as much shoreline (of any type) as the entire west coast of the continental United States. Seagrass meadows provide a wealth of ecosystem services, with benefits to the regional economy and social-ecological system, including habitat for fishes and invertebrates, many of which are commercially and traditionally harvested (Hughes et al. 2014, Lefcheck et al. 2019). Southeast Alaska's sea otter population is recovering from local extinction resulting from the commercial fur trade. After reintroduction in the late 1960s the sea otter population was estimated at 25,000 animals in 2011 (Burris and McKnight 1973, USFWS 2014, Tinker et al. 2019). Despite the well-known ecological role of sea otters in kelp forests (Estes et al. 1978, Duggins 1980, Estes and Duggins 1995), little is known about their role in seagrass habitats (Hughes et al. 2019), other than the dramatic patterns seen in Elkhorn Slough, CA (Hughes et al. 2013).

Here we test for generality of a four-level trophic cascade across a vast seagrass ecosystem in Southeast Alaska. We applied a conceptual model for the ecological relationships within apex predator - seagrass trophic cascades described in California (Hughes et al. 2013) and in the Baltic Sea (Jephson et al. 2008, Moksnes et al. 2008, Baden et al. 2010, 2012). For a true trophic cascade to be present we expected sea otters to ultimately show a positive relationship with seagrass, but also for each member of the cascade to have a negative relationship with its closest trophic neighbor, linking the system together. Here we advance the study of sea otter ecosystem effects and the larger study of the role of apex predators by testing this conceptual model in two ways. One, we examined the overlap in distribution of sea otters and seagrass in Southeast Alaska, spanning approximately 700 km of coast. Two, we conducted an in-depth characterization of seagrass communities across 21 sites that span ~100 km of coast and a gradient of sea otter occupation and activity to test for the ecological relationships of the hypothesized trophic cascade.

2.2 Results

2.2.1 Seagrass Extent With and Without Sea Otters

Our comparison of seagrass extent relative to the current sea otter population across 37,681 km of shoreline in Southeast Alaska revealed a positive association between seagrass extent and sea otter occupation (Fig. 2.1). Of the 14,705 km of shoreline identified as suitable seagrass habitat within the sea otter range (Gill and Burn 2007, USFWS 2014), 5,793 km (39%) were defined as patchy or continuous seagrass and 3,361 km (23%) were defined only as continuous. In contrast, where sea otters were absent, 22,976 km of shoreline were identified as suitable for seagrass, 4,371 km (19%) were defined as patchy or continuous seagrass, and 1,725 km (8%) were defined only as continuous (Fig. 2.1).

2.2.2 Sea Otter Index

Infrequent population assessments (7-10 years) and variable population growth (Tinker et al. 2019) make accurate estimates of the Southeast Alaska sea otter population difficult. To overcome this, we developed a sea otter index from various sea otter related measures which provided a robust metric of seagrass site-level sea otter occupation and ranged across our study sites (Table S2.1). The first principal component of the principal components analysis accounted for 67.5% of the variation in sea otter measures, with the highest loading on sea otter surveys as (0.575), followed by the population model of sea otter density (0.530), number of sea otter pits (0.527), and the proportion of sea otter cracked clam shells (0.337). The index allowed us to test for hypothesized ecological relationship across a gradient of apex predator occupation.

2.2.3 Seagrass Communities

We identified many ecological relationships among components of the seagrass community predicted by the trophic cascade hypothesis, but these varied in their intensity and strength of evidence (Table 2.1, S2.2; Fig. 2.2). As predicted, the sea otter index was negatively associated with crab biomass (weight = 1.00, p = 0.002; Table 2.1, S2.2; Fig. 2.2A) and positively associated with seagrass biomass (weight = 1.00, p = 0.027; Table 2.1, S2.2; Fig. 2.2E). We found a negative relationship between epifauna load and epiphyte load (weight = 1.00, p = 0.067; Table 2.1, S2.2; Fig. 2.2C), a positive relationship between epiphyte load and nitrate (weight = 0.76, p = 0.058; Table 2.1, S2.2; Fig. 2.2D), and a weak negative relationship between seagrass biomass and epiphyte load (weight = 0.55, p = 0.091; Table 2.1, S2.2; Fig. 2.2F). However we did not find evidence of a relationship between epifauna load and crab biomass (Fig. 2.2B), as these variables were not included in top models with either as a response variable (Table 2.1, S2.2).

Correlation analysis among trophic cascade variables generally supported the linear modeling results above (Fig. 2.3). We found relatively strong correlations between the sea otter index and crab biomass ($R^2 = -0.63$), sea otter index and seagrass biomass ($R^2 = 0.43$), and between epifauna and epiphytes ($R^2 = -0.41$). In general, we found low correlation between non-trophic cascade community measures (fish biomass, macroalgae and diatom cover, and sediment score) and the trophic cascade variables (sea otter index, crab biomass, seagrass biomass, epifauna load, epiphyte load, and nitrate), with some exceptions. We found a relatively strong negative correlation between sea otter index and sediment score ($R^2 = -0.66$) indicating smaller sediment grain sizes at sites with high sea otter index values. Conversely we found a positive correlation between crab biomass and sediment score ($R^2 = 0.49$). Considering correlations among the non-trophic cascade community measures, we found moderate positive correlation between fish biomass and diatom cover ($R^2 = 0.45$), sediment score and macroalgae ($R^2 = 0.47$) and negative correlation between sediment score and diatom cover ($R^2 = -0.43$).

2.2.4 Environmental Patterns

Environmental variables ranged in their variability among sites but were relatively consistent considering the dynamic nature of shallow intertidal ecosystems (Table S2.3). Light transmittance varied across sites, ranging from 0.29 to 0.83 (0.54 +/- 0.15 SD) but did not vary across the sampling season (linear regression against sample date April 29th – August 22nd; $p = 0.166$). Sediment score across sites ranged from 1.0 (mud) to 5.2 (coarse sand) (2.6 +/- 1.4 SD) (Table S2.3). Water temperature increased through the sampling season and ranged from 8.0° to 16.6° C (linear regression against sample date April 29th – August 22nd; $p < 0.001$). A coordinated effort to quantify sea water temperatures for all sites on the same day, August 14, 2017, showed little evidence of variation across sites with a mean of 13.6°C (+/- 0.8 SD) at 1 m depth and 13.3°C (+/- 0.9 SD) at 4 m depth (Table S2.3). Nitrate measured throughout the sampling season ranged from 0.10 to 2.79 µmol (1.00 µmol +/- 0.81 SD) and did not show a relationship with sampling date ((linear regression against sample date April 29th – August 22nd ; p = 0.239). On August 14, 2017, nitrate concentration across all sites ranged from 0.08 to 2.63 µmol (0.76 +/- 0.75 SD) at 1 m depth and from below the detection limit to 2.43 µmol (0.86 +/- 0.80 SD) at 4 m depth (Table S2.3). Salinity ranged from 24.3 to 31.5 ppt (29.7 +/- 1.6 SD) across all sites and showed little change through the sampling season (linear regression against sample date April 29th – August 22nd; p = 0.164). Salinity on August 14, 2017 showed greater variation at 1 m depth ranging from 19.0 to 31.5 ppt (29.0 ppt +/- 3.5 SD) but was more consistent at 4 m depth ranging from 30.4 to 32.0 ppt (31.5 ppt +/- 0.7 SD) (Table S2.3).

2.3 Discussion

Many of the ecological relationships predicted by the apex predator – seagrass trophic cascade conceptual model were present across the large spatial scale of our study, including a positive relationship between sea otters and seagrass and a negative relationship between sea otters and crabs. We found some evidence for the direct relationships among the nitrate – seagrass – epiphyte – epifauna portion of the community, consistent with the model and similar to other large scale studies (Duffy et al. 2015). However, we did not find the expected negative relationship between crabs and epifauna, a critical link in the trophic cascade. Our correlation analyses indicate little influence of the bottom-up forces of nitrate and sediment size on components of the trophic cascade suggesting the importance of top-down forces in the system. Given the lack of evidence for all relationships in the trophic cascade, our results suggest that the trophic mechanisms leading to increased seagrass biomass may differ in Southeast Alaska and/or at large spatial scales. The positive relationship between sea otters and seagrass could have ecosystem-scale and conservation consequences including benefits to harvested fishes and shellfish as well as carbon sequestration. Furthermore, our results advance the growing body of research on the ecosystem effects of recovering apex predators (Silliman et al. 2018) by assessing their ecological role against a continuous measure of occupation and across a large geographic scale.

The lack of a relationship between crabs and epifauna in our study suggests decoupling between high and low trophic levels and may be a result of the relative abundance of epifauna and crabs compared to Elkhorn Slough (Hughes et al. 2013), the availability of alternative food sources, and/or spatial scale-induced variability in trophic relationships. We measured lower epifauna loads (termed 'grazer load' in Hughes et al. 2013) in our system than observed in the Elkhorn Slough study, which ranged from 0.0 – 0.80 mg cm-1 in Elkhorn Slough (Hughes et al. 2013), compared to <0.001 – 0.002 mg cm-1 in Southeast Alaska. Elkhorn Slough epifauna assemblages were dominated by the large-bodied herbivorous sea hare (*Phyllaplysia taylori*) which are absent in Southeast Alaska. Crab biomass also differed, ranging from 0.4 (+/- 0.4 SEM) to 270.2 (+/- 190.9 SEM) g day-1 across sites in Southeast Alaska compared to approximately 100 to 700 g day-1 in Elkhorn Slough. It may be that epifauna in Southeast Alaska system do not provide a reliable and consistent prey resource for crabs, therefore, decreasing the interaction strength between these two groups. Given their mobility and the generalist feeding strategy of crabs, it is possible that they consume a variety of prey within and outside of seagrass meadows, which would further weaken their relationship with seagrass-associated epifauna. Furthermore, trophic relationships among species may uncouple when the scale at which each species functions differs (Van De Koppel et al. 2005). As described above, the mobility of crabs may suggest that they function at fundamentally different scales than epifauna, further contributing to the lack of evidence for a relationship between them.

Fishes are common in seagrass ecosystems worldwide and are known to consume seagrass-associated epifauna, sometimes leading to cascading effects (Moksnes et al. 2008, Baden et al. 2010, Lewis and Anderson 2012); however, we did not find evidence of this relationship (Fig. 2.2B; Fig. 2.3; R2 = 0.18). This may be due to similar reasons as for crabs (above), including mobility, generalist feeding strategy, and scale-induced uncoupling. Other factors may have influenced our fish biomass measures as well. Fish biomass was highly variable across sites, as is common in the region (Murphy et al. 2000, Johnson et al. 2012), potentially masking any effect of the fish assemblage on epifauna or other variables. We also conducted only one beach seine set at each site, potentially precluding detection of seasonal trends in diversity, abundance, and biomass that may influence the epifaunal community. Given the support for the important role of mesopredators, including both crabs and fishes, in seagrass ecosystems from other regions and at smaller scales, further research is needed to identify the trophic relationships of these species in Southeast Alaska.

Our study system varied in other notable ways from Elkhorn Slough at the time of the Hughes et al. (2013) study, including sea otter density, eelgrass biomass, epiphyte load, nitrate concentration, and spatial scale which may have contributed to the lack of evidence for a full trophic cascade. Sea otter densities were higher in Elkhorn Slough ranging from approximately 0.25 to nearly 400 sea otters km^{-2}, compared to 0.0 to 13.75 sea otters km^{-2} at our sites. Seagrass biomass was higher in Elkhorn Slough ranging from approximately 100 – 400 g m^{-2} compared to 6.9 – 155.9 g m^{-2} at our sites. Epiphyte loads were also higher in Elkhorn Slough ranging from approximately 0.25 – 3.5 mg cm^{-1}, compared to < 0.01 – 0.14 mg cm^{-1} at our sites. Water nitrate concentrations were drastically higher in Elkhorn Slough and measured 10.0 µmol to 600 µmol, compared to a maximum of 2.76 µmol at our sites. This difference in available nitrate likely contributes to large differences in epiphyte load (Burkholder et al. 2007). These large differences may explain why we did not observe stronger trophic relationships predicted by Hughes et al. (2013). Despite these differences we still found that the overall effect of sea otters on seagrass may be generalizable across a much larger spatial scale and that sea otters may have a beneficial effect to seagrass in the absence of eutrophication. However, the trophic mechanisms leading to that effect may depend on local biotic and abiotic conditions.

The lack of evidence of a full trophic cascade may also be due to spurious correlations which we are unable to resolve in the natural experiment approach of our study. In our whole Southeast Alaska shoreline comparison it remains to be seen if sea otters prefer seagrass habitats or if the current sea otter population just so happens to be in close proximity to seagrass shoreline. Notably, all sea otter reintroduction sites are along the outer coast (Fig. 2.1), providing no comparison of sea otter population dynamics in inside waters across the same time period. Furthermore, our substrate and exposure criteria for selecting suitable seagrasses may not account for other physical and biological factors that influence the presence, absence, or density of seagrasses. Temperature and sedimentation, for example, may affect the ability of seagrass to thrive (Zimmerman et al. 2015) and could be greatly influenced by the proximity of glaciated watersheds which are common in the inside waters on Southeast Alaska. To date, how these factors influence seagrasses in Southeast Alaska are not well understood.

Seagrass communities are subject to seasonal changes affecting the seagrass itself (Nelson and Waaland 1997, Clausen et al. 2014) and the abundance and diversity of seagrass-associated species (Heck et al. 1989, Douglass et al. 2010). We found seasonal variation in seagrass biomass and epiphyte load and were able to account for it by detrending these variables before analysis. Furthermore, seagrass communities can vary at both small (< 100 m) and large spatial scales (>10 km) (Whippo et al. 2018) introducing further variability to the system. Our sampling regime was designed to focus on the spatial variability of sea otter presence and precluded assessment of seagrass community variability at a site through time. Seagrass community phenology coupled with spatial variability may have introduced variability in our data that we are unable to account for and may influence our results. However, we sampled across the sea otter gradient through time to avoid confounding the sea otter effect with the seasonal effect (Fig. 3; $R^2 = -0.08$). While seasonal variation in in seagrass community phenology likely occurs in Southeast Alaska and deserves further study, our analyses still support generality in portions of the sea otter – seagrass trophic cascade across a large spatial scale.

Sea otters can cause a significant amount of physical disturbance to seagrass meadows, as we measured through counts of sea otter pits (Table S2.2), suggesting an alternative interaction pathway between sea otters and seagrass. We observed that sea otters digging for clams removed seagrass, particularly at the upper edge of intertidal seagrass meadow. The strong correlation between sea otter index and sediment score (Fig. 2.3; $R^2 = -0.66$) may also reflect effects of disturbance. Finer sediments were associated with a higher sea otter index, but we are unsure of the mechanism. Sea otters may be more active in areas of finer sediments, finer sediments may result from higher sea otter activity, or the relationship may be spurious. As our sampling occurred within seagrass beds, this study was not designed to evaluate the effect of sea otter disturbance on seagrass distribution and abundance. Parallel studies suggest sea otter disturbance results in reduced seagrass extent in the intertidal in our study region (Stephens et al. *in prep*).

The beneficial effects of sea otters in seagrass meadows could have broad impacts both in Southeast Alaska and in other regions where the two species co-occur, as seagrass provides valuable habitat for commercially important fish and shellfish and can serve as a carbon sink. Healthy and vibrant seagrass beds provide nursery habitat to fish and invertebrates (Beck et al. 2003, Lefcheck et al. 2019), meeting that standard of 'essential fish habitat' (EFH) in the United States (NOAA 2006). In Southeast Alaska, seagrasses support many commercially harvested species including four Pacific salmon species (*Oncorhynchus* spp.), multiple rockfish species (Sebastes spp.), Walleye pollock (*Gadus chalcogrammus*), Pacific cod (*G. macrocephalus*), Lingcod (*Ophiodon elongatus*), and Pacific herring (*Clupea pallasii*) (Murphy et al. 2000, Johnson et al. 2003). The expansion of sea otters in Southeast Alaska could benefit fish through increased seagrass biomass. Sea otters may also play an important role in carbon sequestration as seagrasses meadows in the region have some of the highest sediment organic matter in the coastal northeast Pacific (Prentice et al. 2020) and are known carbon sinks worldwide (Fourqurean et al. 2012). As seagrasses cover 10,164 km of shoreline in Southeast Alaska, these local effects may have global implications.

As predator populations continue to recover, an understanding of their effects in multiple ecosystems and across multiple scales will be essential for their successful conservation and management (Roman et al. 2015, Silliman et al. 2018). Our study directly addressed this questions and found that sea otters' effect on seagrass and the relationships among seagrass, epiphytes, and epifauna in seagrass to be consistent with the trophic cascade model across a broad scale in Southeast Alaska. However, our results do not support the full trophic cascade, and the mechanisms leading to the patterns described here remain to be resolved. This and other studies provide evidence for the ecological importance of apex predators and highlights the need to integrate this information into management and conservation across diverse habitats and spatial scales. While the recovery of sea otters is a conservation success story, it has generated conflicts with human shellfish harvesters (Carswell et al. 2015). To date it remains unclear if the indirect benefits to commercial, recreational, and subsistence fisheries of the positive effects of sea otters on seagrass or kelp forests (Estes and Duggins 1995) outweigh their direct negative effects (Larson et al. 2013, Carswell et al. 2015, Hoyt 2015).

2.4 Materials and Methods

2.4.1 Seagrass Extent With and Without Sea Otters

We tested for a relationship between sea otters and seagrass by comparing the amount of seagrass shoreline in areas with and without sea otters. We determined total seagrass shoreline in Southeast Alaska, using the publically-available shoreline-characterization database, Shorezone (Harper and Morris 2004, NOAA 2019). The database defines all seagrasses in protected shorelines as *Zostera marina*; however, the region is known to hold intermixed *Z. marina* and surfgrass (*Phyllospadix* spp.) habitats (Stephens et al. 2019). Due to this discrepancy, we define all shoreline defined by Shorezone as *Z. marina* as ‘seagrass’. We defined regions of Southeast Alaska with and without sea otters using United States Fish and Wildlife Service survey data from Yakutat Bay in 2005 (Gill and Burn 2007) and for the rest of Southeast Alaska in 2010 and 2011 (USFWS 2014). Glacier Bay was excluded from analysis due to a lack of shoreline characterization data; however, sea otters have been present in the bay since at least 1993

(Esslinger and Bodkin 2009). First we calculated the length of suitable seagrass shoreline in all of Southeast Alaska defined as shoreline with 1) exposure classifications of 'semi-protected', or 'protected', or 'very-protected' and 2) with substrate classified as 'partially mobile sediment' or 'rock and sediment', or 'mobile sediment', or 'estuarine sediment'. These shoreline segments were summed in areas with and without sea otters. We calculated total seagrass extent (km) by summing shoreline defined as seagrass, both patchy and continuous, in regions with and without sea otters. Finally, we selected only continuous seagrass and summed that extent in regions with and without sea otters. Proportions of shoreline defined as suitable seagrass shoreline that were actually characterized as seagrass are reported between areas with and without sea otters.

2.4.2 Sea Otter Index

We created a sea otter index that combined current observations with historical sea otter survey data as an overall measure of sea otter occupation and use at each seagrass survey site. The index combined four measures: 1) boat-based sea otter surveys conducted for this study, 2) model estimates of sea otter density from historical population surveys, 3) sea otter pits and 4) shell-litter predation assays. (1) Two replicate boat-based sea otter abundance surveys were conducted by driving a small boat at 14 km/h and counting all sea otters within a 3.8 km distance (over water) from each seagrass site. Sea otter counts were converted to density based on the total surveyed area and averaged. (2) The estimated sea otter population density was drawn from modeling efforts which fitted all available Southeast Alaska sea otter survey data to a spatially-explicit density dependent population model (Tinker et al. 2019). (3) We counted pits generated by sea otters foraging for clams at each site across three shore parallel 100 m × 2 m transects located inside the seagrass bed, on the upper edge, and outside and above the upper edge of the seagrass bed. Sea otter pits were defined as depressions greater than ~30 cm diameter. (4) Along the same 100 m transects, but within a 1 m swath, we collected all clam shell litter that had a complete valve hinge, was not fouled or scarred, and was resting on top of the substrate. We calculated the proportion of shells that showed break patterns consistent with sea otter predation, as opposed to crabs, predatory snails, and sea stars/natural death (Boulding 1984, Ambrose et al. 1988, Kvitek et al. 1991, 1992). The combination of sea otter dug pits and the proportion of sea otter cracked bivalve shells helped account for ambiguity surrounding whether or not a pit was actually created by a sea otter (Traiger et al. 2016). The sea otter index is the first principal component of the four sea otter variables that were transformed via natural log (for counts) or arcsine-square root (for proportions) and standardized to the maximum value across all sites. Principal component analysis was performed using the 'princomp' function in R v.3.5.1 (Team 2018).

2.4.3 Seagrass Communities

We sampled seagrass communities at 21 sites on the west coast of Prince of Wales Island from April through August 2017 (Fig. 2.1). Sites were randomly selected using the shoreline characterization in Shorezone (Harper and Morris 2004, NOAA 2019) targeting sites with continuous seagrass, without canopy kelps, and either semi-protected, or protected, or very protected exposure, and with no upland development such as roads or buildings. Exact site locations were refined by groundtruthing to identify meadows with at least 100 m of continuous seagrass. Areas with intermixed surfgrass (*Phyllospadix* spp.) were avoided.

At each site, we characterized the composition of the seagrass community including seagrass, seagrass epiphytes, seagrass-associated invertebrate epifauna (hereafter 'epifauna'), crabs, and fishes. We sampled seagrass, epiphytes, and epifauna in eight 0.5 m × 0.5 m quadrats evenly spaced along a 100 m transect placed at least 5 m linear distance below the upper intertidal edge of the continuous seagrass bed. Given these criteria this transect was placed at approximately -0.5 m relative to mean lower low water (MLLW) across all sites. In each quadrat we measured percent cover of living attached macroalgae, benthic diatoms mats, and seagrass shoot density. From each quadrat we randomly collected five seagrass shoots in a 400 μm mesh bag, which was kept cool and transported back to the laboratory for analysis. In the lab, each shoot was floated in freshwater to collect epifauna and then scraped to collect epiphytes. The total length of all seagrass leaves per shoot was also measured. Epifauna primarily consisted (by mass) of isopods (*Pentidotea resecata*) and limpets (*Lottia paralella*) and also included gammarid amphipods (Suborder Gammaridea), caprellid amphipods (Family Caprellidae), and other gastropods (primarily *Littorina* spp. and *Lacuna* spp.). For analysis all taxa were pooled together. Seagrass leaves, epiphytes and epifauna were dried for at least 24 hr at 60° C and weighed to the nearest 0.0001 g. For analysis, aboveground seagrass leaf mass was converted to mass per square meter using the shoot density estimates per quadrat. Epiphyte and epifauna load were calculated as mass per gram of total seagrass biomass of the five shoots collected from each quadrat. All seagrass, epiphyte, and epifauna data were then averaged across the eight quadrats at each site for analysis. For comparison to Elkhorn Slough (Hughes et al. 2013) we also calculated epiphyte and epifauna loads in terms of mg cm^{-1} seagrass.

Crabs were sampled by setting three strings of three pots at each site for 24 hr within the seagrass bed. Each string consisted of one 61 cm × 61 cm × 33 cm rectangular pot with 10 cm ×

10 cm wire mesh and four 20 cm openings, one 71 cm diameter × 33 cm circular pot with 2.5 cm × 2.5 cm fabric mesh and two 7.5 cm diameter openings, and one 'fukui' pot measuring 60 cm × 45 cm × 20 cm with 1 cm × 1 cm fabric mesh and two 20 cm openings. All pots were baited with approx. 0.5 l chopped frozen herring. When pots were collected, all crabs were identified to species and carapace width measured. Carapace widths were converted to biomass using species-specific conversion factors (Table S2.4) using Eq. 2.1. Crab biomass was summed for each string and then averaged across the three strings at each site.

$$mass(g) = a \quad length(cm)^{b} \qquad (2.1)$$

Fish abundance, biomass, and species composition were quantified following methods described in Johnson et al. (2012). Briefly, fish were captured using a 37 m beach seine designed to capture a wide range of fish with variable mesh (10 m sections of 32 mm mesh, 4 m sections of 6 mm mesh, 9 m section of 3.2 mm mesh). The seine tapered from 5 m tall at the center to 1 m tall at the ends and was set as a round haul by holding one end on the beach while backing around the other end in a small boat to the beach. The catch was sorted, identified to species, counted, and a subsample (up to 30 fish) of each species was measured to the nearest mm (fork or total length). Unmeasured fish were assigned lengths based on the distribution of lengths from measured fish of that species at a given site. Fish lengths were converted to biomass using species specific length – weight conversion factors (Table S2.4) using Eq. 2.1.

We tested predicted ecological relationships among seagrass community variables (nitrate, aboveground eelgrass biomass, epiphyte load, epifauna load, crab biomass and sea otters via sea otter index) using linear models. Given that sampling spanned the summer growing season, we first evaluated the effect of time by fitting a linear model between Julian day and each response variable. We found significant positive linear relationships between Julian day and aboveground seagrass biomass ($p < 0.001$) and significant negative relationship with epiphyte load ($p = 0.005$) and thereafter used the residuals of this analysis as a detrended form of the data. All variables were examined for normality; epifauna load was natural log-transformed and crab biomass was square-root transformed.

In order to identify which predictors were most important for explaining a given response, we fit all possible combinations of explanatory factors and then ranked each model using the Akaike Information Criterion adjusted for small sample size (AICc). Since our study was aimed at describing the primary ecological relationships among different components of the seagrass community, we did not include interaction terms in linear models. Full models included all variables in the hypothesized trophic cascade: nitrate, seagrass biomass, epiphyte load, epifauna load, crab biomass, and sea otter index and are detailed in Table S2. We averaged model coefficients from all models with $\Delta\text{AICc} < 2$ (hereafter 'top models') (Burnham and Anderson 2002) using only models where a given factor was included, as is recommended when factors may have weak interactions with the response (Grueber et al. 2011). To account for different scales of measurement between response and among predictor variables in a given model, we standardized model coefficients in the model-averaging procedure to the standard deviation of the response of interest (Barton 2019). These standardized coefficients are reported in Table 2.1 and Table S2.2. We interpret model coefficients based on both the coefficient weight calculated from the model-averaging procedure and the p-value from the averaged model. We interpret the coefficient weight as a measure of the relative importance of that factor in explaining a response and the p-value as a measure of the amount of support of the direction and magnitude of the coefficient. Together these values provide an overall measure of the relationship between a response and a given factor. All statistical analyses were performed using the R v.3.5.1 statistical environment (Team 2018) and models were fit and ranked using the 'dredge' function in the 'MuMIn' package (Barton 2019).

In addition to the hypothesized trophic cascade relationships we also investigated the relationship among biological and abiotic features of Southeast Alaska eelgrass communities. We evaluated these relationships by calculating pairwise Pearson correlations among variables listed above as well as Julian day, macroalgae and diatom cover, fish biomass, and sediment score. Macroalgae and diatom cover were arcsine-square root transformed, fish biomass was natural log transformed, and other variables were transformed as described above.

2.4.4 Environmental Patterns

At the time of seagrass sampling we measured water temperature, salinity, and light transmittance, and collected a 50 ml water sample for nitrate concentration analysis in the eelgrass bed at approximately 1 m water depth on the outgoing tide. We also sampled each of these parameters, except light transmittance, at 1 and 4 m water depths at all 21 sites within a single 8 hr period on August 14, 2017 to better understand if these parameters varied across space while controlling for seasonal variation. Water samples were immediately filtered through a 0.4 µm Whatman GF/F filter into sample vials and then frozen at -20□ C until analysis on October 11th 2017 using a Lachat QuikChem 8000 Flow Injection Analyzer. We measured seawater temperature and salinity using an YSI Pro2030 meter. Light transmittance was calculated as the proportion of light measured at 1m to light measured at the surface. Light was measured as µmol s-1 m-2 using a LI-COR LI-193R spherical quantum sensor. We characterized primary surface sediment type along the same transect used for eelgrass collections using a qualitative score (1 = mud, 2 = sandy mud, 3 = muddy sand, 4 = sand, 5 = course sand, 6 = pebble, 7 = gravel, 8 = cobble, 9 = boulder, 10 = bedrock) characterized at ten 10 m intervals that were averaged per site.

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2.7 Figures

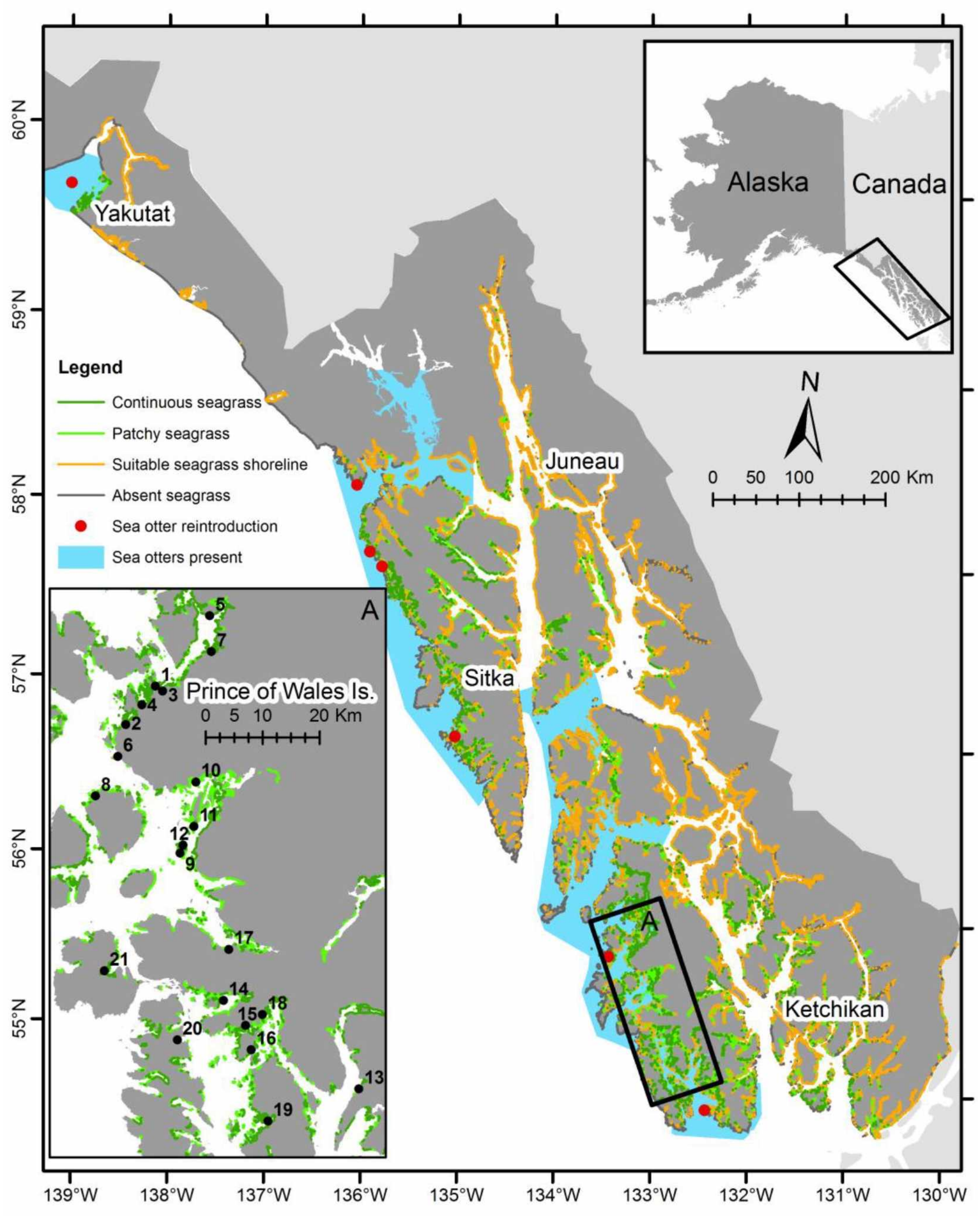


Fig. 2.1: Seagrass distribution (continuous, patchy, or absent), along shoreline with exposure and sediment identified as suitable for seagrass (Harper and Morris 2004, NOAA 2019) and sea otter presence (USFWS 2014). A) Sites of intensive seagrass community surveys on the west coast of Prince of Wales Island, ordered from high (#1) to low (#21) in terms of the sea otter index.

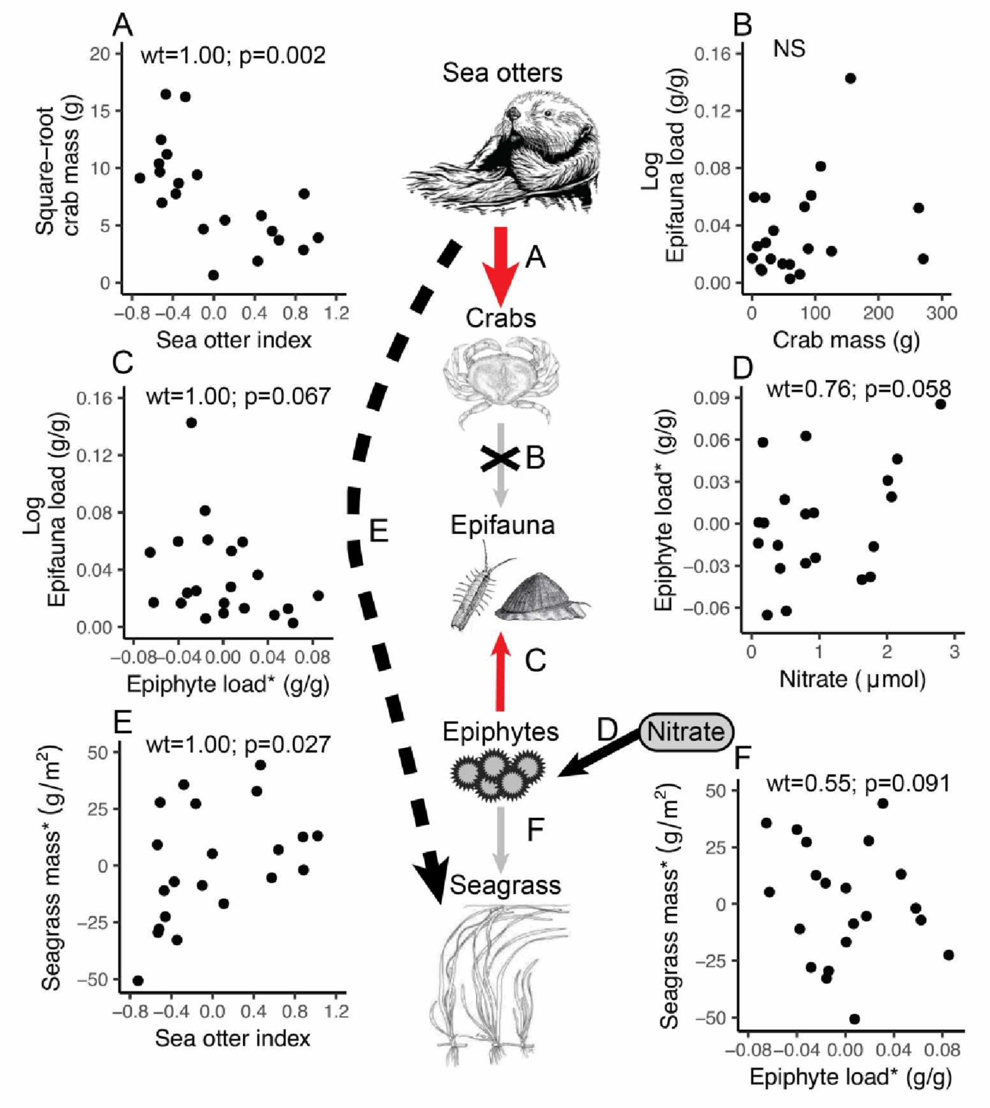
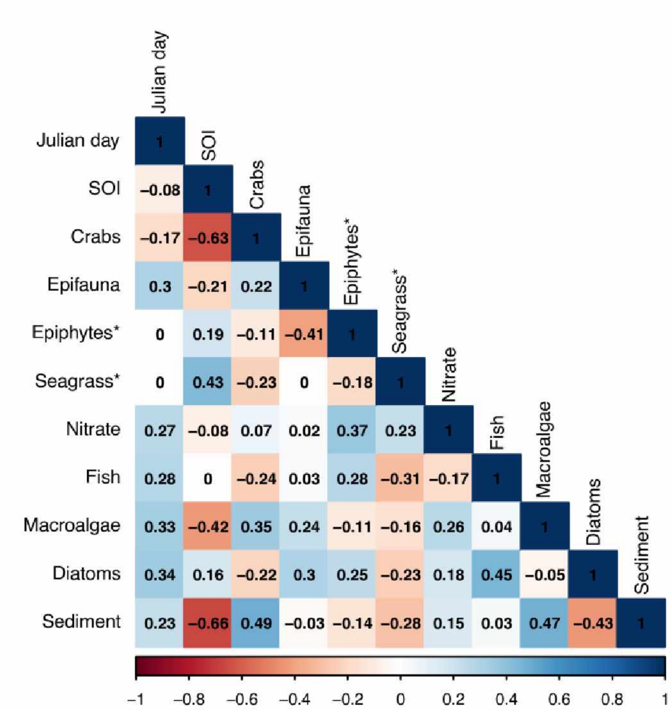


Fig 2.2: Interaction web among Southeast Alaska seagrass community. In the diagram, arrow width is proportional to model weight between species. Black arrows (D, E) represent positive relationships. Red arrows (A, C) represent negative relationships. Grey arrows (F) represent weak relationships. Crossed arrow (B) represents no relationship. Variables that end in (*) were detrended for the effect of Julian day. wt = averaged coefficient weight.



	Julian day	SOI	Crabs	Epifauna	Epiphytes*	Seagrass*	Nitrate	Fish	Macroalgae	Diatoms	Sediment
Julian day	1										
SOI	−0.08	1									
Crabs	−0.17	−0.63	1								
Epifauna	0.3	−0.21	0.22	1							
Epiphytes*	0	0.19	−0.11	−0.41	1						
Seagrass*	0	0.43	−0.23	0	−0.18	1					
Nitrate	0.27	−0.08	0.07	0.02	0.37	0.23	1				
Fish	0.28	0	−0.24	0.03	0.28	−0.31	−0.17	1			
Macroalgae	0.33	−0.42	0.35	0.24	−0.11	−0.16	0.26	0.04	1		
Diatoms	0.34	0.16	−0.22	0.3	0.25	−0.23	0.18	0.45	−0.05	1	
Sediment	0.23	−0.66	0.49	−0.03	−0.14	−0.28	0.15	0.03	0.47	−0.43	1

Fig 2.3: Pearson correlations calculated on transformed data (Materials and Methods) among seagrass community variables. Variables that end in (*) were detrended for the effect of Julian day

2.8 Tables

Table 2.1: Statistical results for response variables (crab biomass, grazer and epiphyte load, and aboveground seagrass biomass) in top performing linear models. The number of top models (≤ Δ2 AICc) is reported along with the sum of the Akaike weights from top models, the number of top models containing a given factor, and the sum of weights across top models for each factor. Model-averaged coefficients were standardized to the standard deviation of a given response. Variables that end in (*) were detrended for the effect of Julian day. Detailed model fit provided in Table S2.2.

Response	N top models	Sum Akaike weights of top models	Factor	N containing models	Sum of weights	Estimate	Standard Error	p-value
Crabs	1	1	Sea otter index	1	-	-0.632	0.178	0.002
Epifauna	2	0.37	Epiphytes*	1	0.63	-0.409	0.209	0.067
Epiphytes*	12	0.72	Nitrate	9	0.76	0.434	0.214	0.058
			Seagrass	5	0.40	-0.396	0.231	0.107
			Epifauna	4	0.33	-0.108	0.195	0.589
			Crabs	3	0.22	-0.069	0.163	0.682
			SOI	3	0.22	0.080	0.187	0.068
Seagrass*	4	0.53	Sea otter index	4	1.00	0.489	0.207	0.027
			Nitrate	2	0.55	0.393	0.217	0.090
			Epiphytes*	2	0.55	-0.397	0.221	0.091

2.9 Supporting Information

2.9.1 Supplemental Tables

Table S2.1: Values used to calculate sea otter index at each intensive seagrass site. Average sea otter density was calculated from two boat-based sea otter surveys conducted in the present study. Sea otter population model densities are drawn from Tinker et al. 2019. Number of sea otter pits and proportion of sea otter cracked shells were evaluated at each site (Materials and Methods). Sea otter index is taken as the first principal component of these four measures.

Site number	Average sea otter density	Sea otter population model density (km-2)†	n sea otter pits	Proportion of sea otter cracked shells	Sea otter index
1	13.75	3.663	244	0.37	1.021
2	7.59	3.663	114	0.49	0.885
3	13.22	3.663	49	0.41	0.880
4	5.83	3.663	23	0.38	0.639
5	1.74	3.663	83	0.40	0.574
6	3.92	1.443	128	0.51	0.465
7	5.00	3.663	3	0.35	0.429
8	2.03	0.163	64	0.50	0.109
9	0.71	0.163	190	0.29	-0.003
10	3.65	0.163	11	0.20	-0.101
11	0.42	0.163	51	0.30	-0.163
12	2.32	0.163	8	0.07	-0.278
13	0.00	1.443	5	0.14	-0.345
14	0.68	1.443	0	0.19	-0.374
15	0.00	1.443	1	0.12	-0.458
16	0.00	1.443	2	0.06	-0.470
17	0.05	0.163	1	0.37	-0.507
18	0.00	1.443	0	0.13	-0.517
19	0.12	1.443	0	0.08	-0.528
20	0.00	1.443	0	0.11	-0.536
21	0.10	0.163	0	0.08	-0.722

Table S2.2: Detailed model fits of all top models (≤ Δ2 AICc) for each response. Model coefficients were standardized to the standard deviation of a given response. 'X' indicates factors that were excluded from full model passed to 'dredge' function. 'I' indicates factors that were included in the full model but were not included in any top models. Variables that end in (*) were detrended for the effect of Julian day.

Response	Rank	Crabs	Seagrass*	Epiphytes*	Epifauna	Nitrate	Sea otter index	R^2	Adjusted R^2	df	Log Likelihood	AICc	ΔAICc	Akaike weight
Crabs	1	X	I	I	I	I	-0.632	0.400	0.401	3	-54.463	116.337	-	0.440
													sum of weights	0.440
Epifauna	1	I	I	-0.409	X	I	I	0.167	0.179	3	-26.752	60.916	-	0.234
	2 - null			-				0.000	0.000	2	-28.673	62.013	1.097	0.135
													sum of weights	0.369
Epiphytes*	1	-	-	X	-	0.375	-	0.140	-0.004	3	39.683	-71.954	-	0.089
	2	-	-0.492		-	0.523	0.438	0.367	-0.010	5	42.891	-71.782	0.171	0.082
	3 - null	-	-		-	-	-	0.000	0.000	2	38.095	-71.523	0.431	0.072
	4	-	-		-0.319	0.367	-	0.242	-0.007	4	41.009	-71.518	0.436	0.072
	5	-	-0.344		-0.371	0.446	-	0.351	-0.010	5	42.638	-71.275	0.678	0.063
	6	-0.305	-		-	0.394	-	0.233	-0.006	4	40.881	-71.263	0.691	0.063
	7	-	-		-0.328	-	-	0.108	-0.003	3	39.293	-71.174	0.779	0.060
	8	-0.353	-0.337		-	0.476	-	0.338	-0.009	5	42.428	-70.855	1.098	0.051
	9	-	-0.284		-	0.441	-	0.217	-0.006	4	40.659	-70.817	1.137	0.050
	10	-0.280	-		-	-	-	0.078	-0.002	3	38.950	-70.488	1.465	0.043
	11	-	-0.498		-0.287	0.511	0.352	0.441	-0.012	6	44.205	-70.410	1.544	0.041
	12	-	-		-	0.391	0.216	0.187	-0.005	4	40.264	-70.029	1.925	0.034
													sum of weights	0.720
Seagrass*	1	I	X	-0.449	I	0.444	0.549	0.422	0.422	5	-91.270	196.540	-	0.205
	2			-		-	0.592	0.186	0.186	3	-94.865	197.142	0.602	0.152
	3			-		0.269	0.432	0.258	0.258	4	-93.897	198.293	1.753	0.085
	4			-0.271		-	-	0.257	0.257	4	-93.912	198.324	1.784	0.084
													sum of weights	0.526

Table S2.3: Environmental parameters measured at each site during seagrass community sampling and on our coordinated effort on August 14, 2017 at 1 m and 4 m depth. BDL = below detection limit.

				Temperature (°C)			Nitrate (µmol)			Salinity (ppt)		
Site number	Date seagrass sampling	Mean sediment type score	Light availability	seagrass	1 m	4 m	seagrass	1 m	4 m	seagrass	1 m	4 m
1	7/24/2017	1.2	0.64	11.8	12.3	12.1	0.17	0.15	0.33	31.4	31.4	31.5
2	4/29/2017	1.6	0.62	8.0	14.0	14.1	0.18	0.58	0.25	28.0	30.6	31.0
3	6/24/2017	1.2	0.57	11.0	12.5	12.4	1.63	0.16	0.51	30.6	31.4	31.3
4	5/29/2017	1.3	0.54	10.3	13.6	12.8	0.94	0.30	2.43	30.9	30.6	31.4
5	7/25/2017	1.0	0.32	13.7	14.9	14	0.49	0.15	2.24	29.7	29.7	30.4
6	8/20/2017	3.1	0.57	12.9	13.3	13.3	2.15	0.08	1.00	30.6	30.3	30.7
7	6/25/2017	1.0	0.43	12.8	14.5	14.2	2.01	1.70	0.61	29.5	30.0	30.7
8	7/26/2017	3.5	0.76	16.6	12.4	12	0.80	2.62	0.13	31.5	32.0	33.0
9	5/25/2017	3.4	0.71	10.7	14.7	14.7	1.75	0.30	0.17	30.3	31.0	31.0
10	6/23/2017	1.0	0.64	13.5	14.0	12.4	2.79	0.46	0.05	28.0	29.0	31.0
11	6/22/2017	1.0	0.83	12.4	14.0	13.9	0.80	1.61	BDL	29.7	31.0	32.0
12	5/24/2017	3.3	0.46	10.0	14.0	13.8	0.10	2.63	BDL	24.3	31.0	32.0
13	7/22/2017	5.2	0.29	13.4	13.4	13.6	1.80	0.75	BDL	29.3	19.0	31.0
14	4/30/2017	2.9	0.47	10.0	14.3	13.7	0.38	0.42	0.93	30.0	24.0	32.0
15	5/26/2017	2.9	0.32	9.9	13.0	12.8	0.23	0.36	0.41	30.0	30.0	31.0
16	5/27/2017	4.0	0.48	11.1	14.1	13.7	0.51	0.71	0.72	30.9	28.0	32.0
17	8/21/2017	4.7	0.65	12.4	13.6	12.6	0.42	0.89	1.36	31.1	31.0	32.0
18	6/28/2017	4.6	0.37	12.5	13.4	12.7	0.80	0.42	1.64	29.8	27.0	31.0
19	6/27/2017	2.0	0.74	13.1	14.0	13.7	2.07	0.56	2.09	30.1	21.0	31.0
20	7/23/2017	3.8	0.55	12.4	12.9	12.2	0.77	0.74	1.27	28.7	29.0	32.0
21	8/22/2017	3.4	0.43	12.6	12.4	12.0	0.91	0.35	1.81	29.4	32.0	33.0

Table S2.4: Length – weight relationships for crab and fish species used in Eq. 2.1.

Common name	Scientific name	Family	a	b	Notes
Dungeness crab	*Metacarcinus magister*	Cancridae	0.00531	2.1949	Oftedal et al. 2007
Decorator crab	*Oregonia gracilis*	Oregoniidae	0.00882	2.1525	kelp crab (*Pugettia producta*) values used
Red rock crab	*Cancer productus*	Cancridae	0.00142	2.4625	Oftedal et al. 2007
Helmet crab	*Telmessus cheiragonus*	Cheiragonidae	0.00882	2.1525	kelp crab (*Pugettia producta*) values used
Graceful rock crab	*Metacarcinus gracilis*	Cancridae	0.00531	2.1949	Oftedal et al. 2007, dungeness crab used
Unknown rock crab		Cancridae	0.00337	2.3287	average of red rock and dungeness crab
Cabezon	*Scorpaenichthys marmoratus*	Cottidae	0.0291	3.0000	Froese et al. 2014
Slender cockscomb	*Anoplarchus insignis*	Stichaeidae	0.0039	3.1200	Froese et al. 2014
Pacific cod	*Gadus macrocephalus*	Gadidae	0.0095	3.1153	Gunderson and Dygert 1988, Nielsen 1992, Orlov et al. 2009
Dolly varden	*Salvelinus malma*	Salmonidae	0.0052	3.1150	Froese et al. 2014, Underwood et al. 1997
Starry flounder	*Platichthys stellatus*	Pleuronectidae	0.0109	3.1059	Froese et al. 2014
Kelp greenling	*Hexagrammos decagrammus*	Hexagrammidae	0.0156	3.0000	Froese et al. 2014
Masked greenling	*Hexagrammos octogrammus*	Hexagrammidae	0.0046	3.1300	Froese et al. 2014
Whitespotted greenling	*Hexagrammos stelleri*	Hexagrammidae	0.0031	3.4278	Froese et al. 2014
Crescent gunnel	*Pholis laeta*	Pholidae	0.0018	3.1500	Froese et al. 2014
Penpoint gunnel	*Apodichthys flavidus*	Pholidae	0.0018	3.1500	Froese et al. 2014
Pacific Herring	*Clupea pallasii*	Clupeidae	0.0067	3.1509	Froese et al. 2014, Park and Huh 2015
Lingcod	*Ophiodon elongatus*	Hexagrammidae	0.0133	3.0000	Froese et al. 2014
Shiner perch	*Cymatogaster aggregata*	Embiotocidae	0.0195	3.0200	Froese et al. 2014
Bay Pipefish	*Syngnathus leptorhynchus*	Syngnathidae	0.0002	3.1200	Bayer 1980
Pygmy poacher	*Odontopyxis trispinosa*	Agonidae	0.0039	3.1200	Froese et al. 2014
Sturgeon poacher	*Podothecus accipenserinus*	Agonidae	0.0039	3.1200	Froese et al. 2014
Tubenose poacher	*Pallasina barbata*	Agonidae	0.0039	3.1200	Froese et al. 2014
Walleye pollock	*Gadus chalcogrammus*	Gadidae	0.0195	2.8753	Froese et al. 2014
Snake prickleback	*Lumpenus sagitta*	Stichaeidae	0.0019	2.9900	Froese et al. 2014
Black rockfish	*Sebastes melanops*	Sebastidae	0.0211	3.0000	Froese et al. 2014
Brown rockfish	*Sebastes auriculatus*	Sebastidae	0.0102	3.0700	Froese et al. 2014
Copper rockfish	*Sebastes caurinus*	Sebastidae	0.0175	3.0000	Froese et al. 2014, Colton 2006
Quillback rockfish	*Sebastes maliger*	Sebastidae	0.0297	3.0000	Froese et al. 2014, Colton 2006
Unknown rockfish	*Sebastes sp.*	Sebastidae	0.0172	3.0492	and mean values of known *Sebastes sp.*
Chinook salmon	*Oncorhynchus tshawytscha*	Salmonidae	0.0133	3.0000	Froese et al. 2014
Chum salmon	*Oncorhynchus keta*	Salmonidae	0.0185	3.1000	Froese et al. 2014
Coho salmon	*Oncorhynchus kisutch*	Salmonidae	0.0112	3.0000	Froese et al. 2014

Table S2.4 continued

Pink salmon	*Oncorhynchus gorbuscha*	Salmonidae	0.0137	3.2500	Erokhin 1990
Pacific sand lance	*Ammodytes personatus*	Ammondytidae	0.0404	3.0060	Froese et al. 2014
Buffalo sculpin	*Enophrys bison*	Cottidae	0.0091	3.0900	Froese et al. 2014
Great sculpin	*Myoxocephalus polyacanthocephalus*	Cottidae	0.0125	3.1356	Froese et al. 2014 , Orlov 2009
Grunt sculpin	*Rhamphocottus richardsonii*	Rhamphocittidae	0.0100	3.0400	Froese et al. 2014 , Karpov and Kwiecien 1988
Longhorn sculpin	*Myoxocephalus octodecemspinosus*	Cottidae	0.0071	3.1300	Froese et al. 2014
Manacled sculpin	*Synchirus gilli*	Cottidae	0.0071	3.1300	Froese et al. 2014
Padded sculpin	*Artedius fenestralis*	Cottidae	0.0071	3.1300	Froese et al. 2014
Pacific staghorn sculpin	*Leptocottus armatus*	Cottidae	0.0400	2.8200	Froese et al. 2014, Ruiz-Campos et al. 2006
Sailfin sculpin	*Nautichthys oculofasciatus*	Hemitripteridae	0.0045	3.1100	Froese et al. 2014
Shorthorn sculpin	*Myoxocephalus scorpius*	Cottidae	0.0160	3.0560	Froese et al. 2014
Silverspotted sculpin	*Blepsias cirrhosus*	Hemitripteridae	0.0088	3.0278	Froese et al. 2014
Smoothhead sculpin	*Artedius lateralis*	Cottidae	0.0071	3.1300	Froese et al. 2014
Tidepool sculpin	*Oligocottus maculosus*	Cottidae	0.0071	3.1300	Froese et al. 2014
Pacific sanddab	*Citharichthys sordidus*	Paralichthyidae	0.0093	3.0800	Froese et al. 2014
Speckled sanddab	*Citharichthys stigmaeus*	Paralichthyidae	0.0071	3.1500	Froese et al. 2014
Butter sole	*Isopsetta isolepis*	Pleuronectidae	0.0091	3.0900	Froese et al. 2014
C-O Sole	*Pleuronichthys coenosus*	Pleuronectidae	0.0091	3.0900	Froese et al. 2014
English sole	*Parophrys vetulus*	Pleuronectidae	0.0091	3.0153	Froese et al. 2014 , Gunderson and Dygert 1988
Rock sole	*Lepidopsetta spp.*	Pleuronectidae	0.0206	2.8580	Froese et al. 2014
Threespine stickleback	*Gasterosteus aculeatus*	Gasterostaeidae	0.0114	3.1160	Froese et al. 2014, Ruiz-Campos et al. 2006
Tubesnout	*Aulorhynchus flavidus*	Aulorhynchidae	0.0004	3.4300	Bayer 1980
Brown Irish lord	*Hemilepidotus spinosus*	Hexagrammidae	0.0071	3.1300	Froese et al. 2014
Giant wrymouth	*Cryptacanthodes giganteus*	Cryptacanthodidae	0.0039	3.1200	Froese et al. 2014
Unknown sculpin		Cottidae	0.0138	3.0815	mean values of known Cottidae
Unknown flatfish		Pleuronectidae	0.0106	3.0657	mean values of known Pleuronectidae
Unknown greenling		Hexagrammidae	0.0077	3.1859	mean values of known Hexagrammidae
Unknown Myoxocephalus	*Myoxocephalus sp.*	Cottidae	0.0137	3.1018	mean values of known *Myoxocephalus sp.*
Unknown gunnel		Pholidae	0.0018	3.1500	mean values of known Pholidae
Unknown Artedius	*Artedius sp.*	Cottidae	0.0071	3.1300	mean values of known *Artedius sp.*

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Chapter 3: Sea otter effects on trophic structure of seagrass communities in Southeast Alaska[3]

Abstract

Community trophic structure is a function of both top-down and bottom-up forces and the energetic pathways transferring primary production to consumers. Seagrass communities are often characterized as being top-down controlled by invertebrate grazers and top predators through trophic cascades. Seagrass communities are also noted for their diverse sources of primary production and energetic pathways to consumers. In Southeast Alaska, sea otter (*Enhydra lutris*) abundance is positively related to seagrass (*Zostera marina*) biomass; however, the ecological connections in the hypothesized sea otter - seagrass trophic cascade are weak. This raises questions on both the trophic structure of Southeast Alaska seagrass communities and the extent to which sea otters affect seagrass trophic structure in the region. We addressed this question by comparing biomass, carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope (SI), and fatty acid (FA) data from 16 taxa at three sites with high (8.2 ± 4.2 sea otters/km^2) and three sites with low (0.01 ± 0.02 sea otters/km^2) sea otter density. We found lower crab and clam biomass in the high sea otter region but little difference between regions in other seagrass community constituents. Stable isotopes indicated similar overall isotopic niche space between sea otter regions. Two taxa differed in $\delta^{13}C$ between sea otter regions, and seven species differed in $\delta^{15}N$. Fatty acid analysis suggested multivariate dissimilarity in 14 of the 16 conspecifics between sea otter regions. Several essential FA, including 20:5ω3 (EPA) and 22:6ω3 (DHA), were common in discriminating conspecifics, suggesting subtle differences in energetic pathways between regions. The sum of our results suggest that sea otters may have a strong effect on the abundance of certain species, which does not translate to a large difference in energy flow among

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community constituents, but rather provides nuanced evidence for differing trophic structure between sea otter regions. These results highlight the complex trophic dynamics in seagrass communities not necessarily evident from biomass and SI data alone.

3.1 Introduction

Seagrass ecosystems support diverse communities that are considered to be primarily structured by top-down forces (Duffy et al. 2014). The consumption of seagrass epiphytes by invertebrate epifauna (“grazers”) is, on average, stronger than the bottom-up forces of nutrients, leading to positive indirect effects of herbivores to seagrass (Hughes et al. 2004, Valentine and Duffy 2006, Heck and Valentine 2007). In seagrass, *Zostera marina*, communities the top-down forcing from grazers appears relatively consistent around the world suggesting consistent structuring forces regardless of region (Duffy et al. 2015). Such strong interactions are not limited to lower trophic levels. Grazers may be consumed by mesopredators, such as fishes and crabs, which can modulate their top-down effect on epiphytes (Duffy et al. 2005, Douglass et al. 2007, Lewis and Anderson 2012). In systems with dominant apex predators, yet another level of trophic control can be added. Apex predators can control mesopredator abundance, which can cascade down the food web and lead to overall positive indirect effects from apex predators to seagrass (Moksnes et al. 2008, Baden et al. 2010, Hughes et al. 2013). The studies that have informed these conclusions usually rely on relative biomass or abundance comparisons to describe these trophic controls. While an intuitive and time-tested metric of trophic ecology, biomass, considered alone, may mask weak interactions among taxa, therefore skewing our perspective of trophic structure.

Trophic biomarkers such as stable isotopes (SI) and fatty acids (FA) can provide an alternative perspective on trophic structure by focusing on energetic pathways. Biomarkers can reflect the diet of a consumer, and investigations into the trophic structure of communities often rely on trophic biomarkers to assess the dietary resources and trophic level of a given species or a community at large (Peterson et al. 1985, Peterson 1999, Dalsgaard et al. 2003, Kelly and Scheibling 2012). Biomarkers can reveal ecosystem dynamics not necessarily evident from traditional biomass measures or abundance data alone. For example, the combination of stable isotope and biomass data from eutrophic and non-eutrophic seagrass communities revealed both a difference in biomass of some primary producers and consumers and a difference in overall trophic structure as measured by isotopic niche space (Thormar et al. 2016). Common biomarkers include the SI of carbon and nitrogen, as well as FA. The ratio of the stable isotope of carbon, ^{13}C to ^{12}C, is commonly used to reflect the ultimate energy source of consumers at a coarse resolution and is assumed to change little with trophic level (Peterson and Fry 1987). Conversely, the ratio of the SI of nitrogen, ^{15}N to ^{14}N, enriches with consumption, making it a useful measure of the relative trophic position of species and food chain length (Cabana and Rasmussen 1996, Layman et al. 2007).

Fatty acids are particularly useful biomarkers in benthic aquatic ecosystems because many aquatic primary producers have distinct FA signatures (Kelly and Scheibling 2012, Galloway et al. 2012, Galloway and Winder 2015). Certain FA, especially highly unsaturated fatty acids (HUFA) and polyunsaturated fatty acids (PUFA), are only synthesized *de novo* in biologically relevant amounts by primary producers, and therefore consumers must obtain them from their diet (Brett and Müller-Navarra 1997, Kelly and Scheibling 2012). Furthermore, many C_{18} PUFA are found in relatively high proportions in benthic sources of primary production, such as seagrasses and brown and green algae (Galloway et al. 2012). Therefore, these and other "essential fatty acids" (EFA) can serve as dietary tracers in benthic food webs and can help reveal trophic relationships that may not be apparent by biomass comparisons alone. These FA, and the tight link of specific FA to certain primary producers, can provide detail on the diets of consumers not possible with SI. Therefore, the combination of relatively coarse resolution SI and finer resolution FA biomarkers in the same study can build a more comprehensive understanding of consumer diets, especially in systems with many possible food sources (e.g. Jankowska et al. 2018). This approach has been used in a variety of ecosystems, including nearshore planktonic communities (Lowe et al. 2014), nearshore suspension-feeder diets (Allan et al. 2010), kelp-dominated benthic communities (Galloway et al. 2013), and seagrass communities (references below), to help reveal trophic dynamics not necessarily apparent by just one measure alone.

The trophic structure of seagrass communities has been investigated using SI and FA trophic biomarker approaches in a variety of regions. These studies indicate complex food webs, where many consumers show evidence of diverse ultimate energy sources, including macroalgae, epiphytes (macro and microalgae) and bacteria (Kharlamenko et al. 2001, Alfaro et al. 2006, Jaschinski et al. 2008, Jephson et al. 2008, Douglass et al. 2011, Thormar et al. 2016, Jankowska et al. 2018). Both SI and FA data support the top-down control hypothesis that grazers are important for controlling epiphytic and ephemeral macroalgae, and that seagrass biomarkers are only found in very small amounts or not at all in grazers or higher consumers (Alfaro et al. 2006, Jaschinski et al. 2008, Jephson et al. 2008, Thormar et al. 2016, Jankowska et al. 2018). SI analyses on entire seagrass communities indicate that trophic structure can vary with abiotic conditions (Thormar et al. 2016) or top-down forces (Jephson et al. 2008), and that mesopredators, such as crabs and fishes, often consume a diverse diet (Douglass et al. 2011).

Many common seagrass community consumers, such as gastropods, bivalves, and crabs, have high proportions of FA that are common in bacteria, suggesting consumption of detrital food sources (Kharlamenko et al. 2001, Alfaro et al. 2006, Jankowska et al. 2018). Taken together these biomarker studies indicate that the trophic structure of seagrass communities may be affected by top-down forcing, bottom-up forcing or a combination of the two. Given the complexity in dietary sources and structuring forces, any single metric of trophic structure may omit underlying trophic pathways and food sources essential for functioning of seagrass communities.

Most research on the structure of seagrass communities has focused on biomass-driven comparisons of lower trophic levels (Duffy et al. 2014). Multiple reviews of the literature and meta-analyses describe seagrass communities as being structured by top-down forces, namely through herbivory of seagrass epiphytes by invertebrate grazers (Hughes et al. 2004, Heck and Valentine 2007, Duffy et al. 2014). However, the role of higher-order predators has recently gained more attention. Hughes et al. (2013) documented how the return of sea otters (*Enhydra lutris*) to Elkhorn Slough, CA triggered cascading top-down effects that altered seagrass community structure. Other top predators in seagrass communities, such as cod (*Gadus morhua*) in the Baltic Sea, can drive trophic cascades (Jephson et al. 2008, Moksnes et al. 2008, Baden et al. 2010, 2012). In Chapter 2, myself and co-authors tested the generality of these patterns in Southeast Alaska and found evidence for a positive relationship between sea otters and seagrass and predicted, albeit weak, direct relationships among epifauna, epiphytes, eelgrass, and nitrate. In Chapter 2 we did not find a relationship between crabs or fish and epifauna (including grazers), an essential step in the trophic cascade described in Elkhorn Slough, CA and the Baltic Sea. These results suggest that while some of the forces present in the linear trophic cascade are present at some level, other relationships may also be present in Southeast Alaska seagrass communities that may influence community and trophic structure.

In summary, studies using biomass metrics generally describe seagrass communities as top-down controlled, in contrast to studies using biomarkers that largely characterize seagrass communities as having diverse primary energy sources and consumer diets. These two perspectives reveal different attributes of food webs. Biomass patterns may be more indicative of species interactions, while biomarkers reveal energetic pathways that originate from primary producers. Here, we use biomass and biomarkers to describe and compare the trophic structure of seagrass (*Zostera marina*) communities in Southeast Alaska in regions of high and low sea otter density. This approach allows us to build a comprehensive picture of seagrass community trophic structure from both the species interactions (biomass) and energetic pathways (biomarkers) perspectives. Specifically, we evaluated whether biomass, SI of carbon (^{13}C) and nitrogen (^{15}N), whole FA profiles, and specific classes of FA of the primary producers and consumers differed within conspecifics between regions with high and low sea otter density. Biomass data provide a classic ecological metric to compare to previous studies and to contextualize the biomarker data. SI and FA data were used to compare the primary carbon sources, relative trophic level, food chain length, and primary dietary sources of conspecifics.

We hypothesize that differences in conspecific biomass would follow results from Chapter 2 and from other studies on the effect of sea otters on clam and crab communities (Kvitek et al. 1992, Hughes et al. 2013, Hoyt 2015), where sea otters have a positive relationship with seagrass and a negative relationship with clam and crab biomass. In contrast to biomass data, we hypothesize that conspecific consumer biomarker values will not differ between sea otter regions because we do not expect sea otters to drive variation in primary producer biomarkers. Alternatively, if we do observe conspecific differences in biomarker values, we hypothesize that three factors could lead to these differences. First, conspecific primary producer biomarkers may differ between sea otter regions leading to differences in consumers. Second, the presence of sea otters could alter the diet of consumer conspecifics between regions. For example, if sea otters greatly reduce clam abundance, that may reduce or eliminate that food source to other consumers like crabs. Finally, any differences could be the result of natural variability in conspecific biomarkers as a result of variability in diet sources and/or relative proportions. Given the consistency in environmental conditions across the study area (Chapter 2), we do not expect biomarker differences in primary producer conspecifics between sea otter regions. However, we acknowledge that SI and FA values can vary across time and space (Guest et al. 2010, Dethier et al. 2013). We are particularly interested in tracking patterns of essential fatty acids (EFA) of consumers between sea otter regions, as EFA may be the best indicators of different diets of conspecifics.

3.2 Methods

3.2.1 Study area

Our study took place on the west coast of Prince of Wales Island in southern Southeast Alaska, USA (Fig. 3.1). Southeast Alaska contains over 10,000 km of seagrass shoreline (Harper and Morris 2004, NOAA 2019), primarily in protected, soft-sediment shorelines composed of eelgrass (*Z. marina*, hereafter 'seagrass'), surfgrass (*Phyllospadix serrulatus*) and a mixture of the two (Stephens et al. 2019). Seagrass beds in the region are often in close proximity to other habitats, such as canopy and understory kelp forests, sand flats, and estuaries, creating a mosaic of nearshore habitats (NOAA 2019). Southeast Alaska is home to a large sea otter population, which after near extinction from the maritime fur trade has expanded to an estimated population of over 25,000 individuals (USFWS 2014, Tinker et al. 2019). Sea otters are unevenly distributed across Southeast Alaska, including Prince of Wales Island, creating a heterogeneous seascape of sea otter occupation time, abundance, and population status with respect to estimated carrying capacity (USFWS 2014, Tinker et al. 2019). We identified six study sites, three in a region of high sea otter occupation and three in a region of low sea otter occupation (described further below), all sites with similar seagrass bed size, underlying substrate, and exposure. At each site, we measured the biomass of major seagrass community constituents and collected tissue samples for SI and FA analysis (Fig. 3.1, Table S3.1).

3.2.2 Sea otter occupation

We used U.S. Fish and Wildlife Service aerial sea otter surveys (USFWS 2014) paired with a recent analysis of these survey data (Tinker et al. 2019) to identify areas of high and low sea otter density. We supplemented these measures with two replicate boat-based sea otter surveys at each site. These surveys were conducted following methodology described in Chapter 2. Briefly, we counted all sea otters within a 3.4 km radius (over water distance) of each site twice between June and August 2018. Sea otter counts were converted to density based on the total water area surveyed for each site.

3.2.3 Biomass

In July 2018 at each site, we surveyed the seagrass community including measurements of seagrass, seagrass epiphytes, seagrass-associated invertebrate epifauna, clams, crabs, fishes and particulate organic matter (hereafter ‘POM’) (Table 3.1). At each site we placed one 100 m transect in the seagrass meadow at least 5 m linear distance below the upper edge of the continuous seagrass meadow and at least 10 m from the edge of the meadow at approximately -0.6 m mean lower low water (MLLW) tidal elevation. Along the transect we counted seagrass shoot density in eight 0.5 m × 0.5 m evenly spaced quadrats. We characterized the primary sediment type in each quadrat using a qualitative scoring system ranging from soft to hard substrates (1 - mud to 10 - bedrock; see Chapter 2). Scores were averaged across the transect at each site. Adjacent to each quadrat we conducted a grab sample to collect seagrass and associated epifauna. The grab was accomplished by affixing a 400 µm mesh bag measuring approximately 28 cm × 60 cm to a 0.018 m^2 circular metal ring. The ring and bag were carefully lowered over the seagrass and the seagrass was cut at the sediment interface. The bag was inverted and brought to the surface taking care to avoid loss of eelgrass or associated grazers. Collection bags were placed in coolers until further processing later that day.

We processed seagrass collection bags in the laboratory to quantify biomass of seagrass, epiphytes, and epifauna. Collection bags were emptied into trays and gently rinsed with fresh water to release epifauna. Epiphytes from individual seagrass leaves were collected on pre-dried and weighed cotton pads. Epifauna were grouped into the following taxonomic groups: the isopod *Pentidotea resecata*, limpet *Lottia parallela* and all other epifauna including gammarid amphipods (Suborder Gammaridea), caprellid amphipods (Family Caprellidae) and other gastropods (primarily *Lacuna* sp. and *Littorina* sp.). Seagrass leaves, epiphytes and epifauna from each grab sample were dried for at least 24 h at 60° C and weighed to the nearest 0.0001 g. For analysis, seagrass leaf mass was converted to mass per square meter by multiplying mass measured in our sampling ring by 55.55. Epiphyte and epifauna mass were converted to epiphyte and epifauna load defined as grams of epiphyte or epifauna per gram of seagrass in each grab sample, and averaged for each site. For analysis, epifauna were grouped as total epifauna load, *Pentidotea* load, and limpet load.

We measured clam abundance, species composition and biomass by digging eight 0.25 m × 0.25 m × 0.25 m pits evenly spaced along a 100 meter transect at approximately 0 m MLLW at each site (Table 1). Clams and sediment were passed through a 1 cm sieve and all retained clams were identified to species and measured to the nearest mm. Clam lengths were converted to biomass using species-specific conversion coefficients (Table S3.2) using Equation 3.1, where m is clam width and a and b are conversion factors. Clam density (g/m^2) was calculated for each species and for the total clam assemblage and averaged for each site.

$$mass(g) = a \times m_{taxa}(cm)^b \text{ (3.1)}$$

We found a variety of clam species but focused analyses on total clam mass, as well as mass and tissue samples (below) from butter clams (*Saxidomus giganteus*) and *Macoma* spp. clams, which were the most dominant taxa by biomass.

We measured relative crab abundance, species composition and biomass by setting four strings of two crab pots each at approximately -3 m MLLW for 24 h at each site (Table 3.1). Each string consisted of one 61 cm × 61 cm × 33 cm pot with 10 cm × 10 cm wire mesh and four 20 cm openings, and one “Fukui” type pot measuring 60 cm × 45 cm × 20 cm with 1 cm × 1 cm fabric mesh with two 20 cm openings. All pots were baited with approx. 0.5 l of chopped herring. Upon collection all crabs were identified to species, and we measured carapace width to the nearest mm. Carapace widths were converted to biomass using species-specific conversion factors (Table S3.2) using Equation 3.1 above, where m is carapace width. Total and species-specific crab biomass were summed for each string and then averaged across the four strings at each site.

We measured fish abundance and species composition in terms of numbers and biomass following methods described in Johnson et al. (2012) (Table 3.1). Fish were captured using a 37 m variable-mesh beach seine. Outer panels were 10 m sections of 32 mm mesh, intermediate panels were 4 m sections of 6 mm mesh, and the center panel was 9 m section of 3.2 mm mesh. The seine tapered from 5 m tall at the center to 1 m tall at the ends to conform to the shape of the beach slope when set. The seine was set as a round haul by holding one end on the beach while backing around the other end in a small boat to the beach approximately 18 m from the start. Once the seine was pulled onshore the catch was sorted, identified to species, counted and a subsample (up to 30 fish) of each species was measured to the nearest mm (fork length). For species with more than 30 individuals, we counted all remaining members of that species. These unmeasured fish were assigned lengths in proportion to the size-frequency distribution of measured fish of that species at the same site. Fish lengths were converted to biomass using species specific length–weight conversions coefficients (Table S3.2) and Equation 3.1 above, where m is fork length. We searched the FishBase (www.fishbase.org) database and other literature for published length-weight conversion coefficients. Species that did not have any published values, and/or species that we were only able to identify to genus or family in the field, were assigned conversion factors first based on the congeners, or if not available, based on other species with similar overall body plans (e.g., fusiform). Once all coefficients were compiled, we calculated the mean of each factor for each species, if applicable, and assigned a single a and b value to each species.

Particulate organic matter was measured from three replicate oblique plankton tows at each site using a 0.5 m diameter, 20 μm mesh plankton net (Table 3.1). The net was dropped to a depth of 5 m and then slowly raised to the surface over the period of one minute at horizontal speed of approximately 1 m/s. Once at the surface the net was raised and rinsed to collect all material in the cod end. One hundred ml of the collected water was filtered through pre-burned (400° C for 4 hours) and weighed 0.4 µm Whatman GF/F filters to calculate the proportion of organic matter. Filters with retained material were frozen at -20° C until later processing. Filters were dried at 60° C for 24 hours then at 400° C for four hours and weighed to calculate proportion organic matter. POM biomarker samples were obtained by filtering seawater collected from the plankton tow through separate filters until a visible layer formed on the filter (150 – 400 ml seawater). This layer was scraped off and saved for biomarker processing described below. We were only able to obtain one tow and one POM biomarker sample at site H3 due to a conspicuous coccolithophore bloom. Our seawater sample from this water mass quickly clogged (< 50 ml) our filtering apparatus rendering further POM operations at that site infeasible. See further description of this bloom event in Results.

Concurrent with POM sampling we collected environmental parameters at each site. We used an YSI Pro2030 meter to measure water temperature (°C), salinity (ppt) and dissolved oxygen (mg l^{-1}) at 1 m and 5 m depths. With a LI-COR LI-193R spherical quantum sensor, we measured photosynthetic active radiation (PAR, as µmol s^{-1} m^{-2}) at the surface (air) and at 1 m and 5 m depth water depth. We calculated the percent of light transmittance as the percent of PAR measured at 5 m divided by PAR measured at 1m. We collected 50 ml of seawater at 1 and 5 m depths for nitrate and phosphate concentration analysis. Seawater was immediately filtered through a 0.4 µm Whatman GF/F filter into sample vials and then frozen at -20° C for approximately one month and then at -80° C until nutrient analyses were conducted on March 28, 2019 using an Astoria Pacific Analyzer at University of Alaska Southeast.

3.2.4 Biomarker sampling and processing

Given that SI and FA values can vary across relatively small spatial and time scales (Guest et al. 2010, Dethier et al. 2013), our tissue sample scheme was designed to (1) collect tissue samples within the smallest time window possible, especially for a given taxon, (2) balance capturing biomarker variability within and among sites (e.g. Galloway et al. 2013), and (3) balance logistical constraints in each sea otter density region. Our goal was to obtain two replicate tissues samples for each taxon from each site in each sea otter region, for a total of six tissue samples in each sea otter region and twelve tissue samples for each taxon. For all biomarker comparisons we did not test for site effects, rather our emphasis is on any difference between sea otter regions. Due to logistical constraints, we were not always able to meet this sample size goal, leading to an imbalance in sample sizes within some taxa (Table 3.1).

We collected species for biomarker sampling that represented the trophic range of organisms found in Southeast Alaska seagrass meadows, are relatively common and are important components of the hypothesized sea otter—seagrass trophic cascade at each site described above (Table 3.1). We selected species that fell into three general categories: primary producers, primary consumers and secondary consumers. Whenever possible, we collected the same species at all sites. For primary producers, we collected seagrass (*Z. marina*), seagrass epiphytes consisting primarily of diatoms (Class = Bacillariophyceae), POM, rockweed *Fucus distichus* (hereafter *Fucus*), sugar kelp (*Saccharina latissima*) and sea lettuce *Ulva* sp. (hereafter *Ulva*). For primary consumers, we collected the isopod *Pentidotea rascata* (hereafter *Pentidotea*), eelgrass limpets (*Lottia paralella*), butter (*Saxidomus giganteus*) and *Macoma* spp. clams. For secondary consumers we collected dock shrimp (*Pandalus danae*), helmet crabs (*Telmessus cheiragonus*), graceful crabs (*Metacarcinus gracilis*), red rock crabs (*Cancer* *productus*), shiner perch (*Cymatogaster aggregata*), snake prickleback (*Lumpenus sagitta*) and Pacific staghorn sculpin (*Leptocottus armatus*). The tissue or tissues sampled from each species varied with regard to the organism's size and body plan. Seagrass and macroalgae tissues were collected distal from meristematic regions, to avoid relatively older or fouled tissues. Animal tissues included all soft body tissues (excluding shell) of limpets, foot muscle tissue from clams, whole *Pentidotea*, leg muscle tissue from crabs and dorsal muscle tissue from fish. Tissue samples were frozen at -20°C for one month and then at -80°C for five months. Samples identified for biomarker analysis were lyophilized for 48 hours and stored at -80°C until further processing. For both SI and FA analysis, lyophilized tissues were ground to a fine powder with mortar and pestle. This processes also served to homogenize pooled samples (Table 3.1).

We determined carbon and nitrogen SI ratios using the procedures of the NOAA Auke Bay Laboratories - Fisheries Recruitment Energetics and Coastal Assessment Chemistry Laboratory in Juneau, Alaska described below. Subsamples of ground tissues (approx. 1.0 mg) were weighed with a microbalance and placed into tin capsules for analysis. SI analysis was performed using a FlashSmart elemental analyzer coupled to a Delta V continuous-flow isotope ratio mass spectrometer (Thermo Scientific, Waltham, Massachusetts, USA). SI are reported in delta (δ) notation as the per mille of the ratio of heavy to light isotope relative to international standard of Vienna Peedee Belemnite for carbon and atmospheric nitrogen for nitrogen. The instrument was calibrated using certified reference materials from the International Atomic Energy Agency and the U.S. Geological Survey. Internal laboratory standards (purified methionine and homogenized Chinook salmon muscle) were used as quality controls and yielded long-term precision estimates of ±0.12 ‰ for carbon and ±0.13 ‰ for nitrogen (M. Rogers, NOAA, Juneau, *personal communication*).

Fatty acids were extracted and analyzed with gas chromatography coupled with mass spectrometry from ground tissues following methods found in Yoshioka et al. (2019) which are modified from Taipale et al. (2013, 2016). All FA analyses were conducted at the Oregon Institute of Marine Biology (OIMB) in Charleston, Oregon. Following lyophilization, samples of each tissue were homogenized, lipid extracted and transesterified to produce FA methyl esters (FAME) for analysis (Taipale et al. 2016). During the initial lipid extraction, we added C19:0 as an internal standard to each sample. To extract total lipids, homogenized tissue samples were digested in a 4:2:1 chloroform:methanol:0.9% NaCl solution twice. From the resulting pooled organic layers, 1 ml was removed for transesterification, evaporated under N_2 flow, and the organics were re-suspended in a toluene and 1% sulfuric-acid methanol solution and maintained at 90°C for 90 min to trans-esterify FAME. FAME solutions were then neutralized with 2% $KHCO_3$, diluted with hexane, vortexed and centrifuged before carefully transferring the FAME layer to 2 ml glass vials for gas chromatography. FAME dissolved in hexane were analyzed, identified and quantified using gas chromatography mass spectrometry following Taipale et al. (2016). We quantitatively measured FAME concentrations using a serial dilution of a mixed external FA standard (Nu-chek Prep 566C) and calculated relative proportions of each identified FA from the area under each sample peak.

3.2.5 Statistical analyses

To test for a difference in trophic structure, we compared biomass, SI and FA data between regions with high and low sea otter density for all but three taxa. We were not able to obtain tissues from red rock crabs in the high sea otter region, so we were unable to present conspecific comparisons of red rock crab SI and FA. We present only biomass and FA data for limpets because we had trouble obtaining consistent SI values from those tissues. Finally, we did not obtain biomass estimates of dock shrimp across sites; however, they were abundant where we collected individuals for tissue samples (Table 3.1).

We compared conspecific biomass using linear mixed effects models with a fixed effect of sea otter region, with the high sea otter region as the reference group, and site as a random effect. As only one beach seine set was conducted per site, we did not include a random effect of site for total and species-specific fish biomass. Biomass data were transformed such that the residuals were approximately normal. The proportion of organic matter of POM is constrained between zero and one, so we applied an arcsine-square root transformation to these data. We natural log transformed seagrass biomass and total fish biomass. We square root transformed epiphyte load, epifauna load and helmet crab biomass; cube-root transformed limpet load, total clam density and red rock crab biomass; and fourth-root transformed *Pentidotea* load, *Macoma* spp. density, total crab, and graceful crab biomass, and shiner perch, snake prickleback, and staghorn sculpin biomass. Butter clam density was not transformed. We note that biomass responses for limpets, butter clams, helmet crabs, graceful crabs and red rock crabs included multiple measures of zero biomass; however, our transformations were aimed at normalizing positive values. Given that the inclusion of zeros resulted in minor normality violation and that zeros were not distributed across all sites and sea otter regions, we proceeded to fit standard linear mixed effects models. All models were fit and assessed in R (v3.5.1) (R Core Team 2018).

We analyzed $\delta^{13}C$ and $\delta^{15}N$ data in two ways. First, we compared the overall seagrass community isotopic niche space between the two sea otter regions (Layman et al. 2007) using the 'convexhull' function in the siar package in R (Parnel and Jackson 2013) on mean $\delta^{13}C$ and $\delta^{15}N$ values for each taxon and by plotting $\delta^{13}C$ and $\delta^{15}N$ values in a bi-plot. This analysis provided an overall comparison of the breadth of carbon source and food chain length of each seagrass community. Second, we directly compared mean $\delta^{13}C$ and $\delta^{15}N$ values of conspecifics between high and low sea otter regions using t-tests. Unlike biomass analyses, we did not fit mixed effects models with a random site effect due to a lack of site level replication for some taxa (above) leading to model convergence issues, reflecting an inability to separate among-site variability from within-site variability. This analysis would indicate differences in ultimate carbon source through $\delta^{13}C$ and relative trophic position through $\delta^{15}N$. We recognize that performing multiple t-tests on our SI dataset may increase the probability of type-I errors; however, we elected to not correct for multiple comparisons and present t-statistics and p-values in their raw form (Moran 2003). Initial analysis revealed that the $\delta^{13}C$ value of POM collected at site H3 was highly enriched (-1.59‰) compared to all other POM samples (mean = -18.98 +/- 0.80 SD), likely due to the presence of a coccolithophore bloom (see Results). For this reason, we excluded this sample from SI and FA analysis; however, we recognize the potential of this water mass to influence our results (see Discussion).

Analyses of FA profiles for each taxon were split into three stages including PERMANOVA to compare profiles between sea otter regions, similarity percentage analysis (SIMPER) to identify FA important to discriminating between sea otter regions, and direct comparison of specific FA and FA groups. Before these analyses we filtered all FA identified from gas chromatography to those unique FA with a mean proportional peak area ≥ 0.5% for a given taxon. This resulted in 42 FA on which we conducted FA analyses. First, we used PERMANOVA to test the effect of sea otter region on whole FA profiles of each taxon except red rock crabs. Second, for those taxa whose FA profiles differed significantly between sea otter regions (PERMANOVA, $p < 0.05$), we conducted SIMPER analysis. SIMPER ranked FA on their individual contribution to multivariate discrimination and therefore could highlight ultimate energy sources and trophic pathways in the community. Finally, we summarized the proportion of eight FA or FA groups commonly used to describe trophic relationships and dietary variability among consumers. We were particularly interested if EFA contributed to dissimilarity between sea otter regions. Essential fatty acids defined here as PUFA with greater than 18 carbon atoms, these FA must be obtained from a consumer's diet. Therefore, differences in EFA proportions within a taxon would suggest differences in diet between sea otter regions.

FA and FA groups (Table 3.2) were based on previous studies of benthic community FA markers and similar seagrass trophic structure studies. FA composition of seagrass-associated species that indicate high proportions of FA known to be produced by bacteria suggests that bacterial/detrital energy pathways may be an important aspect of seagrass food webs (Kharlamenko et al. 2001, Alfaro et al. 2006, Jaschinski et al. 2008, Jankowska et al. 2018). The C_{18} polyunsaturated fatty acids (PUFA) 18:3ω3 (alpha-linolenic acid = ALA) and 18:2ω6 (alpha-linoleic acid = LIN) are highly abundant in vascular plants including seagrass, *Z. marina*, and therefore may serve as a marker for the consumption of seagrass (Kharlamenko et al. 2001, Alfaro et al. 2006, Kelly and Scheibling 2012, Galloway et al. 2012, Jankowska et al. 2018). The monounsaturated FA 16:1ω7 (palmitoleic acid = PAL) is considered a marker for diatoms (Dalsgaard et al. 2003, Kelly and Scheibling 2012, Galloway et al. 2012). The proportion of the PUFA 20:4ω6 (arachidonic acid = ARA) was examined, as it is considered a marker for brown and red algae (Kelly and Scheibling 2012, Galloway et al. 2012) and could suggest alternative dietary sources among consumers compared to the seagrass, bacteria, diatom and dinoflagellates. The PUFA 20:5ω3 (eicosapentaenoic acid = EPA), and 22:6ω3 (docosahexaenoic acid = DHA) are considered biomarkers for diatoms and dinoflagellates, respectively. It is important to note that most of these PUFA discussed above are present in varying levels in multiple producer groups and are not truly discreet source biomarkers. Diatom mats and films are common in Southeast Alaska seagrass beds and are the predominant seagrass epiphyte. Furthermore, diatoms can be a predominant food source to seagrass community epifauna and clams (Kharlamenko et al. 2001, Alfaro et al. 2006, Jephson et al. 2008, Thormar et al. 2016, Jankowska et al. 2018). Alternatively, dinoflagellates can be consumed by filter feeders and planktivorous fishes that are common in Southeast Alaska eelgrass beds. EPA and DHA are also considered indicators of changes in trophic structure in aquatic systems (Müller-Navarra et al. 2000, Litzow et al. 2006).

We compared the mean proportion of these FA and FA groups for each taxon between sea otter regions using Mann-Whitney U tests, which are robust to non-normal distributions such as proportion data. PERMANOVA of FA were performed on Euclidean distances of arcsine-square root transformed proportional FA data, as is common for such datasets (e.g. Raymond et al. 2014, Yoshioka et al. 2019). PERMANOVAs were conducted using the 'adonis2' function in the vegan package (Oksanen et al. 2019) using 9999 permutations. SIMPER analysis was performed on untransformed FA proportions using the 'simper' function in the vegan package (Oksanen et al. 2019) using 9999 permutations. All analyses were performed in R v.3.5.1 (R Core Team 2018).

3.3 Results

3.3.1 Sea otter occupation

Boat-based sea otter counts indicated higher sea otter densities in concordance with USFWS surveys (USFWS 2014) and estimated sea otter density in the region (Tinker et al. 2019) (Table S1). Mean boat-based sea otter density at high sites was 8.2 individuals km^{-2} (± 4.2 SD) compared to 0.01 individuals km^{-2} (± 0.02 SD) at low sites. Estimated sea otter density from historical USFWS surveys in the vicinity of high sites was 3.633 km^{-2} and 0.163 km^{-2} for low sites (Tinker et al. 2019) (Table S3.1). Sea otter densities measured for this study were similar to those measured in 2017 in the same region (Chapter 2).

3.3.2 Environmental parameters

Environmental parameters varied little between sea otter regions and were similar to previous studies in the region (Chapter 2). Since our environmental sampling consisted of point measurements at each site, replication within each sea otter region was only three for each parameter. Therefore, we elected not to conduct statistical comparisons of environmental parameters but out data are reported in full here (Table S3.1; Fig. S3.1). We consider these environmental parameters to be fairly similar across sites, especially considering the dynamic nature of nearshore ecosystems, with at least one exception. While variable, water nitrate concentrations appeared to be greater in the high sea otter region with a mean of 0.025 µmol/L (+/- 0.017 SD) at 1 m and 0.032 µmol/L (+/- 0.027 SD) at 5 m, compared to a mean of 0.007 µmol/L (+/- 0.008 SD) at 1m and 0.015 µmol/L (+/- 0.004 SD) at 5 m across low sea otter region sites (Fig. S1d). However, nitrate concentrations in the present study were lower than those observed in Chapter 2 (0.08 – 2.79 µmol/L), which measured nitrate concentration across 21 sites on the west coast of Prince of Wales Island. We note that during our data collection a large coccolithophore bloom occurred across much of western Prince of Wales Island that lasted for much of the month of July. All study sites were outside of the visible bloom for all sampling activities, except site H3 during POM and environmental data collection and collection of butter clams for biomarker analysis. The coccolithophore bloom noticeably reduced water clarity, therefore increasing the variability in percent light transmittance at high sea otter region sites (Table S1; Fig. S1g).

3.3.3 Biomass

Biomass differed between sea otter regions for a few taxa, including total clam biomass, butter clam biomass, total crab biomass and red rock crab biomass (Table 3.3; Fig. 3.2). Total clam and butter clam biomass were lower in the high sea otter region ($p = 0.007$, $p = 0.032$; Fig. 3.2g, h). Similarly, total crab and red rock crab biomass were lower in the high sea otter region ($p = 0.004$, $p < 0.001$; Fig. 3.2j, m). We did not find evidence of an effect of sea otter density region on seagrass biomass, epiphyte load, POM percent organic matter, epifauna, *Pentidotea*, and limpet load, *Macoma* spp. biomass, graceful and helmet crab biomass, total fish, staghorn sculpin, shiner perch, and snake prickleback biomass (Table 3.3). We did find greater within-site variation than among-site variation of seagrass biomass, epiphytes, limpet load, total, butter, and *Macoma* spp. clam biomass, and graceful and helmet crab biomass (Table 3.3).

3.3.4 Stable isotopes

Convex hull isotopic niche area in the high sea otter region was 42.853 compared to 48.241 in the low sea otter region. This represented an 11% greater isotopic niche area in the low sea otter region than the high sea otter region (Fig. 3.3a). $\delta^{13}C$ values of primary producers ranged from -18.12‰ to -7.50‰ in the high sea otter region and from -19.55‰ to -8.20‰ in the low sea otter regions, suggesting a similar breadth of dietary sources between the two regions. $\delta^{15}N$ of all taxa ranged from 6.18‰ to 14.00‰ in the high sea otter region and from 5.69‰ to 13.45‰ in the low sea otter region, suggesting similar food chain length between the regions.

We found conspecific differences in $\delta^{13}C$ and $\delta^{15}N$ between sea otter regions for multiple taxa (Table S3; Fig. 3.3b, c). Among primary producers we found more depleted $\delta^{13}C$ values of POM in the low sea otter region (Fig. 3.3b; $p < 0.001$). There were no differences in $\delta^{13}C$ among primary consumers but we did find more depleted $\delta^{13}C$ in the secondary consumer staghorn sculpin in the high sea otter region (Fig. 3.3b; $p = 0.021$). We found differences in $\delta^{15}N$ in seven of our 15 taxa, ranging from primary producers to secondary consumer (Table S3.3; Fig. 3.3c). There were more depleted $\delta^{15}N$ values in the low sea otter region in POM, *Fucus*, sugar kelp, dock shrimp and shiner perch ($p < 0.001$, $p = 0.031$, $p = 0.010$, $p = 0.044$, $p = 0.015$, respectively) and more enriched $\delta^{15}N$ values in the low sea otter region in seagrass epiphytes and butter clams ($p = 0.054$, $p < 0.001$, respectively).

3.3.5 Fatty acids

We found evidence for differences in the FA profiles in 14 out of 16 taxa, ranging from primary producers to secondary consumers (Fig. 3.4, Table 3.4). Conspecific FA composition differed between sea otter regions for *Fucus*, POM, limpet, dock shrimp and graceful crab (Fig. 3.4b, c, f, h, j; Table 3.4; $p < 0.01$) and for seagrass, *Ulva*, *Pentidotea*, butter clam, helmet crab, snake prickleback and staghorn sculpin (Fig. 3.4a, d, e, g, i, k, j; Table 3.4; $p < 0.05$). We found marginal evidence of an effect of sea otter region on the FA composition for seagrass epiphyte and *Macoma* spp. (Table 3.4; $p < 0.1$) and no evidence of a sea otter region effect on the FA composition for sugar kelp and shiner perch (Table 3.4; $p > 0.1$).

SIMPER analyses identified EFA as important in FA discrimination of conspecifics between sea otter regions (Table 3.5). Of the top five discriminating FA for each taxon, one (limpet) to four (*Ulva* and snake prickleback) of those FA were EFA. The cumulative percentage that EFA contributed to dissimilarity for each taxon ranged from 13.8% (limpet) to 47.8% (staghorn sculpin) with a mean of 30.7 % (+/- 12.0 SD). Eicosapentaenoic acid (EPA, 20:5ω3) ranked in the top five FA for all species except seagrass and *Ulva*, accounting for 6.0% – 15.9% of the total dissimilarity. However, we did not find a pattern of consistently higher or lower EPA propositions across taxa collected from each region. Docosahexaenoic acid (DHA, 22:6ω3) substantially contributed to FA dissimilarity between regions among secondary consumers including dock shrimp (8.4%), helmet crab (11.6%), graceful crab (9.0%), snake prickleback (21.6%) and staghorn sculpin (26.1%), with greater proportions found in all secondary consumers except snake prickleback and staghorn sculpin in the high sea otter region (Table 3.5). SIMPER results further indicated a range of 10 to 20 unique FA which sum to 90% dissimilarity between groups (Table S3.4).

Our comparison of marker FA among conspecifics found that all taxa showed at least some evidence of differing FA proportions between high and low sea otter density regions (Table S3.5; Fig. 3.5). POM showed the greatest number of differences between sea otter regions. We found evidence for a difference in the proportion of POM bacterial FA, the sum of ALA and LIN, PAL, ARA and DHA (Fig. 3.5; $p = 0.014$, $p = 0.014$, $p = 0.014$, $p = 0.014$, $p = 0.014$ respectively) and C_{18} PUFA and EPA ($p = 0.043$, $p = 0.070$ respectively). We also found evidence for proportional differences in multiple dock shrimp marker FA, including the proportion of bacterial FA, total C_{18} PUFA, total PUFA, ARA and EPA (Fig. 3.5; $p = 0.005$, $p = 0.005$, $p = 0.008$, $p = 0.005$, $p = 0.013$ respectively) and little evidence of a difference in the proportion of PAL ($p = 0.093$). Across all taxa we found total PUFA made up greater than 20% of total FA, especially for primary producers (Fig. 3.5). We found evidence for a difference in total PUFA between sea otter regions in seagrass ($p = 0.054$), *Fucus* ($p = 0.031$), *Ulva* (p =

0.066) and dock shrimp (p = 0.008). The EFA, EPA, differed in three out of six primary producers, including seagrass (p = 0.027), *Fucus* (p = 0.020) and POM (p = 0.070), however there was not a consistent pattern of higher or lower proportions between sea otter regions. In contrast, the essential FA DHA was found to be in significantly lower proportion in the low sea otter region in *Fucus* (p = 0.003) and POM (p = 0.014). EPA differed in only two out the ten consumers, including limpets and dock shrimp, both with lower proportions in the low sea otter region. Similarly, we found lower proportions of DHA in the low sea otter region for limpets (p = 0.027), butter clams (p = 0.036) and staghorn sculpin (p = 0.013).

3.4 Discussion

Contrary to our predictions, we did not observe that sea otters conferred the same patterns on seagrass biomass as Chapter 2 or a similar study in Elkhorn Slough (Hughes et al. 2013). Overall we found few differences in conspecific biomass between sea otter density regions, suggesting limited indirect effects of sea otters on patterns of seagrass community biomass. However, there were clear direct negative effects of sea otter density on clam and crab biomass. While we did find some differences in conspecific δ^{13}C and δ^{15}N, our comparison of overall trophic niche space indicated similar total area and range of δ^{13}C and δ^{15}N between sea otter regions, suggesting little difference in overall trophic structure inferred from SI. We found evidence for differences in FA profiles for 14 out of 16 taxa including primary producers, primary consumers and secondary consumers. These differences appear to be driven in large part by EFA, including EPA and DHA, and suggest subtle differences in diets of conspecifics between regions with high and low sea otter density. This pattern was further supported by our direct comparison of marker FA and FA groups. In total, our FA results provide the most evidence of differing trophic structure between sea otter regions and highlight their ability to detect such patterns not evident from the biomass or SI perspective alone. However, given the lack of a theoretical mechanism by which sea otters could induce changes to primary producer FA and similar environmental conditions between sea otter regions, we suggest that it is likely that we captured the natural variability in energetic pathways in Southeast Alaska seagrass communities. These variable results highlight that while top-down forces from sea otters can have large effects on the biomass of certain taxa, they may not necessarily translate to a difference in energy flow among other community constituents.

Conspecific differences in whole FA profiles, specific FA and FA groups provide the most evidence of differing trophic structure between sea otter density regions. These results reveal three potential scenarios for Southeast Alaska seagrass communities. One, that primary producers vary in their FA profiles across our study area, which then propagate to consumers; two, that the diets of consumers vary across our study area as a function of the natural variation in diet composition; or three, a sea otter induced change in consumer diets. As evidence for scenario one, four out of the six primary producers analyzed differ in their whole FA profile between sea otter regions. These differences may be the result of natural variability in primary sources rather than sea otters, because we do not know of a mechanistic link between sea otters and primary producer FA. We did not find overall evidence that these differences in primary producer FA propagate to consumers leading to different consumer FA. Combining PERMANOVA results with our examination of marker FA and FA groups, we found only two instances where FA differences in primary producers may have directly translated to differences in a primary consumer. We found lower proportions of EPA in low sea otter region samples of both seagrass and *Fucus*, and in the consumer limpets. The primary driver of this pattern is unclear, as limpets likely do not rely on seagrass as a major dietary source (see below), and we have not observed them attached to or consuming *Fucus*. The lack of concurrence between primary producer and likely consumer FA may also reflect that many consumers rely on diverse diets (Kharlamenko et al. 2001, Alfaro et al. 2006, Douglass et al. 2011, Jankowska et al. 2018) and could obtain FA from a variety of sources, including many that were not measured in this study.

Primary producer SI and FA biomarkers can also vary as a function of environmental conditions, space, and season (Dethier et al. 2013, Lowe et al. 2014). Environmental parameters measured for this study were relatively consistent across sites and sea otter regions except water nitrate concentrations, which were slightly higher in the high sea otter region. Measurements for this study were similar to those measured in seagrass meadows in the region previously (Chapter 2) across a larger spatial and temporal range, further supporting that these environmental parameters vary little across these sites. Geographic location could affect environmental conditions not captured by our sampling, potentially introducing unaccounted affects and variation in biomarker values. Given the distribution of sea otters in the region, we were unable to control for geographic location in our sampling regime and therefore rely on the environmental measures at our sites alone. However, we took care to select sites with qualitatively similar geomorphology and seagrass bed size. We also constrained biomarker sampling to the shortest time frame possible with a given taxon, ranging from one to three days. Assuming that environmental or temporal factors did not affect primary producer biomarkers, our observed differences could be reflective of natural variability or some effect of sea otters. While there is support for location-associated variability in biomarker values in nearshore ecosystems (Dethier et al. 2013), we know of no evidence of sea otter-mediated effects on biomarker values in primary producers. As FA synthesis of primary producers is a function of a taxon's physiology and environmental setting (Dalsgaard et al. 2003), a mechanistic relationship between sea otters and primary producer biomarker values is unclear.

Another possible driver of conspecific FA differences between sea otter regions may be variation in diet composition and therefore trophic structure of the seagrass community that is not mechanistically tied to sea otters. The FA primarily responsible for discriminating conspecifics between sea otter regions highlights this pattern. The consistency of EPA as an important discriminating FA supports a growing consensus of EPA as a critical FA in describing trophic variability in ecosystems (Arts et al. 2001, Litzow et al. 2006, Galloway et al. 2013). While EPA is often considered a biomarker for diatoms, is it also present in elevated proportions in other sources of nearshore primary production including dinoflagellates (Kelly and Scheibling 2012) and brown and red macroalgae (Galloway et al. 2012). Given that we see variable directional patterns of EPA proportions within taxa between two sea otter regions, it may be that even if sea otters have an effect on EPA availability in the community, consumers are buffered from this by EPA availability from other sources within or outside the seagrass community. DHA also appeared to be an important discriminating FA, especially in secondary consumers, further supporting the importance of DHA as a trophic marker for many species (Arts et al. 2001, Dalsgaard et al. 2003). Generally, these differences in FA profiles in conspecifics could result from differences in diet composition, either unique source and/or proportions, between sea otter regions. At present we are unable to evaluate which of these scenarios is occurring is Southeast Alaska; however, given the evidence for diverse diets of consumers in this study and other seagrass ecosystems (Kharlamenko et al. 2001, Alfaro et al. 2006, Jaschinski et al. 2008, Jephson et al. 2008, Douglass et al. 2011, Jankowska et al. 2018), it is likely a combination of different sources and relative contribution of those sources to a given consumer's diet.

Patterns of DHA may be explained by the coccolithophore bloom observed near one of our high sea otter density sites. DHA occurs in relatively high proportions in coccolithophores (Class Prymnesiophyceae) and can be useful in distinguishing them from other phytoplankton (Dalsgaard et al. 2003, Fiorini et al. 2010, Galloway and Winder 2015). While not included in our analyses, the single POM FA sample from the coccolithophore bloom measured a DHA proportion of 0.176, compared to a mean of 0.082 (± 0.016 SD) across all other high sea otter sites. However, mean DHA proportions at low sea otter density sites were notably lower at 0.038 (± 0.007 SD). This may indicate a difference in the trophic structure between sea otter regions; however, we believe this is unlikely for two reasons. One, the coccolithophore bloom was an ephemeral and unanticipated event, and is not necessarily a consistent feature of nearshore ecosystems in the region. Two, POM FA signatures are known to vary in space and time (Lowe et al. 2014), which was not likely captured by our limited sampling. Therefore, while our POM FA samples may be indicative of planktonic food sources in general, they likely do not capture the variability in the POM FA signature within and across our study sites and region.

Our comparison of isotopic niche space suggested little difference between overall trophic structures between sea otter density regions. Other studies of the trophic structure of seagrass communities have reported a 60% difference in isotopic niche space between sites (Thormar et al. 2016); however, these were largely attributed to differences in nutrient loading, i.e. bottom-up forces. The authors suggested that SI values of seagrass community species may be more susceptible to change from bottom-up forces than top-down ones. The similarity in $\delta^{13}C$ of most conspecifics in our study is likely due to no observed difference in the $\delta^{13}C$ primary producers between regions. The exception being the $\delta^{13}C$ values of POM. Even though POM was more enriched at high sea otter sites, this pattern does not appear to transfer to consumers of POM, butter clams and *Macoma* spp. clams, whose $\delta^{13}C$ are nearly identical between sea otter treatments. The only other taxa that differed in $\delta^{13}C$ were staghorn sculpins. While this could be due to a direct or indirect sea otter effect, as seen in other fishes influenced by sea otters (Markel and Shurin 2015), our results could reflect natural variability of the species. Staghorn sculpins are known generalist predators in the region (Whitney et al. 2017, Duncan and Beaudreau 2019), which could result in a wide range of $\delta^{13}C$ values (Whitney et al. 2018). Furthermore, our results could be reflective of the slightly larger individuals sampled in the low sea otter region, as body size can reflect ontogenetic diet shifts and therefore changes in SI. While we observed more differences between sea otter regions in $\delta^{15}N$, they were not consistent in direction and did not appear to propagate up the food chain. However, regardless of direction differences in $\delta^{15}N$, these patterns suggest that some taxa may occupy different relative trophic positions between sea otter density regions.

Sea otters had strong negative effects on total crab and clam biomass, and little effect on other species in the hypothesized sea otter-seagrass trophic cascade that were expected based on Chapter 2 and from Elkhorn Slough (Hughes et al. 2013). Notably we failed to find a positive relationship between sea otters and seagrass, contrary to Chapter 2. This may be due to the reduced number of study sites, geographic area and seasonal time frame in this study compared to Chapter 2. Sea otter density region had the greatest effect on total clam and crab biomass, on butter and *Macoma* spp. clams, and helmet and red rock crabs, confirming results from Chapter 2 and previous research in the region (Hoyt 2015). We found greater helmet crab biomass at high sea otter sites, while overall crab biomass was lower. This may be due to interference competition between helmet and red rock crabs. At low sea otter density sites, where red rock crabs were abundant and relatively large (mean carapace width 150.5 mm ± 4.7 SD), red rock crabs may have entered the crab pots first, discouraging entrance by the much smaller helmet crabs (mean carapace width 40.0 mm ± 4.0 SD). While no helmet crabs were caught through our crab pot sampling at low sea otter density sites, we were able to easily obtain them via snorkel, confirming their presence. Assuming that these observations are evidence of interference competition between these two species, there is a potential that helmet crabs occupy different trophic niches when red rock crabs are present versus absent. Our SI data indicate some difference in $\delta^{13}C$ and $\delta^{15}N$ of helmet crabs where red rock crabs are present (low sea otter sites) and absent (high sea otter sites); however, this difference is not statistically significant. We found good evidence for a difference in FA profile of helmet crabs between regions driven by three EFA, EPA, DHA and ARA, suggesting differences in diet and supporting a different ecological niche for this species between sea otter regions.

An essential component of the top-down structuring theory in seagrass communities is that epifaunal grazers predominantly consume seagrass epiphytes and other ephemeral macroalgae rather than seagrass itself (Hughes et al. 2004, Heck and Valentine 2007). Our SI and FA results support this hypothesis in Southeast Alaska, in line with similar studies (e.g. Jaschinski et al. 2008). We found little evidence that *Pentidotea* or limpets contain large amounts of the sum of LIN and ALA, which are relatively abundant in *Zostera marina* (Fig. 3.5). Instead, *Pentidotea* and limpets contained relatively high proportions of ARA, EPA and DHA, which are relatively high in *Fucus*, sugar kelp (Fig. 3.5) and other brown algae (Kelly and Scheibling 2012, Galloway et al. 2012). Furthermore, the dietary proportions of these FA correlate well to *Pentidotea* FA composition described in other studies (Galloway et al. 2014), further supporting that *Pentidotea* likely consume a diverse macroalgae diet. The FA profile of gastropods, including limpets and snails in our study, follow a similar pattern of ARA, EPA and DHA as that described in other studies (Kharlamenko et al. 2001, Jankowska et al. 2018) and suggest that seagrass community epifaunal gastropod diets likely consist of a variety of sources. Our FA and SI results contrast to those of McConnaughey and McRoy (1979), who suggested that seagrass itself may make up a large portion of the base of Alaska seagrass community food webs based on $\delta^{13}C$ data. Our data indicate $\delta^{13}C$ values of consumers, especially *Pentidotea*, align more closely to other sources of primary production than seagrass. Bacterial sources may be an important primary food source in Southeast Alaska seagrass communities. The proportion of total bacterial FA among primary and secondary consumers ranged from 0.027 to 0.116, which is similar to other seagrass meadows, ranging from approximately 0.02 to 0.11 in the Sea of Japan (Kharlamenko et al. 2001), from 0.02 to 0.05 in the Baltic Sea (Jankowska et al. 2018). Our results contrast with higher proportions reported from northern New Zealand, ranging from 0.132 to 0.146 in (Alfaro et al. 2006); however, these high values may be due to a diverse estuarine habitat that included multiple foundational species in a relatively small area.

Predation of mesopredators on epifauna is an essential element of seagrass trophic cascades that include higher order predators, as described in the Baltic Sea and Elkhorn Slough, CA (Jephson et al. 2008, Moksnes et al. 2008, Baden et al. 2010, 2012, Hughes et al. 2013). Our previous research in Southeast Alaska, however, failed to find an association between mesopredators and seagrass epifauna (Chapter 2). Our SI and FA comparison of crabs (including helmet and graceful crabs) and fishes (snake prickleback and staghorn sculpin) suggest that these taxa consume diets with a wide variety of ultimate sources, regardless of sea otter region. While it is possible that fishes and crabs consume seagrass epifauna, FA analyses indicate that they likely consume a variety of other species that lie outside the current hypothesized sea otter – seagrass trophic cascade. In addition to the references above on the diets of staghorn sculpins, seagrass-associated fishes often consume a diverse diet consisting of detritus, epibenthic and planktonic prey (Adams 1976). Seagrass-associated crabs can also exhibit diverse diets, not necessarily tightly linked to seagrass epifauna (Douglass et al. 2011).

Considering biomass, SI, and FA results, no single taxon differed in biomass, $\delta^{13}C$, $\delta^{15}N$ and FA between the two sea otter regions. The two taxa which differed in SI and FA biomarker measures, POM and staghorn sculpin did not differ in biomass. These variable results highlight that while top-down forces from sea otters can have large effects on the biomass of certain taxa, this does not necessarily translate to a difference in energy flow among other community constituents. Our results support the diverse trophic structure of seagrass ecosystems, similar to previous studies (Kharlamenko et al. 2001, Alfaro et al. 2006, Douglass et al. 2011, Jankowska et al. 2018) that showed that at the whole community level, these ecosystems have a similar breadth of carbon sources (range of $\delta^{13}C$) and food chain length (range of $\delta^{15}N$). This result was only identifiable through FA data and to a lesser extent SI and biomass data. The variation in conspecific biomarkers that we found appears to be more of a feature of the complexity of seagrass food webs and natural variability than some sea otter induced effect. We did not find evidence in Southeast Alaska for a sea otter-mediated effect on trophic structure at the biomarker level, such that might come about through sea otter-mediated diet switching among consumers. Future research could identify potential diet shifts through experimental manipulation and feeding trials. Furthermore, our results highlight that regions like Southeast Alaska, where communities are relatively open and composed of a mosaic of habitats (O’Clair et al. 1997), may be resilient to localized perturbations to the food chain as consumers appear to utilize diverse diet resources (Mccann 2000, Bellmore et al. 2015). From this perspective it may be an over-simplification to consider seagrass ecosystems in Southeast Alaska as only influenced by top-down forces and in isolation from other habitats and characterized by simple linear food chains. Taking this into account, future research should consider the resources available in adjacent habitats and the flux of those resources among habitats.

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3.7 Figures

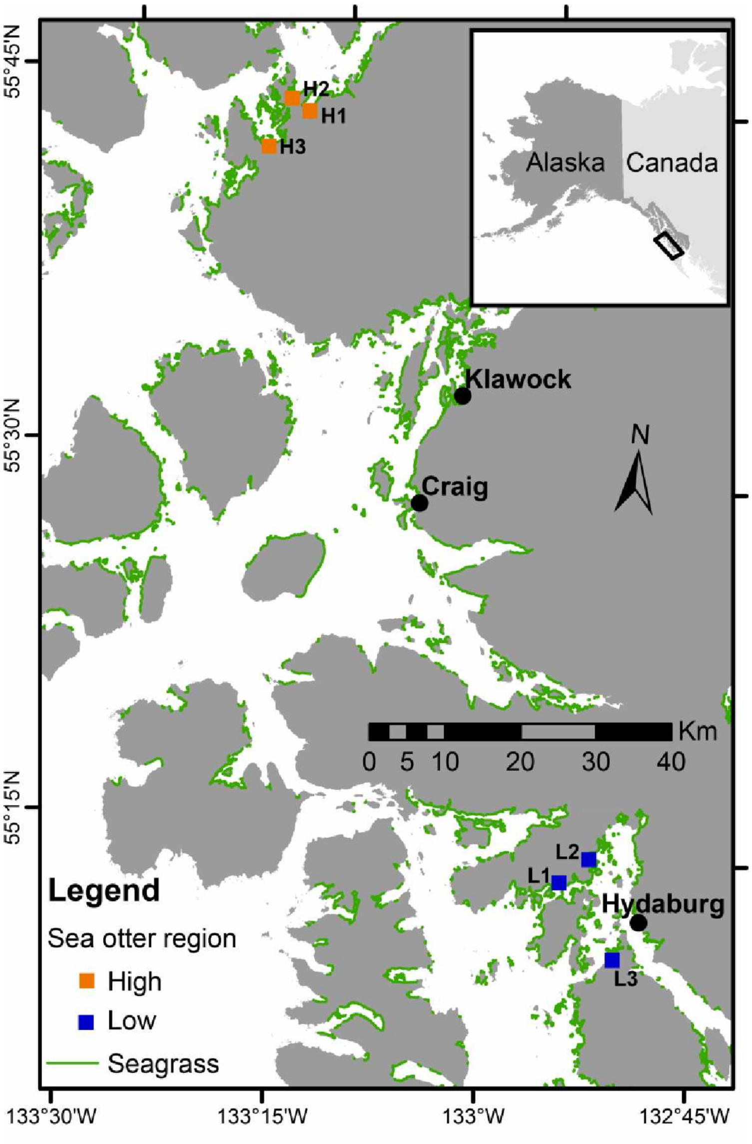

Fig. 3.1: Study area on the west cost of Prince of Wales Island, Alaska including seagrass extent (Harper and Morris 2004, NOAA 2019), and high and low sea otter study sites.

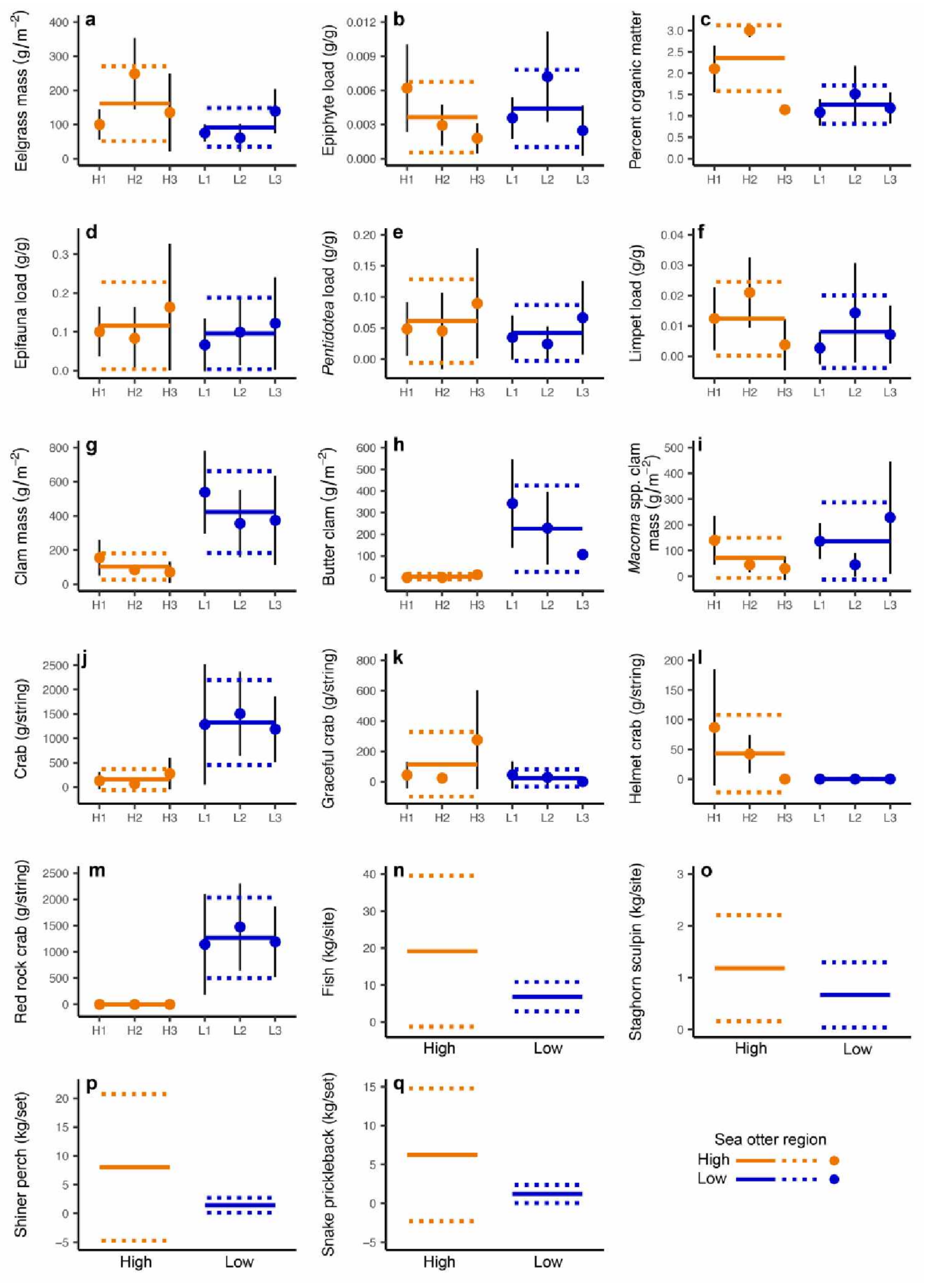

Fig. 3.2: Mean biomass (solid lines) and error (SD, dashed lines) of sampled seagrass community taxa at high (orange) and low (blue) sea otter regions. Points represent site level means with vertical error (SD) bars. Seagrass (a), epiphyte load (b), percent organic matter of particulate organic matter (c), total epifauna load (d), *Pentidotea* load (e), limpet load (f), total clam density (g), butter clam biomass (h), *Macoma* spp. biomass (i), total crab biomass (j), graceful crab biomass (k), Helmet crab biomass (l), red rock crab biomass (m), total fish biomass (n), staghorn sculpin biomass (o), shiner perch biomass (p), and snake prickleback biomass (q). Due to conducting one beach seine at each site, only regional fish biomass is presented. All biomass data are presented in grams except for fishes (n – q) which are presented in kilograms.

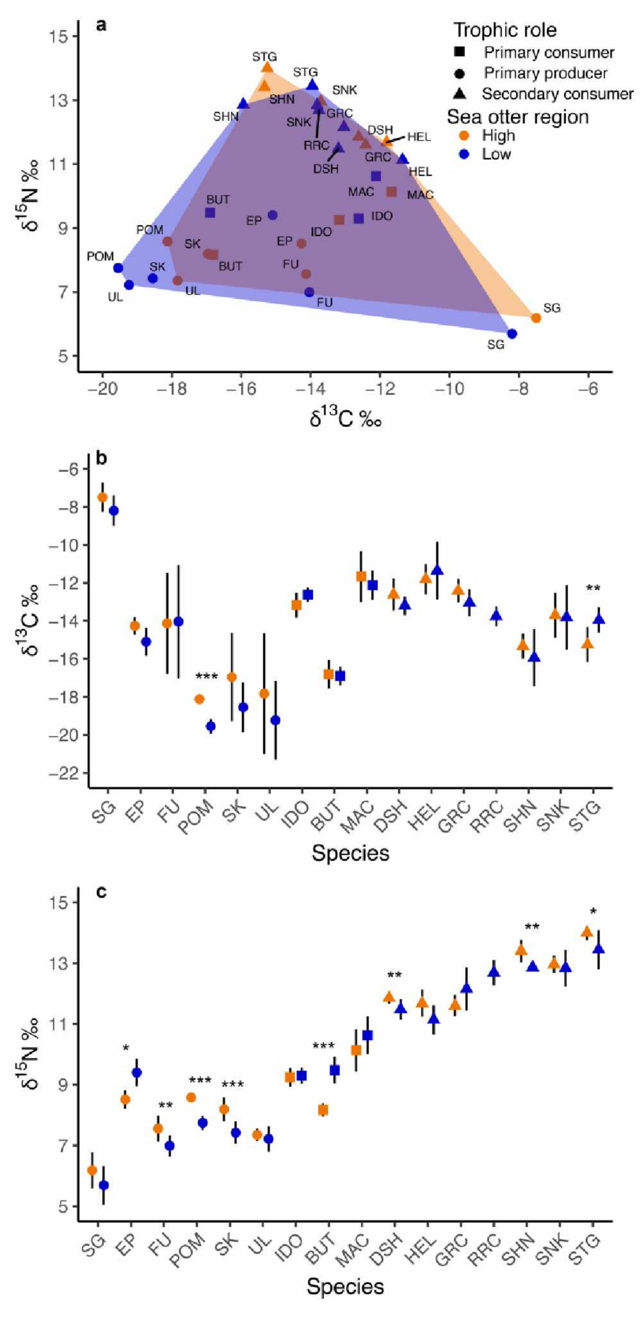

Fig. 3.3: Mean δ^{13}C and δ^{15} biplot of sampled species with convex hull overlay (a) and mean (+/- SD) δ^{13}C (b) and δ^{15}N (c) and for sampled taxa between high and low sea otter density regions. Asterisks indicate p-values from t-tests where* p-value ≤ 0.1, ** p-value ≤ 0.05, and *** p-value ≤ 0.01.

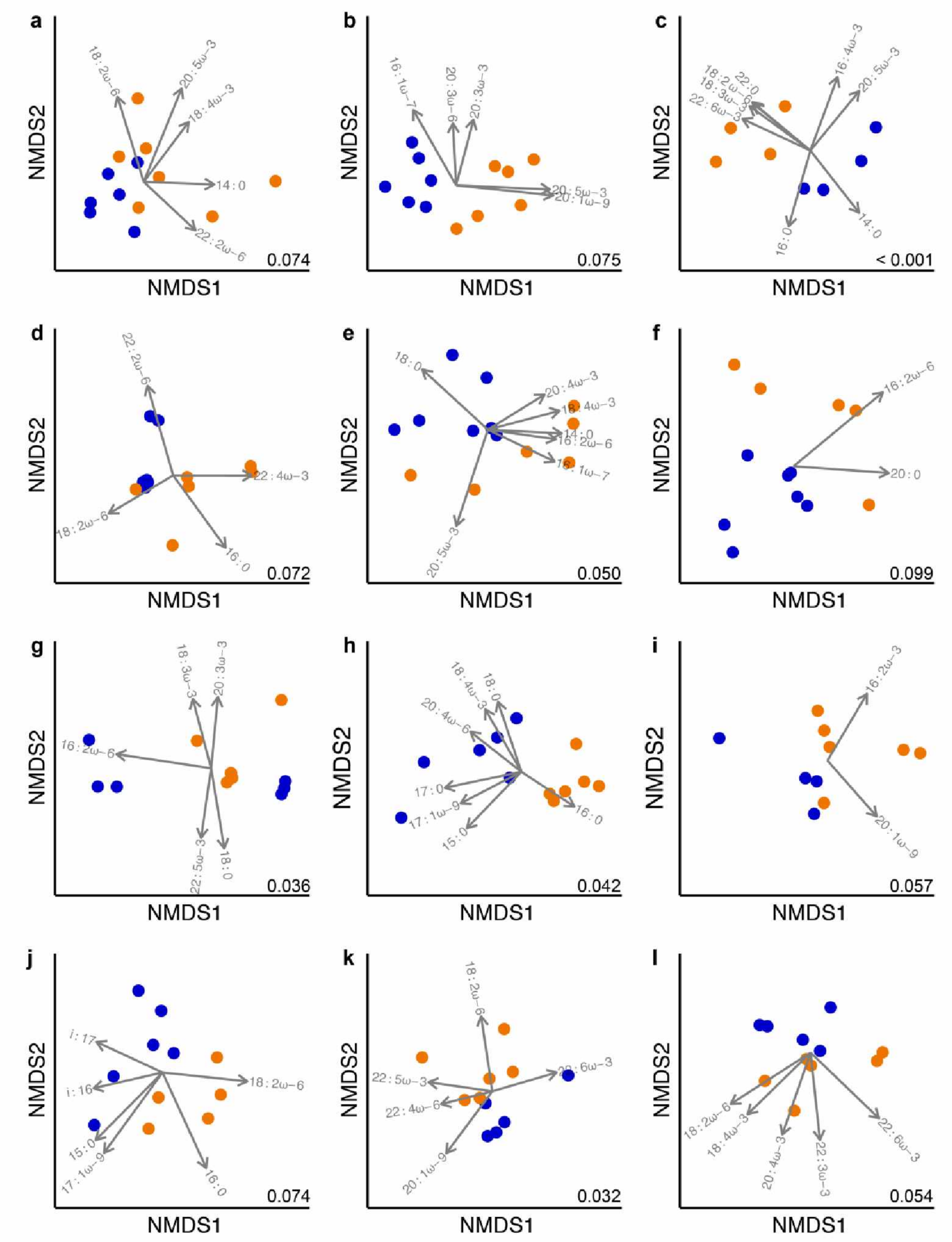

Fig. 3.4: Non-metric multidimensional scaling (NMDS) plots of FA profiles for taxa with evidence for a sea otter region effect determined from PERMANOVA analysis (p-value ≤ 0.05), including seagrass (a), *Fucus* (b), POM (c), *Ulva* (d), *Pentidotea* (e), limpet (f), butter clam (g), dock shrimp (h), helmet crab (i), graceful crab (j), snake prikleback (k), and staghorn sculpin (l). Points represent unique tissue samples form high (orange) and low (blue) and sea otter density regions. Two-dimensional stress listed in lower right of each plot. Vectors reflect FA with r-squared values ≥ 0.8 with NMDS axes. Vectors for POM (c) reflect FA with r-squared values ≥ 0.95 with NMDS axes.

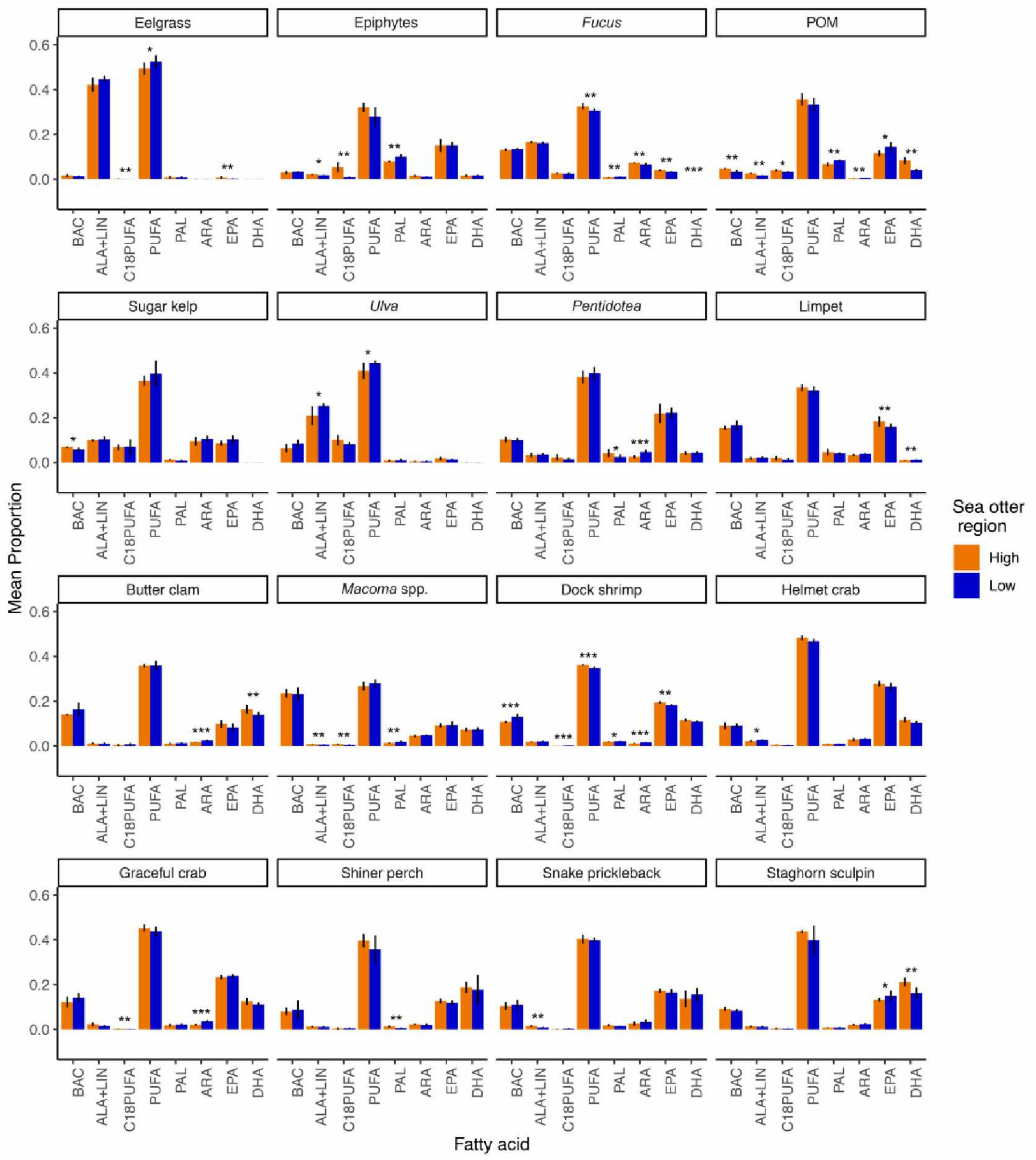

Fig. 3.5: Mean proportions (+/- SD) of marker FA and FA groups for all taxa measured between high and low sea otter density regions. BAC = bacterial FA including 15:0, iso-15:0, isto-16:0, 17:0, iso-17:0, anteiso-17:0, 17:1ω9, anteiso-18:0, 18:1ω7, 18:1ω9, 20:1ω7, 20:1ω9, and 22:1ω9. ALA + LIN = sum on alpha-linolenic acid 18:3ω3 and alpha-linoleic acid18:2ω6. C18PUFA = other C_{18} carbon essential FA including 18:3ω6 and 18:4ω3. PUFA = all polyunsaturated FA including all FA with ≥ 2 double bonds. PAL = palmitoleic acid 16:1ω7. ARA = arachidonic acid 20:4ω6. EPA = eicosapentaenoic acid 20:5ω3. DHA = docosahexaenoic acid 22:6ω3. Asterisks indicate p-values from t-tests where *p-value ≤ 0.1, **p-value ≤ 0.05, and ***p-value ≤ 0.01. Full Mann-Whitney U test results are presented in Table S5.

3.8 Tables

Table 3.1: Summary of taxa tissue collections including sampling date and replication of biomass, SI, and FA analysis. *Three replicate POM tows were taken at two high sea otter density sites but only one tow at the remaining site (H3). Tissue indicates whole body (WB), all soft tissues (ST), foot muscle (FM), and muscle (M). Sample measurement (Meas.), if applicable, indicates specimen total length (TL), shell width (SW), carapace width (CW) or fork length (FL). Mean (± SD) specimen lengths are given for each species where applicable.

					n per site		n per region								
Common name	Scientific name	Abbr.	Sample date(s) - high	Sample date(s) - low	Biomass - high	Biomass - low	SI - high	SI - low	FA - high	FA - low	Tissue	Tissues pooled	Meas.	Size (mm) - high	Size (mm) - low
Primary producers															
Seagrass	*Zostera marina*	SG	7/14 - 7/16	7/11 - 7/13	8	8	7	6	7	6	WB				
Eelgrass epiphytes	Class Bacillariophyceae	EP	7/14 - 7/16	7/11 - 7/13	8	8	5	3	5	3	WB				
Particulate organic matter		POM	7/25	7/24	3*	3	4	6	4	6	WB				
Rockweek	*Fucus distichus*	FU	7/14 - 7/16	7/11 - 7/13			6	6	6	6	WB				
Sugar kelp	*Saccharina latissima*	SK	7/14 - 7/16	7/11 - 7/13			5	6	5	6	WB				
Sea lettuce	*Ulva* spp.	UL	7/14 - 7/16	7/11 - 7/13			6	5	6	6	WB				
Primary consumers															
Eelgrass isopod	*Pentidotea rascata*	IDO	7/14 - 7/16	7/11 - 7/13	8	8	6	7	6	7	WB	X	TL	36.5 (4.6)	36.1 (2.4)
Eelgrass limpet	*Lottia parallela*	LMP	7/14 - 7/16	7/11 - 7/13	8	8	-	-	6	7	ST	X			
Butter clam	*Saxidomus giganteus*	BUT	8/15	7/11 - 7/13	8	8	6	6	5	6	FM	X	SW	29.8 (5.6)	70.2 (6.3)
Macoma clam	*Macoma* spp.	MAC	7/14 - 7/16	7/11 - 7/13	8	8	6	6	6	6	FM	X	SW	41.3 (7.3)	39.1 (4.0)
Secondary consumers															
Dock shrimp	*Pandalus danae*	DSH	7/29 - 7/31	7/26 - 7/28			6	6	6	6	M	X	TL	85.8 (3.9)	83.3 (3.3)
Helmet crab	*Telmessus cheiragonus*	HEL	7/22	7/28	4	4	6	4	6	4	M		CW	44.5 (2.3)	40.0 (4.5)
Graceful crab	*Metacarcinus gracilis*	GRC	7/22	7/28	4	4	5	6	5	6	M		CW	62.8 (3.6)	72.0 (11.5)
Red rock crab	*Cancer productus*	RRC	7/22	7/28	4	4	-	6	-	6	M		CW	-	150.5 (4.7)
Shiner perch	*Cymatogaster aggregata*	SHN	7/29 - 7/31	7/26 - 7/28	1	1	6	6	6	6	M		FL	122.8 (3.7)	122.7 (4.2)
Snake prickleback	*Lumpenus sagitta*	SNK	7/29 - 7/31	7/26 - 7/28	1	1	6	4	6	5	M		FL	158.0 (21.5)	162.3 (57.4)
Staghorn sculpin	*Leptocottus armatus*	STG	7/29 - 7/31	7/26 - 7/28	1	1	6	6	6	6	M		FL	160.3 (14.8)	144.8 (35.6)

Table 3.2: Key to marker FA used in analysis. References 1 - Dalsgaard et al. 2003, 2 - Volkman et al. 1980, 3 - Jaschinski et al. 2011, 4 - Kharlamenko et al. 2001, 5 - Galloway et al. 2012, 6 - Kelly and Scheibling 2012, 7 – Ackman et al. 1968, 8 - Alfaro et al. 2006.

Abbreviation	FA	Marker for	Reference
BAC	15:0	Bacterial	1
	iso-15:0		1
	iso-16:0		1
	17:0		1
	iso-17:0		1
	anteiso-17:0		1
	17:1w9		1
	anteiso-18:0		1
	18:1ω7		2, 3
	18:1ω9		1
	20:1ω7		1
	20:1ω9		1
	22:1ω9		1
LIN	18:2ω6	Seagrass, vascular plants	4, 5, 6
ALA	18:3ω3	Seagrass, vascular plants	4, 5, 6
PUFA	≥ 2 double bonds		5, 6
ARA	20:4ω6	Brown and red algae	5, 6
EPA	20:5ω3	Diatoms, dinoflagellates, brown and red algae	5, 6, 7
PAL	16:1ω7	Diatoms	1, 5, 6
DHA	22:6ω3	Zooplankton	1, 4, 8

Table 3.3: Results from mixed effects models of taxa biomass for the fixed effect of sea otter region (high sea otter region as reference group) and random effect of site. Since only one beach seine was conducted at each site, random site effects were not evaluated.

Factor	Transformation	Fixed effects	Estimate	Std. Error	df	t-value	p-value	Random effect of site	SD
Seagrass	log	Intercept	4.864	0.280	42	17.370	< 0.001	Intercept	0.446
		Low sea otter	-0.522	0.396	4	-1.319	0.268	Residual	0.540
Epiphytes	square-root	Intercept	0.054	0.010	42	5.342	< 0.001	Intercept	0.016
		Low sea otter	0.007	0.014	4	0.486	0.652	Residual	0.023
POM	arcsine - square root	Intercept	0.147	0.013	10	11.659	< 0.001	Intercept	0.017
		Low sea otter	-0.036	0.017	4	-2.070	0.107	Residual	0.019
Epifauna	square-root	Intercept	0.306	0.031	42	9.969	< 0.001	Intercept	< 0.001
		Low sea otter	-0.033	0.043	4	-0.752	0.494	Residual	0.150
Pentidotea	forth-root	Intercept	0.391	0.037	42	10.588	< 0.001	Intercept	< 0.001
		Low sea otter	0.002	0.052	4	0.045	0.966	Residual	0.181
Limpet	cube-root	Intercept	0.171	0.049	42	3.480	0.001	Intercept	0.075
		Low sea otter	-0.050	0.070	4	-0.726	0.508	Residual	0.116
Clams	cube-root	Intercept	4.332	0.364	42	11.903	< 0.001	Intercept	0.402
		Low sea otter	2.684	0.515	4	5.214	0.007	Residual	1.373
Butter clam	none	Intercept	4.949	48.233	42	0.103	0.919	Intercept	70.134
		Low sea otter	220.854	68.212	4	3.238	0.032	Residual	128.391
Macoma spp. clam	forth-root	Intercept	2.348	0.533	42	4.409	< 0.001	Intercept	0.856
		Low sea otter	0.635	0.753	4	0.843	0.447	Residual	0.974
Crabs	forth-root	Intercept	2.969	0.337	18	8.820	< 0.001	Intercept	< 0.001
		Low sea otter	2.833	0.476	4	5.951	0.004	Residual	1.166
Graceful crab	forth-root	Intercept	2.116	0.631	18	3.354	0.004	Intercept	0.833
		Low sea otter	-1.392	0.892	4	-1.560	0.194	Residual	1.414
Helmet crab	square-root	Intercept	4.336	1.581	18	2.743	0.013	Intercept	2.264
		Low sea otter	-4.336	2.235	4	-1.940	0.124	Residual	3.078
Red rock crab	cube-root	Intercept	0.000	0.447	18	0.000	1.000	Intercept	< 0.001
		Low sea otter	10.150	0.632	4	16.069	< 0.001	Residual	1.547
Fish	log	Intercept	2.417	0.622	4	3.884	0.018		
		Low sea otter	-0.610	0.880	1	-0.693	0.527		
Shiner perch	forth-root	Intercept	1.324	0.320	4	4.135	0.014		
		Low sea otter	-0.292	0.453	1	-0.644	0.555		
Snake prickleback	forth-root	Intercept	1.357	0.322	4	4.211	0.014		
		Low sea otter	-0.502	0.456	1	-1.102	0.332		
Staghorn sculpin	forth-root	Intercept	0.769	0.360	4	2.137	0.099		
		Low sea otter	-0.106	0.509	1	-0.208	0.845		

Table 3.4: PERMANOVA results on the effect of sea otter region on FA profiles of sampled taxa. All PERMANOVA were conducted with 9999 permutations.

	df	SS	R^2	pseudo - F	p-value
Seagrass					
Sea otter	1	0.021	0.210	2.929	0.017
Residual	11	0.078	0.790		
Epiphytes					
Sea otter	1	0.067	0.367	3.477	0.054
Residual	6	0.116	0.633		
Fucus					
Sea otter	1	0.010	0.325	4.806	0.002
Residual	10	0.021	0.675		
POM					
Sea otter	1	0.058	0.643	14.387	0.005
Residual	9	0.032	0.357		
Sugar kelp					
Sea otter	1	0.025	0.133	1.390	0.251
Residual	9	0.164	0.866		
Ulva					
Sea otter	1	0.106	0.245	3.239	0.019
Residual	10	0.327	0.755		
Pentidotea					
Sea otter	1	0.075	0.240	3.471	0.042
Residual	11	0.239	0.760		
Limpet					
Sea otter	1	0.041	0.226	3.211	0.005
Residual	11	0.140	0.774		
Butter clam					
Sea otter	1	0.079	0.245	2.920	0.047
Residual	9	0.243	0.755		
Macoma spp. clam					
Sea otter	1	0.031	0.168	2.020	0.068
Residual	9	0.154	0.832		
Dock shrimp					
Sea otter	1	0.024	0.445	8.026	0.003
Residual	10	0.030	0.555		
Helmet crab					
Sea otter	1	0.008	0.201	2.015	0.040
Residual	8	0.032	0.799		
Graceful crab					
Sea otter	1	0.032	0.295	3.766	0.003
Residual	9	0.076	0.705		
Shiner perch					
Sea otter	1	0.019	0.156	1.659	0.166
Residual	9	0.102	0.844		
Snake prickleback					
Sea otter	1	0.027	0.218	2.506	0.034
Residual	9	0.098	0.782		
Staghorn sculpin					
Sea otter	1	0.018	0.242	2.873	0.026
Residual	9	0.057	0.758		

Table 3.5: SIMPER results on the top 5 FA contributing most to multivariate dissimilarity for taxa with evidence of an effect of sea otter region on whole FA profiles ($p < 0.05$ from PERMANOVA). Essential FA (EFA) are listed in bold. Full SIMPER results can be found in Table S4.

						Mean FA %					
Taxon	Overall dissimilarity %	N FA to sum > 90% dissimilarity	N EFA	sum EFA contribution %	FA	High sea otter	Low sea otter	Mean dissimilarity % (SD)	Dissimilarity	Cumulative dissimilarity	p
Seagrass	6.3	10	3	44.4	**18:3ω3**	**36.0**	**37.6**	**1.2 (1.0)**	**19.7**	**19.1**	**0.378**
					16:0	33.1	32.2	0.9 (0.6)	14.1	33.2	0.394
					16:3ω3	**5.7**	**7.0**	**0.8 (0.5)**	**12.4**	**45.6**	**0.026**
					18:2ω6	**6.2**	**7.0**	**0.8 (0.6)**	**12.3**	**57.9**	**0.482**
					14:0	1.6	0.6	0.5 (0.5)	7.9	65.8	0.420
Fucus	4.3	15	2	17.4	16:0	30.9	31.2	0.7 (0.4)	15.6	15.6	0.42
					18:1ω9	11.3	11.8	0.4 (0.3)	10.2	25.8	0.235
					20:4ω6	**7.3**	**6.5**	**0.4 (0.3)**	**9.5**	**35.3**	**0.032**
					14:0	19.1	19.5	0.4 (0.3)	9.4	44.7	0.354
					20:5ω3	**4.0**	**3.3**	**0.3 (0.2)**	**7.9**	**52.5**	**0.010**
POM	12.1	15	2	30.9	14:0	20.9	25.6	2.3 (0.6)	19.4	19.4	0.005
					22:6ω3	**8.3**	**3.9**	**2.2 (0.8)**	**18.3**	**37.7**	**0.005**
					20:5ω3	**11.6**	**14.4**	**1.5 (1.0)**	**12.6**	**50.3**	**0.099**
					16:0	27.5	26.9	1.1 (0.7)	8.8	59.1	0.745
					16:1ω7	6.7	8.4	0.9 (0.4)	7.2	66.3	0.005
Ulva	14.3	14	4	43.8	**18:2ω6**	**5.5**	**10**	**3.0 (2.0)**	**21.0**	**21.0**	**0.114**
					16:0	45.6	41.8	2.1 (1.5)	14.9	36.0	0.032
					18:4ω3	**8.9**	**7.3**	**1.2 (1.1)**	**8.5**	**44.5**	**0.412**
					18:3ω3	**15.6**	**15.4**	**1.1 (0.8)**	**7.7**	**52.3**	**0.631**
					16:3ω3	**3.4**	**4.4**	**1.0 (0.6)**	**6.6**	**58.9**	**0.131**
Pentidotea	13.9	18	2	21.6	14:0	6.4	2.5	2.2 (1.3)	16.1	16.1	0.016
					20:5ω3	**21.9**	**22.2**	**1.9 (1.2)**	**13.6**	**29.7**	**0.387**
					18:0	11.1	13.7	1.7 (1.0)	12.6	42.3	0.059
					20:4ω6	**2.5**	**4.7**	**1.1 (0.6)**	**8.0**	**50.3**	**0.002**
					16:1ω7	4.2	2.5	1.1 (0.7)	7.9	58.1	0.077
Limpet	9.6	20	1	13.8	**20:5ω3**	**18.4**	**16**	**1.3 (1.1)**	**13.8**	**13.8**	**0.039**
					16:0	26.6	28.5	0.9 (0.5)	9.9	23.7	0.001
					18:0	10.8	9.5	0.8 (0.6)	8.5	32.2	0.051
					16:1ω7	4.7	4.2	0.7 (0.4)	7.0	39.2	0.062
					20:1ω9	2.9	4.2	0.6 (0.6)	6.6	45.8	0.044
Butter clam	13.2	18	3	28.2	16:0	34.6	31.1	1.7 (0.8)	13.1	13.1	0.002
					22:6ω3	**16.5**	**13.8**	**1.4 (0.9)**	**10.8**	**23.9**	**0.036**
					22:2ω6	**1.2**	**2.3**	**1.2 (1.0)**	**8.8**	**32.7**	**0.353**
					20:5ω3	**9.8**	**8.3**	**1.1 (0.8)**	**8.6**	**41.3**	**0.148**
					22:1ω9	0.1	2.1	1.0 (1.0)	7.7	49	0.136
Dock shrimp	5.7	16	2	19.1	16:0	38.0	35.8	1.2 (0.7)	20.3	20.3	0.017
					20:5ω3	**19.5**	**18.3**	**0.6 (0.3)**	**10.7**	**31.0**	**0.007**
					18:0	9.4	10.5	0.6 (0.4)	10.1	41.1	0.014
					15:0	0.8	1.8	0.5 (0.5)	8.5	49.5	0.005
					22:6ω3	**11.6**	**10.9**	**0.5 (0.3)**	**8.4**	**58.0**	**0.069**
Helmet crab	5.7	18	3	35.7	**20:5ω3**	**27.8**	**26.5**	**1.0 (0.6)**	**17.9**	**17.9**	**0.106**
					16:0	28.9	30.4	0.9 (0.7)	15.7	33.6	0.174
					22:6ω3	**11.7**	**10.5**	**0.7 (0.6)**	**11.7**	**45.2**	**0.292**

Table 3.5 continued

					18:0	11.1	11.1	0.5 (0.3)	9.4	54.6	0.053
					20:4ω6	**2.9**	**3.3**	**0.3 (0.2)**	**6.1**	**60.7**	**0.643**
Graceful crab	9.0	19	3	22.7	16:0	30.4	27.8	1.3 (0.9)	14.9	14.9	0.029
					18:0	8.8	10.7	1.1 (1.0)	12.5	27.5	0.293
					22:6ω3	**12.5**	**11.2**	**0.8 (0.7)**	**9.0**	**36.5**	**0.148**
					20:4ω6	**2.1**	**3.5**	**0.7 (0.3)**	7.7	**44.2**	**0.003**
					20:5ω3	**23.3**	**23.8**	**0.5 (0.4)**	**6.0**	**50.3**	**0.379**
Snake prickleback	8.8	20	4	42.8	**22:6ω3**	**13.6**	**15.5**	**1.9 (1.4)**	**21.6**	**21.6**	**0.558**
					16:0	33.1	34.3	1.0 (0.8)	11.1	32.8	0.389
					20:5ω3	**17.3**	**16.5**	**0.7 (0.6)**	**8.0**	**40.7**	**0.325**
					20:4ω6	**2.6**	**3.3**	**0.6 (0.4)**	**6.7**	**47.4**	**0.204**
					22:5ω3	**2.8**	**2**	**0.6 (0.5)**	**6.5**	**53.9**	**0.578**
Staghorn sculpin	8.1	16	3	47.8	**22:6ω3**	**17.1**	**21.2**	**2.1 (1.1)**	**26.1**	**26.1**	**0.009**
					20:5ω3	**15.9**	**13.3**	**1.3 (0.7)**	**15.9**	**42**	**0.007**
					16:0	32.5	30.7	1.1 (0.9)	13.7	55.7	0.087
					18:0	14.4	14.1	0.5 (0.3)	6.4	62.1	0.626
					22:5ω3	**4.0**	**3.5**	**0.5 (0.3)**	**5.8**	**67.9**	**0.165**

3.9 Supporting information

3.9.1 Supplementary Figures

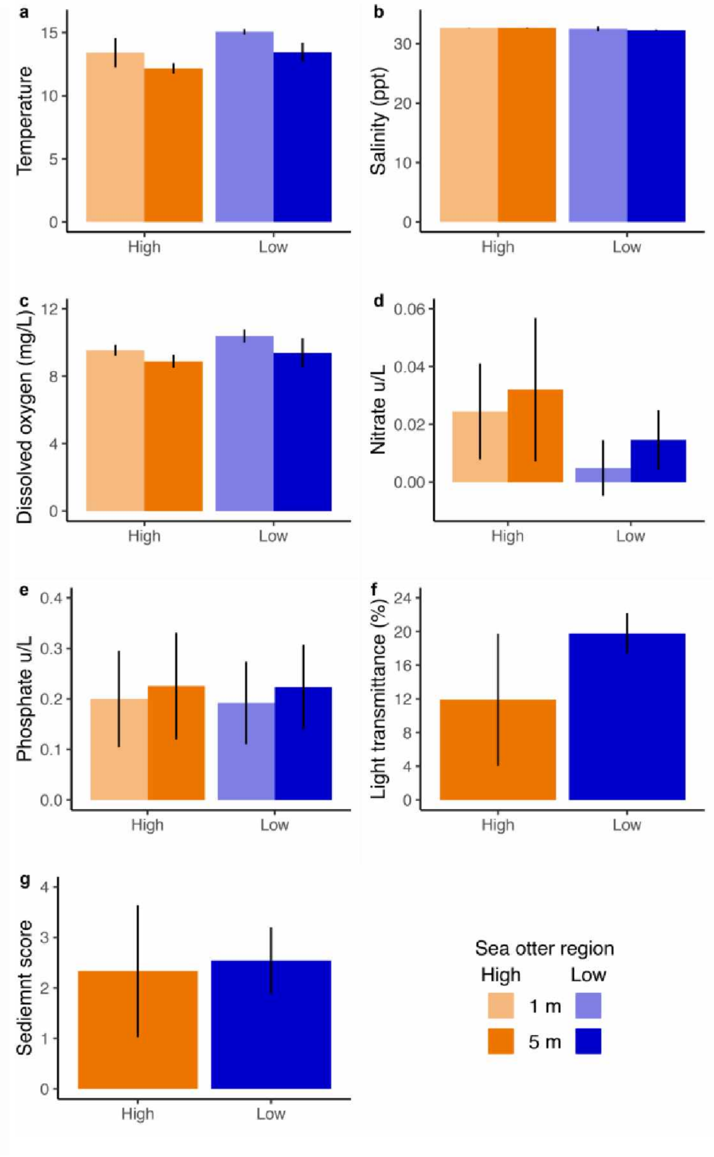

Fig. S3.1: Mean and error (SD) of environmental variables measured at sites in the high (n=3) and low (n=3) sea otter regions. (a) Water temperature measured at 1 and 5 m depth. (b) Salinity measured at 1 and 5 m depth. (c) Dissolved oxygen measured at 1 and 5 m depth. (d) Water nitrate concentration measured at 1 and 5 m depth. (e) Water phosphate concentration measured at 1 and 5 m depth. (f) Percent light transmittance. (g) Qualitative sediment score.

3.9.2 Supplemental Tables

Table S3.1: Summary of site data including location, sea otter density, and environmental data. 2018 sea otter density reflects sea otter densities measured for this study. Model sea otter density represent estimated from Tinker et al. (2019). Mean sediment scores (+/-SD). BLD = below detection limit.

			Sea otter density				Water temperature (°C)		Salinity (ppt)		DO (mg/l)		Light (PAR)				Nitrate (µmol/L)		Phosphate (µmol/L)	
Site	Latitude	Longitude	2018	Model	Environmental sampling date	Sediment score	1 m	5 m	1 m	5 m	1 m	5 m	Surface	1 m	5 m	%	1 m	5 m	1 m	5 m
H1	55.735	-133.295	10.7	3.663	7/25	4.0 (0.0)	13.3	12.1	32.6	32.6	9.63	9.34	2319.0	1445.6	281.4	19.5	0.023	0.037	0.194	0.279
H2	55.739	-133.314	10.7	3.663	7/25	1.3 (0.46)	12.3	11.8	32.7	32.7	9.18	8.60	2245.0	1169.9	145.8	12.5	0.042	0.057	0.286	0.285
H3	55.706	-133.342	3.4	3.663	7/25	1.8 (0.71)	14.6	12.6	32.7	32.7	9.82	8.73	2448.0	1501.1	56.9	3.8	0.009	0.003	0.121	0.112
L1	55.230	-132.924	0	0.163	7/24	2.8 (0.89)	14.9	14.2	32.9	32.2	10.33	9.40	2250.0	1229.1	263.7	21.5	0.001	0.011	0.142	0.249
L2	55.249	-132.881	0	0.163	7/24	2.4 (0.52)	15.3	12.7	32.1	32.2	10.04	8.50	1984.8	901.5	153.6	17.0	BDL	0.019	0.171	0.260
L3	55.189	-132.843	0.04	0.163	7/24	2.5 (0.53)	15.0	13.4	32.5	32.4	10.79	10.25	2288.0	1206.6	251.6	20.9	0.013	0.015	0.247	0.192

Table S3.2: Length – weight relationships for crab and fish species used in Equation 3.1.

Common name	Scientific name	Family	a	b	References and notes
Cockle	*Clinocardium nuttalli*	Cardiida	0.0004	2.9453	Bradbury et al. 2005
Hiatella clam	*Hiatella sp.*	Hiatellidae	0.1660	3.1350	Robinson et al. 2010
Baltic macoma	*Macoma baltica*	Tellinidae	0.0046	2.5212	Oftedal et al. 2007; used *Macoma nasuta* values
Pointed macoma	*Macoma inquinata*	Tellinidae	0.0046	2.5212	Oftedal et al. 2007; used *Macoma nasuta* values
Bentnose macoma	*Macoma nasuta*	Tellinidae	0.0046	2.5212	Oftedal et al. 2007
Softshell clam	*Mya arenaria*	Myidae	0.0003	2.8956	Bradbury et al. 2015
Steamer clam	*Protothaca staminea*	Veneridae	0.0005	2.7080	Oftedal et al. 2007
Butter clam	*Saxidomus gigantea*	Veneridae	0.0002	3.1559	Bradbury et al. 2015
Horse clam	*Tresus nuttallii*	Mactridae	0.0002	2.0730	Lauzier et al. 1998
Dungeness crab	*Metacarcinus magister*	Cancridae	0.0053	2.1949	Oftedal et al. 2007
Decorator crab	*Oregonia gracilis*	Oregoniidae	0.0088	2.1525	kelp crab (*Pugettia producta*) values used
Red rock crab	*Cancer productus*	Cancridae	0.0014	2.4625	Oftedal et al. 2007
Helmet crab	*Telmessus cheiragonus*	Cheiragonidae	0.0088	2.1525	kelp crab (*Pugettia producta*) values used
Graceful rock crab	*Metacarcinus gracilis*	Cancridae	0.0053	2.1949	Oftedal et al. 2007, Dungeness crab used
Unknown rock crab		Cancridae	0.0034	2.3287	average of red rock and Dungeness crab
Cabezon	*Scorpaenichthys marmoratus*	Cottidae	0.0291	3.0000	Froese et al. 2014
Slender cockscomb	*Anoplarchus insignis*	Stichaeidae	0.0039	3.1200	Froese et al. 2014
Pacific cod	*Gadus macrocephalus*	Gadidae	0.0095	3.1153	Gunderson et al. 1988, Nielsen 1992, Orlov et al. 2009
Dolly varden	*Salvelinus malma*	Salmonidae	0.0052	3.1150	Froese et al. 2014, Underwood et al. 1997
Starry flounder	*Platichthys stellatus*	Pleuronectidae	0.0109	3.1059	Froese et al. 2014, IGFA 2001
Kelp greenling	*Hexagrammos decagrammus*	Hexagrammidae	0.0156	3.0000	Froese et al. 2014
Masked greenling	*Hexagrammos octogrammus*	Hexagrammidae	0.0046	3.1300	Froese et al. 2014
Whitespotted greenling	*Hexagrammos stelleri*	Hexagrammidae	0.0031	3.4278	Froese et al. 2014
Crescent gunnel	*Pholis laeta*	Pholidae	0.0018	3.1500	Froese et al. 2014
Penpoint gunnel	*Apodichthys flavidus*	Pholidae	0.0018	3.1500	Froese et al. 2014
Pacific Herring	*Clupea pallasii*	Clupeidae	0.0067	3.1509	Froese et al. 2014, Park and Huh 2015
Lingcod	*Ophiodon elongatus*	Hexagrammidae	0.0133	3.0000	Froese et al. 2014
Shiner perch	*Cymatogaster aggregata*	Embiotocidae	0.0195	3.0200	Froese et al. 2014
Bay Pipefish	*Syngnathus leptorhynchus*	Syngnathidae	0.0002	3.1200	Bayer 1980
Pygmy poacher	*Odontopyxis trispinosa*	Agonidae	0.0039	3.1200	Froese et al. 2014
Sturgeon poacher	*Podothecus accipenserinus*	Agonidae	0.0039	3.1200	Froese et al. 2014
Tubenose poacher	*Pallasina barbata*	Agonidae	0.0039	3.1200	Froese et al. 2014
Walleye pollock	*Gadus chalcogrammus*	Gadidae	0.0195	2.8753	Froese et al. 2014
Snake prickleback	*Lumpenus sagitta*	Stichaeidae	0.0019	2.9900	Froese et al. 2014
Black rockfish	*Sebastes melanops*	Sebastidae	0.0211	3.0000	Froese et al. 2014
Brown rockfish	*Sebastes auriculatus*	Sebastidae	0.0102	3.0700	Froese et al. 2014
Copper rockfish	*Sebastes caurinus*	Sebastidae	0.0175	3.0000	Colton and Larson 2007, Froese et al. 2014
Quillback rockfish	*Sebastes maliger*	Sebastidae	0.0297	3.0000	Froese et al. 2014
Unknown rockfish	*Sebastes sp.*	Sebastidae	0.0172	3.0492	mean values of known *Sebastes* sp.and Colton and Larson 2007
Chinook salmon	*Oncorhynchus tshawytscha*	Salmonidae	0.0133	3.0000	Froese et al. 2014
Chum salmon	*Oncorhynchus keta*	Salmonidae	0.0185	3.1000	Froese et al. 2014

Table S3.2 continued

Coho salmon	*Oncorhynchus kisutch*	Salmonidae	0.0112	3.0000	Froese et al. 2014
Pink salmon	*Oncorhynchus gorbuscha*	Salmonidae	0.0137	3.2500	Erokhin et al. 1990
Pacific sand lance	*Ammodytes personatus*	Ammondytidae	0.0404	3.0060	Froese et al. 2014
Buffalo sculpin	*Enophrys bison*	Cottidae	0.0091	3.0900	Jeong et al. 1997
Great sculpin	*Myoxocephalus polyacanthocephalus*	Cottidae	0.0125	3.1356	Froese et al. 2014, IGFA 2001, Orlov et al. 2009
Grunt sculpin	*Rhamphocottus richardsonii*	Rhamphocittidae	0.0100	3.0400	Froese et al. 2014, Karpov and Kwiecien 1988
Longhorn sculpin	*Myoxocephalus octodecemspinosus*	Cottidae	0.0071	3.1300	Froese et al. 2014
Manacled sculpin	*Synchirus gilli*	Cottidae	0.0071	3.1300	Froese et al. 2014
Padded sculpin	*Artedius fenestralis*	Cottidae	0.0071	3.1300	Froese et al. 2014
Pacific staghorn sculpin	*Leptocottus armatus*	Cottidae	0.0400	2.8200	Froese et al. 2014, Ruiz-Campos et al. 2006
Sailfin sculpin	*Nautichthys oculofasciatus*	Hemitripteridae	0.0045	3.1100	Froese et al. 2014
Shorthorn sculpin	*Myoxocephalus scorpius*	Cottidae	0.0160	3.0560	Froese et al. 2014
Silverspotted sculpin	*Blepsias cirrhosus*	Hemitripteridae	0.0088	3.0278	Froese et al. 2014
Smoothhead sculpin	*Artedius lateralis*	Cottidae	0.0071	3.1300	Froese et al. 2014
Tidepool sculpin	*Oligocottus maculosus*	Cottidae	0.0071	3.1300	Froese et al. 2014
Pacific sanddab	*Citharichthys sordidus*	Paralichthyidae	0.0093	3.0800	Froese et al. 2014
Speckled sanddab	*Citharichthys stigmaeus*	Paralichthyidae	0.0071	3.1500	Froese et al. 2014
Butter sole	*Isopsetta isolepis*	Pleuronectidae	0.0091	3.0900	Froese et al. 2014
C-O Sole	*Pleuronichthys coenosus*	Pleuronectidae	0.0091	3.0900	Froese et al. 2014
English sole	*Parophrys vetulus*	Pleuronectidae	0.0091	3.0153	Froese et al. 2014, Gunderson et al. 1988
Rock sole	*Lepidopsetta spp.*	Pleuronectidae	0.0206	2.8580	Froese et al. 2014
Threespine stickleback	*Gasterosteus aculeatus*	Gasterostaeidae	0.0114	3.1160	Froese et al. 2014, Ruiz-Campos et al. 2006
Tubesnout	*Aulorhynchus flavidus*	Aulorhynchidae	0.0004	3.4300	Bayer 1980
Brown Irish lord	*Hemilepidotus spinosus*	Hexagrammidae	0.0071	3.1300	Froese et al. 2014
Unknown sculpin		Cottidae	0.0138	3.0815	mean values of known Cottidae
Unknown flatfish		Pleuronectidae	0.0106	3.0657	mean values of known Pleuronectidae
Unknown greenling		Hexagrammidae	0.0077	3.1859	mean values of known Hexagrammidae
Unknown Myoxocephalus	*Myoxocephalus sp.*	Cottidae	0.0137	3.1018	mean values of known *Myoxocephalus sp.*
Unknown gunnel		Pholidae	0.0018	3.1500	mean values of known Pholidae
Unknown Artedius	*Artedius sp.*	Cottidae	0.0071	3.1300	mean values of known *Artedius* sp.

Table S3.3: Mean tissue values (+/- SD) and results of t-test for differences in δ^{13}C and δ^{15}N values for conspecifics between low and high sea otter regions.

	n		δ13C				δ^{15}N			
Abbr.	High	Low	High	Low	t	p	High	Low	t	p
SG	7	6	-7.50 (0.76)	-8.20 (0.80)	1.606	0.138	6.18 (0.60)	5.69 (0.64)	1.427	0.183
EP	5	3	-14.26 (0.45)	-15.10 (0.74)	1.764	0.179	8.52 (0.30)	9.40 (0.45)	-3.036	0.054
POM	4	6	-18.12 (0.18)	-19.55 (0.38)	7.976	< 0.001	8.58 (0.13)	7.75 (0.24)	7.135	< 0.001
FU	6	6	-14.13 (2.66)	-14.04 (2.99)	-0.057	0.956	7.56 (0.43)	6.99 (0.34)	2.522	0.031
SK	5	6	-16.96 (2.33)	-18.55 (1.32)	1.355	0.224	8.19 (0.39)	7.42 (0.37)	3.324	0.010
UL	6	5	-17.83 (3.19)	-19.23 (2.07)	0.875	0.405	7.35 (0.21)	7.22 (0.42)	0.663	0.533
IDO	6	7	-13.18 (0.65)	-12.62 (0.38)	-1.859	0.101	9.25 (0.31)	9.30 (0.27)	-0.300	0.770
BUT	6	6	-16.81 (0.75)	-16.90 (0.49)	0.234	0.821	8.17 (0.21)	9.48 (0.44)	-6.568	< 0.001
MAC	6	6	-11.67 (1.34)	-12.12 (0.77)	0.709	0.498	10.13 (0.70)	10.62 (0.61)	-1.296	0.225
DSH	6	6	-12.62 (0.64)	-13.20 (0.49)	1.474	0.178	11.86 (0.19)	11.48 (0.33)	2.398	0.044
HEL	6	4	-11.81 (0.79)	-11.35 (1.52)	-0.553	0.609	11.68 (0.45)	11.14 (0.48)	1.804	0.120
GRC	5	6	-12.42 (0.62)	-13.04 (0.71)	1.554	0.155	11.60 (0.35)	12.15 (0.71)	-1.693	0.131
RRC	-	6	-	-13.76 (0.53)	-	-	-	12.69 (0.42)	-	-
SHN	6	6	-15.33 (0.66)	-15.94 (1.50)	0.912	0.393	13.40 (0.37)	12.86 (0.07)	3.513	0.015
SNK	6	4	-13.71 (1.17)	-13.81 (1.69)	0.107	0.919	12.96 (0.29)	12.84 (0.61)	0.377	0.726
STG	6	6	-15.25 (0.92)	-13.95 (0.66)	-2.798	0.021	14.00 (0.23)	13.45 (0.64)	1.973	0.094

Table S3.4: Full SIMPER results on FA contributing most to multivariate dissimilarity for taxa with evidence ($P < 0.05$ from PERMANAOVA) of an effect of sea otter region on whole FA profiles. All SIMPER analyses were performed with 9999 permutations.

			Mean FA %			
Taxon	N FA sum > 90%	FA	High sea otter	Low sea otter	Average dissimilarity (SD)	Cumulative dissimilarity
Seagrass	10	18: 3ω3	36.0	37.6	1.2 (1.0)	19.1
		16:0	33.1	32.3	0.9 (0.6)	33.2
		16:3ω3	5.7	7.0	0.8 (0.5)	45.6
		18:2ω6	6.2	7.0	0.8 (0.6)	57.9
		14:0	1.6	0.6	0.5 (0.5)	65.8
		18:0	4.6	4.7	0.4 (0.3)	72.6
		22:0	5.5	5.0	0.3 (0.2)	77.2
		16:1ω7	0.8	0.9	0.3 (0.2)	81.6
		20:5ω3	0.7	0.2	0.3 (0.2)	86.0
		20:0	3.4	2.9	0.3 (0.2)	90.3
Fucus	15	16:0	30.9	31.2	0.7 (0.4)	15.6
		18:1ω9	11.3	11.8	0.4 (0.3)	25.8
		20:4ω6	7.3	6.5	0.4 (0.3)	35.3
		14:0	19.1	19.5	0.4 (0.3)	44.7
		20:5ω3	4.0	3.3	0.3 (0.2)	52.5
		18:2ω6	11.4	11.3	0.3 (0.2)	59.3
		18:3ω3	5.2	4.8	0.3 (0.2)	65.5
		18:0	2.2	2.7	0.2 (0.2)	71.0
		18:4ω3	2.1	1.8	0.2 (0.1)	75.7
		20:1ω9	0.4	0.1	0.1 (< 0.1)	79.2
		20:3ω6	1.1	1.2	0.1 (0.1)	82.1
		20:0	1.0	1.2	0.1 (0.1)	84.7
		16:1ω7	0.9	1.1	0.1 (0.1)	87.3
		15:0	0.8	0.9	0.1 (< 0.1)	89.2
		22:1ω9	0.2	0.0	0.1 (0.1)	91.0
POM	15	14:0	20.9	25.6	2.3 (0.6)	19.4
		22:6ω3	8.3	3.9	2.2 (0.8)	37.7
		20:5ω3	11.6	14.4	1.5 (1.0)	50.3
		16:0	27.5	26.9	1.1 (0.7)	59.1
		16:1ω7	6.7	8.4	0.9 (0.4)	66.3
		18:0	3.4	2.1	0.6 (0.3)	71.6
		16:4ω3	3.4	3.9	0.5 (0.3)	75.8
		20:0	0.8	0.2	0.3 (0.2)	78.4
		18:4ω3	3.3	2.9	0.3 (0.2)	80.6
		18:3ω3	1.0	0.5	0.3 (0.1)	82.9
		16:3ω3	0.8	1.3	0.2 (0.2)	84.9
		16:2ω6	2.2	2.4	0.2 (0.1)	86.6
		18:2ω6	1.5	1.2	0.2 (0.1)	88.0
		18:1ω9	1.0	0.7	0.2 (0.1)	89.3
		15:0	1.3	1.1	0.1 (0.1)	90.5
Ulva	14	18:2ω6	5.5	10.0	3 (2.0)	21.0
		16:0	45.6	41.8	2.1 (1.5)	36.0
		18:4ω3	8.9	7.3	1.2 (1.1)	44.5
		18:3ω3	15.6	15.4	1.1 (0.8)	52.3
		16:3ω3	3.4	4.4	1 (0.6)	58.9
		20:1ω7	0.0	1.7	0.8 (0.9)	64.6
		22:5ω3	1.6	2.3	0.7 (0.6)	69.4
		18:1ω7	4.9	4.8	0.6 (0.4)	73.7
		22:0	1.8	0.7	0.5 (0.5)	77.5
		16:2ω6	1.2	1.1	0.5 (0.3)	80.8

Table S3.4 continued

		18:0	1.9	1.3	0.4 (0.4)	83.5
		18:3ω6	1.1	0.9	0.4 (0.2)	85.9
		20:5ω3	1.8	1.3	0.3 (0.3)	88.2
		20:4ω3	0.7	0.2	0.3 (0.3)	90.1
Pentidotea	18	14:0	6.4	2.5	2.2 (1.3)	16.1
		20:5ω3	21.9	22.2	1.9 (1.2)	29.7
		18:0	11.1	13.7	1.7 (1.0)	42.3
		20:4ω6	2.5	4.7	1.1 (0.6)	50.3
		16:1ω7	4.2	2.5	1.1 (0.7)	58.1
		16:0	28.4	29.3	0.8 (0.5)	63.8
		18:4ω3	1.9	1.1	0.6 (0.4)	68.5
		18:1ω9	4.3	4.0	0.4 (0.3)	71.4
		22:6ω3	4.2	4.4	0.4 (0.3)	74.2
		16:2ω6	1.0	0.3	0.4 (0.3)	77.0
		22:0	0.9	1.6	0.4 (0.3)	79.7
		18:1ω7	2.6	2.8	0.3 (0.3)	82.0
		18:3ω3	1.7	1.6	0.3 (0.2)	84.0
		18:2ω6	1.7	2.0	0.2 (0.2)	85.5
		20:3ω3	0.4	0.8	0.2 (0.2)	86.9
		20:2ω6	0.4	0.8	0.2 (0.1)	88.2
		20:4ω3	0.8	0.5	0.2 (0.1)	89.5
		20:1ω9	0.8	0.7	0.2 (0.2)	90.8
Limpet	20	20:5ω3	18.4	16.0	1.3 (1.1)	13.8
		16:0	26.6	28.5	0.9 (0.5)	23.7
		18:0	10.8	9.5	0.8 (0.6)	32.2
		16:1ω7	4.7	4.2	0.7 (0.4)	39.2
		20:1ω9	2.9	4.2	0.6 (0.6)	45.8
		18:1ω7	6.0	5.0	0.5 (0.7)	51.4
		22:5ω3	1.4	2.2	0.5 (0.5)	56.4
		14:0	7.9	8.0	0.4 (0.3)	60.8
		20:1ω7	2.4	3.1	0.4 (0.3)	64.9
		18:4ω3	1.4	0.9	0.4 (0.3)	68.8
		20:4ω6	3.4	3.9	0.4 (0.2)	72.5
		18:1ω9	1.5	2.0	0.3 (0.2)	75.3
		22:2ω6	1.6	1.3	0.3 (0.2)	77.9
		20:2ω6	0.7	1.0	0.2 (0.2)	80.4
		18:2ω6	1.4	1.6	0.2 (0.1)	82.6
		20:4ω3	1.1	1.1	0.2 (0.1)	84.6
		20:3ω3	0.4	0.7	0.2 (0.1)	86.4
		18:2ω3	0.3	0.0	0.1 (0.2)	87.9
		18:3ω3	0.5	0.7	0.1 (0.1)	89.3
		16:2ω6	0.5	0.3	0.1 (0.1)	90.6
Butter clam	18	16:0	34.6	31.1	1.7 (0.8)	13.1
		22:6ω3	16.5	13.8	1.4 (0.9)	23.9
		22:2ω6	1.2	2.3	1.2 (1.0)	32.7
		20:5ω3	9.8	8.3	1.1 (0.8)	41.3
		22:1ω9	0.1	2.1	1.0 (1.0)	49.0
		22:5ω3	1.9	3.7	0.9 (0.5)	55.5
		22:4ω6	0.5	2.0	0.8 (0.3)	61.3
		18:0	12.7	13.5	0.7 (0.5)	66.5
		20:1ω9	1.9	1.1	0.4 (0.3)	69.7
		14:0	1.6	1.5	0.4 (0.4)	72.7
		20:4ω6	1.7	2.5	0.4 (0.1)	75.5
		iso - 17:0	3.2	3.5	0.3 (0.2)	78.1
		20:2ω6	1.1	0.5	0.3 (0.2)	80.5
		18:4ω3	0.3	0.6	0.3 (0.2)	82.8
		anteiso - 17:0	0.9	1.4	0.3 (0.2)	84.8
		20:1ω7	3.5	3.0	0.2 (0.1)	86.6
		17:0	1.3	1.8	0.2 (0.1)	88.4

Table S3.4 continued

		22:4ω3	0.7	0.4	0.2 (0.2)	90.1
Dock shrimp	16	16:0	38.0	35.8	1.2 (0.7)	20.3
		20:5ω3	19.5	18.3	0.6 (0.3)	31.0
		18:0	9.4	10.5	0.6 (0.4)	41.1
		15:0	0.8	1.8	0.5 (0.5)	49.5
		22:6ω3	11.6	10.9	0.5 (0.3)	58.0
		17:0	1.2	1.9	0.3 (0.2)	63.5
		20:4ω6	1.1	1.6	0.3 (0.1)	68.0
		14:0	3.4	3.3	0.2 (0.2)	72.4
		17:1ω9	0.1	0.5	0.2 (0.1)	75.4
		22:5ω3	0.9	0.9	0.2 (0.1)	78.2
		16:1ω7	1.9	2.2	0.1 (0.1)	80.8
		iso - 17:0	0.5	0.7	0.1 (0.1)	83.3
		18:1ω9	3.9	3.9	0.1 (0.1)	85.4
		18:3ω3	0.4	0.6	0.1 (0.1)	87.1
		18:2ω6	1.5	1.5	0.1 (0.1)	88.8
		18:4ω3	0.0	0.2	0.1 (< 0.1)	90.1
Helmet crab	18	20:5ω3	27.8	26.5	1.0 (0.6)	17.9
		16:0	28.9	30.4	0.9 (0.7)	33.6
		22:6ω3	11.7	10.5	0.7 (0.6)	45.2
		18:0	11.1	11.1	0.5 (0.3)	54.6
		20:4ω6	2.9	3.3	0.3 (0.2)	60.7
		17:0	1.2	1.0	0.2 (0.2)	64.1
		22:5ω3	1.2	1.5	0.2 (0.1)	67.3
		18:1ω7	2.4	2.4	0.2 (0.1)	70.4
		18:1ω9	2.6	2.9	0.2 (0.2)	73.5
		18:3ω3	0.5	0.8	0.2 (0.1)	76.5
		18:2ω6	1.7	1.8	0.1 (0.1)	79.0
		14:0	1.1	0.9	0.1 (0.1)	81.4
		15:0	0.7	0.6	0.1 (0.1)	83.4
		16:1ω7	0.8	0.9	0.1 (0.1)	85.0
		anteiso - 17:0	0.3	0.2	0.1 (0.1)	86.5
		iso - 17:0	0.5	0.5	0.1 (< 0.1)	87.8
		20:0	0.4	0.6	0.1 (0.1)	89.1
		20:1ω9	0.5	0.4	0.1 (< 0.1)	90.4
Graeful crab	19	16:0	30.4	27.8	1.3 (0.9)	14.9
		18:0	8.8	10.7	1.1 (1.0)	27.5
		22:6ω3	12.5	11.2	0.8 (0.7)	36.5
		20:4ω6	2.1	3.5	0.7 (0.3)	44.2
		20:5ω3	23.3	23.8	0.5 (0.4)	50.3
		18:2ω6	1.9	1.2	0.4 (0.3)	54.8
		17:0	2.2	2.2	0.4 (0.3)	59.0
		15:0	1.3	1.8	0.4 (0.3)	63.0
		iso - 17:0	1.1	1.8	0.3 (0.2)	66.8
		16:1ω7	1.9	2.2	0.3 (0.2)	70.4
		20:2ω6	1.2	0.6	0.3 (0.3)	73.7
		18:1ω9	3.0	3.2	0.3 (0.2)	77.0
		22:5ω3	2.1	1.7	0.3 (0.2)	80.1
		18:1ω7	2.3	1.9	0.2 (0.2)	82.5
		anteiso - 17:0	0.7	1.0	0.2 (0.1)	84.9
		17:1ω9	0.5	0.6	0.2 (0.2)	87.2
		14:0	0.8	0.7	0.1 (0.1)	88.6
		anteiso - 18:0	0.0	0.2	0.1 (< 0.1)	89.8
		22:4ω3	0.4	0.3	0.1 (0.1)	91.0
Snake prickleback	20	22:6ω3	13.6	15.5	1.9 (1.4)	21.6
		16:0	33.1	34.3	1.0 (0.8)	32.8
		20:5ω3	17.3	16.5	0.7 (0.6)	40.7
		20:4ω6	2.6	3.3	0.6 (0.4)	47.4
		22:5ω3	2.8	2.0	0.6 (0.5)	53.9

Table S3.4 continued

		18:0	11.5	11.1	0.5 (0.3)	59.7
		18:1ω9	2.9	2.9	0.4 (0.3)	64.4
		14:0	2.5	2.1	0.3 (0.1)	67.4
		18:1ω7	2.3	2.0	0.2 (0.2)	70.1
		20:1ω7	0.7	0.9	0.2 (0.2)	72.6
		16:1ω7	1.9	1.5	0.2 (0.2)	75.1
		18:2ω6	1.0	0.7	0.2 (0.1)	77.4
		17:0	1.2	1.4	0.2 (0.1)	79.6
		15:0	0.9	1.2	0.2 (0.1)	81.6
		20:2ω6	0.4	0.1	0.1 (0.1)	83.3
		18:3ω3	0.5	0.3	0.1 (0.1)	84.9
		iso - 17:0	0.7	0.8	0.1 (0.1)	86.5
		22:4ω6	0.5	0.3	0.1 (0.1)	88.0
		20:1ω9	0.8	0.7	0.1 (0.1)	89.4
		18:4ω3	0.0	0.2	0.1 (0.1)	90.8
Staghorn sculpin	16	22:6ω3	17.1	21.2	2.1 (1.1)	26.1
		20:5ω3	15.9	13.3	1.3 (0.7)	42.0
		16:0	32.5	30.7	1.1 (0.9)	55.7
		18:0	14.4	14.1	0.5 (0.3)	62.1
		22:5ω3	4.0	3.5	0.5 (0.3)	67.9
		18:1ω9	3.3	3.7	0.3 (0.3)	72.1
		20:4ω6	2.5	2.1	0.3 (0.2)	75.5
		14:0	1.2	1.3	0.2 (0.1)	77.8
		20:4ω3	0.3	0.7	0.2 (0.2)	80.0
		18:4ω3	0.3	0.3	0.1 (0.1)	81.9
		17:0	0.8	1.0	0.1 (0.1)	83.6
		15:0	0.5	0.7	0.1 (0.2)	85.2
		iso - 17:0	0.6	0.6	0.1 (0.1)	86.7
		18:2ω6	0.8	0.9	0.1 (0.1)	88.2
		18:3ω3	0.5	0.4	0.1 (0.1)	89.5
		16:1ω7	0.9	0.8	0.1 (0.1)	90.7

Table S3.5: Results of Mann-Whitney U tests for differences in marker FA/FA groups for conspecifics between low and high sea otter regions.

	Bacterial		ALA + LIN		Other C_{18} PUFA		PUFA		PAL		ARA		EPA		DHA	
	stat	p	stat	p	stat	p	stat	p	stat	p	stat	p	stat	p	stat	p
Seagrass	30	0.225	10	0.134	36	0.038	7	0.054	17	0.617	30	0.225	37	0.027	23	0.830
Epiphytes	5	0.551	14	0.074	15	0.037	13	0.136	0	0.037	12	0.233	7	1.000	5	0.551
Fucus	14	0.575	27	0.173	22	0.575	32	0.031	4	0.031	32	0.031	33	0.020	0	0.003
POM	24	0.014	24	0.014	21	0.070	16	0.456	0	0.014	0	0.014	3	0.070	24	0.014
Sugar kelp	26	0.055	7	0.171	13	0.784	6	0.121	23	0.171	8	0.235	6	0.121	19	0.407
Ulva	8	0.128	6	0.066	28	0.128	6	0.066	18	1.000	17	0.936	24	0.378	22	0.575
Pentidotea	23	0.830	20	0.943	30	0.225	16	0.520	34	0.074	2	0.008	18	0.721	17	0.617
Limpet	10	0.134	12	0.225	30	0.225	29	0.284	27	0.432	13	0.284	36	0.038	5	0.027
Butter clams	11	0.523	21	0.315	10	0.411	12	0.648	8	0.235	0	0.008	24	0.121	27	0.036
Macoma spp. clam	17	0.936	31	0.045	31	0.045	11	0.298	4	0.031	10	0.230	18	1.000	17	0.936
Dock shrimp	0	0.005	13	0.471	0	0.005	35	0.008	7	0.093	0	0.005	34	0.013	28	0.128
Helmet crabs	11	0.915	3	0.070	15	0.594	20	0.110	8	0.456	8	0.456	19	0.166	20	0.110
Graceful crabs	8	0.235	23	0.171	27	0.036	20	0.411	10	0.411	0	0.008	10	0.411	22	0.235
Shiner perch	22	0.575	23	0.471	12	0.378	27	0.173	34	0.013	23	0.471	25	0.298	17	0.936
Snake prickleback	12	0.648	28	0.022	9	0.315	16	0.927	21	0.315	11	0.523	22	0.235	13	0.784
Staghorn sculpin	28	0.128	22	0.575	20	0.810	25	0.298	18	1.000	13	0.471	7	0.093	34	0.013

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General Conclusion

The recovery of sea otters to Southeast Alaska (SEAK) is a stunning example of a recovering apex predator population that has led to a variety of social and ecological effects. The SEAK sea otter population represents approximately one fifth of the global population (Doroff and Burdin 2015) and is unique in that is actively hunted by Alaska Natives and overlaps with vast seagrass ecosystems (Harper and Morris 2004, USFWS 2014). The growing sea otter population in SEAK has highlighted a need to better understand both sea otter harvest and population dynamics but also the ecological effects of sea otters in nearshore ecosystems. Through our research we have begun to address these questions by examining the spatial and temporal patterns of sea otter harvest and its effect on the sea otter population and by investigating the community and trophic ecology of seagrass communities in light of this apex predator. Overall we have described the varied roles that sea otters play in the SEAK socio-ecological system and highlight how the recovery of apex predators can have diverse effects in that system.

Our analysis of sea otter harvest and its effects on the sea otter population represent the most comprehensive analysis of the SEAK sea otter harvest data set to date. Overall our analyses revealed how location and spatial scale can greatly influence the patterns and effects of subsistence sea otter harvest in the region. These results highlight a disconnect between the scale of sea otter management and the scale of sea otter population dynamics and effects of harvest. As of 2015, the SEAK sea otter stock shows strong signs of growth (Tinker et al. 2019) and little effect of harvest (Chapter 1). However, this is not the scale at which most people, including commercial and subsistence fishermen, interact with and experience the effects of sea otters. This disconnect highlights a potential need to reframe the current management strategy to incorporate smaller scale sea otter population dynamics to address local concerns on sea otters and their effect on local resources. Furthermore, our analysis demonstrates the utility of subsistence harvest data as a tool for population assessment. Since the SEAK stock is surveyed infrequently (7- 10 years), annual sea otter harvest data many allow managers to “fill-in” data gaps between formal surveys. The SEAK sea otter population is expected to continue to grow (Tinker et al. 2019), potentially exacerbating and expanding existing concerns over the sea otter population. In light of this and our analyses here, taking a new approach to sea otter population assessment may be necessary to support fishery, conservation, and sea otter harvest interests.

The role of apex predators in seagrass ecosystems had gained attention around the world, spurred from the dramatic patterns described in California (Hughes et al. 2013) and the Baltic Sea (Moksnes et al. 2008, Baden et al. 2010, 2012). While this research has expanded the trophic breadth of seagrass ecology, one limitation of these studies is that they were constrained to relatively small spatial scales. Here were address this limitation and build off this research by applying the conceptual apex predator – seagrass community trophic cascade model to a much larger spatial scale in SEAK. Our approach also utilized a gradient of apex predator, sea otter, recovery which is rarely accomplished in apex predator studies providing more realism to results as animal populations are often distributed unevenly (Turner 1989, Dunning et al. 1992). Our results highlight how the recovery of apex predators can affect nearshore ecosystems across a broad scale, which may be an essential next step for the management of recovering apex predator populations (Silliman et al. 2018). While we did find generality in many ecological relationships predicted by the model trophic cascade, including a positive relationship between sea otters and seagrass, we found weak evidence of others, notable the relationship between mesopredators and epifauna. The mechanisms leading to the patterns described may not the result of a trophic cascade and remain to be resolved, and may differ from those from California and the Baltic Sea.

Our results provide a detailed assessment of seagrass communities in SEAK, which will hopefully provide a foundation for future research on all aspects of seagrass ecology in the region. The positive relationship between sea otter and seagrass biomass may have large scale implications, as seagrasses are known to increase finfish biomass, including many commercially harvested species, and act as carbon sink (Lefcheck et al. 2019, Prentice et al. 2020). As seagrasses comprise nearly 10,000 km of nearshore habitat in Southeast Alaska future study on seagrass ecology as well as their role as nurseries, and carbon sinks may fill large gaps in current understanding of SEAK nearshore processes. Furthermore our results add to the growing field of recovering apex predator research, especially to habitats not traditionally associated with the species (Silliman et al. 2018). As the sea otter population in expected to grow throughout SEAK (Tinker et al. 2019), our results from Prince of Wales Island may translate to other regions of SEAK. However, physical factors such as temperature and turbidity, which are greatly influenced by nearby glaciers (Arctic Monitoring and Assessment Programme 2012), could modulate the effect of sea otters. From the perspective of increasing temperatures due to climate change, seagrass in SEAK may be poised to benefit. *Zostera marina* growth can be limited below 10°C (Evans et al. 1986, Zimmerman et al. 2015), and such temperatures appear to persist through April at our study sites (Chapter 2). Therefore, increasing temperatures may expand the seagrass growing season.

Building off our research on the seagrass community relationships, our biomarker analyses found varied patterns of seagrass trophic structure and the effect of sea otters depending on the metric used (biomass, stable isotopes, and fatty acids). Our fatty acid results indicate that seagrass community consumers, such as isopods, gastropods, crabs, and fishes, appear to rely on diverse diets, suggesting that a perturbation from sea otters may be buffered by multiple food web connections. From one perspective these results may suggest that the presence of sea otters confers a change in the biochemical pathways in seagrass ecosystems; however, to date we have little evidence of a mechanistic link between sea otter presence and the patterns of FA in consumers and primary producers. Rather, a more likely explanation is that our biomarker results reflect natural variability of seagrass community trophic structure in SEAK. Further examination of the patterns described in Chapter 3, especially with consideration of environmental variables, may provide greater insight to the trophic dynamics of these seagrass communities.

These data represent the first study to combine biomass, SI, and FA data in SEAK and largely confirm findings of similar studies around the world including the northwest Pacific (Kharlamenko et al. 2001), Baltic Sea (Jaschinski et al. 2008, Jankowska et al. 2018), Chesapeake Bay (Douglass et al. 2010), and Northern New Zealand (Alfaro et al. 2006). Our results raise multiple questions on the trophic dynamics of SEAK seagrass communities, including the role of detrital or bacterial food sources, and whether or not sea otters are mechanistically tied to variation in FA values of primary producers or consumers. The role of apex predators on the FA composition of any taxa has not been experimentally assessed but presents alternative perspectives of trophic structure. From the apex predator perspective it can be assumed that top-down forces will confer changes in the biomass of lower trophic levels. However, the biomarkers of any taxa are a function of an individual's diet, from a more bottom-up perspective. Chapter 2 and 3 underscore these two competing views of seagrass trophic ecology. It is widely accepted that seagrass communities, especially *Zostera marina*, are controlled by top-down forces (Hughes et al. 2004, Heck and Valentine 2007, Duffy et al. 2014).

However, biomarker-directed studies indicate a community with multiple ultimate energy sources, suggesting that any top-down herbivory from one species to another would be weak. Two factors which may contribute to this dichotomy are the role of grazer diversity, which can modulate top-down forcing in seagrass communities (Duffy et al. 2015), and spatial scale. Research in the Baltic Sea examined how spatial scale affected trophic interactions in seagrass communities, and found that the trophic interactions between seagrass epifauna at small scales can be effected by the biomass of fishes at a larger scale (Donadi et al. 2017). These results highlight how scale may affect the results seen in Chapter 2 and 3, compared to other studies.

This dissertation represents research on the sea otter population and sea otter effects in ecosystems for a new phase of their occupation in Southeast Alaska. Sea otters have clearly made it out of the initial stages of recovery, show strong signs of growth across the region despite being harvested, and are only at approximately one-third of their projected carrying capacity in the region (Tinker et al. 2019). Given the state of the sea otter population and sea otters' ecological effects in seagrass ecosystems and kelp forests (e.g. Estes and Duggins 1995), local, state, and federal agencies may consider a new perspective on sea otter and ecosystem management. Sea otters are conspicuous members of the SEAK socio-ecological system through their effects on fisheries and ecosystems and their cultural importance as a subsistence resource. To this end resource management, conservation science, and ecological research can consider sea otters not as a returning part of the ecosystem, but one that is here to stay. This may mean adapting local and regional management strategies to account for the effects of sea otters and their projected growth. While some ecological mechanistic relationships remain unresolved, the research presented here, in addition to the growing body of literature on sea otters in SEAK, is a strong indication of the role of sea otters in the region. This dissertation contributes a detailed assessment of SEAK seagrass ecosystems. Seagrasses make up nearly 10,000 km of nearshore habitat in the region but have received little research attention. As seagrasses are considered essential fish habitats (NOAA 2006), further research on how these communities function and contribute to the larger SEAK socio-ecological system are important.

I hope that this research lays the ground work for further investigations into sea otter population dynamics, the role and interplay of subsistence sea otter hunting, the effect of sea otters in nearshore ecosystems and seagrass community and trophic ecology in general.

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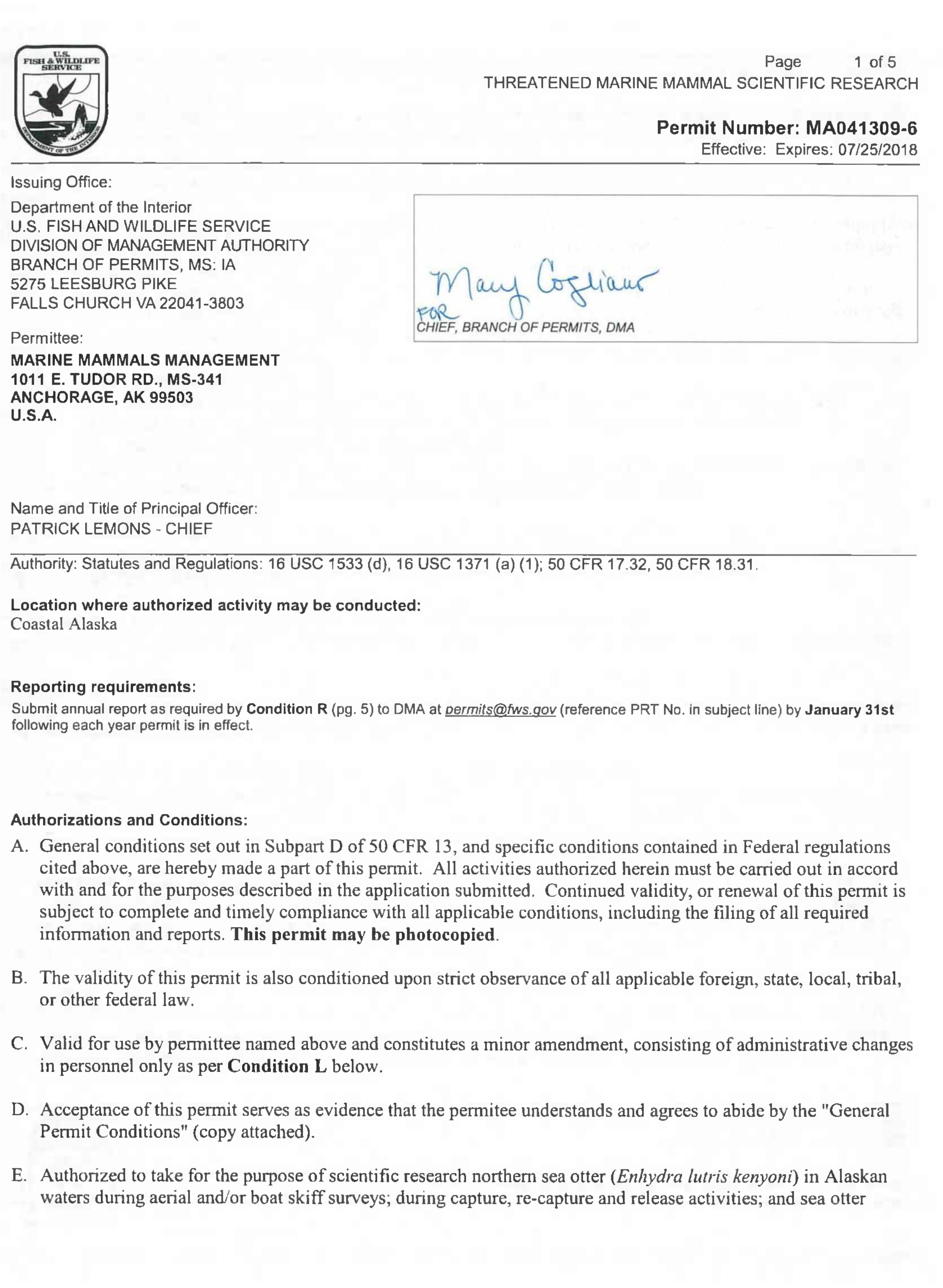
Appendix A

USFWS Marine Mammal Permit



Page 1 of 5
THREATENED MARINE MAMMAL SCIENTIFIC RESEARCH

Permit Number: MA041309-6
Effective: Expires: 07/25/2018

Issuing Office:

Department of the Interior
U.S. FISH AND WILDLIFE SERVICE
DIVISION OF MANAGEMENT AUTHORITY
BRANCH OF PERMITS, MS: IA
5275 LEESBURG PIKE
FALLS CHURCH VA 22041-3803

Mary Cogliano
FOR
CHIEF, BRANCH OF PERMITS, DMA

Permittee:

MARINE MAMMALS MANAGEMENT
1011 E. TUDOR RD., MS-341
ANCHORAGE, AK 99503
U.S.A.

Name and Title of Principal Officer:
PATRICK LEMONS - CHIEF

Authority: Statutes and Regulations: 16 USC 1533 (d), 16 USC 1371 (a) (1); 50 CFR 17.32, 50 CFR 18.31.

Location where authorized activity may be conducted:
Coastal Alaska

Reporting requirements:
Submit annual report as required by **Condition R** (pg. 5) to DMA at *permits@fws.gov* (reference PRT No. in subject line) by **January 31st** following each year permit is in effect.

Authorizations and Conditions:

A. General conditions set out in Subpart D of 50 CFR 13, and specific conditions contained in Federal regulations cited above, are hereby made a part of this permit. All activities authorized herein must be carried out in accord with and for the purposes described in the application submitted. Continued validity, or renewal of this permit is subject to complete and timely compliance with all applicable conditions, including the filing of all required information and reports. **This permit may be photocopied**.

B. The validity of this permit is also conditioned upon strict observance of all applicable foreign, state, local, tribal, or other federal law.

C. Valid for use by permittee named above and constitutes a minor amendment, consisting of administrative changes in personnel only as per **Condition L** below.

D. Acceptance of this permit serves as evidence that the permitee understands and agrees to abide by the "General Permit Conditions" (copy attached).

E. Authorized to take for the purpose of scientific research northern sea otter (*Enhydra lutris kenyoni*) in Alaskan waters during aerial and/or boat skiff surveys; during capture, re-capture and release activities; and sea otter carcass collection (both sexes and all age classes) during beach surveys and necropsies, as described in application file and in Tables 1 - 4 (**Appendix A**), and as conditioned below. Initial takes that include capture and sampling cannot begin until written authorization is received from the Division of Management Authority (DMA).

F. The permittee is authorized to take and release up to 100 per year northern sea otters (*E. l. kenyoni*) of all ages and sexes as follows: capture, immobilize and hold, anesthetize, flipper tag, inject with subcutaneous PIT tag, collect morphometric and biological samples (see Table 4); a subset (up to 50 animals per year) consisting of adults and juveniles (both sexes but no pregnant females) may be captured/re-captured/transported (as per Conditions J & K) and abdominally implanted with radio transmitters and time depth recorders (TDRs).

G. The Permittee is authorized to incidentally harass non-target sea otters, but harassment should be minimized as described in Permittee's application file. Every effort should be made to ensure that other marine mammal species are not in the immediate area prior to commencing authorized activity.

H. Should any marine mammal species other than northern sea otters be encountered during the authorized activities, Permittee must immediately move away from the site and detour around the animals, or if aerial, rise to over 1000 feet (305 meters).

I. Activities are limited to those conducted for the purposes, by the means, in the locations, and during the periods of time as described in the Permittee's application and supplemental information.

J. **CAPTURE/RE-CAPTURE**:

1) Three attending capture personnel must be present during all authorized activities, one of which should be a Principle Investigator with extensive training and previous capture experience (see L. below for co-investigator requirements).
2) Prior to initiating any field captures/re-captures for the instrumentation procedures:
   (a) Each capture and spotting team must have on-hand an up-to-date list (i.e., updated since the most recent implantation surgery) of all animals previously captured;
   (b) This up-to-date list must include each otter's radio frequency and external tag identification;
   (c) Spotters must scan all radio-frequencies of otters likely to occur in the capture area that have been implanted within the past four weeks;
   (d) If a sea otter is positively identified as having undergone surgery within the past four weeks, it may not be targeted for re-capture (unless it is being purposefully targeted as required by Cond. K.5); AND
   (e) Once a captured otter has been brought alongside the capture vessel, the radio frequency and external tag must be checked and compared to the up-to-date animal list, and if it is determined that an otter has been mistakenly re-captured, it must be released immediately at the capture location.
3) Tangle nets may not be set if weather or sea state is, or is forecast to be, such that the recovery of entangled otters may be impeded. Nets must be monitored at least every 6 hours, or every 2 to 4 hours when visibility is poor.
4) Dip nets and underwater capture methods using a diver-held trap and net bag, as described in Permittee's application, may also be used.
5) Permittee may not initiate capture activities in areas where a high number of pregnant otters occur. Permittee must cease capture activities in any area where over 20% of sea otters captured per day are otters in their 3rd trimester of pregnancy.
6) Disturbance of animals should be minimized by exercising caution when approaching and capturing animals,

particularly mother-pup pairs, and the approach must be halted if there is evidence that the activity may be interfering with pair bonding, nursing, reproduction, feeding or other vital functions.

7) To minimize the chance of mother-pup separation, mother and pup should be captured together and released simultaneously following the recovery period. Dependent pups must not be targeted, unless they are targeted along with their mothers. In the event that a pup is captured and not the mother, the pup must be immediately released and allowed to reunite without sampling.
8) Every feasible effort must be made to recover and treat animals showing signs of stress, aberrant behavior, or are orphaned as a result of the permitted activities. The animals must be fully recovered prior to release to ensure that there is no post-operative bleeding. A qualified veterinarian must be consulted any time animals being held are observed shivering or otherwise appear stressed and action shall be taken based on the veterinarian's advice.
9) Captured animals must be released in the proximity of the capture location.
10) In the event that a lactating female is killed or seriously injured as a result of the activities, the female's orphaned or abandoned pup must be humanely provided for (i.e. recovered and cared for or euthanized if absolutely necessary). Such events must be reported to DMA as described in condition N below.

K. **INSTRUMENTING OTTERS**:

1) Only qualified veterinarians are authorized to surgically implant radio transmitters and TDRs; no pregnant females may be radio- or TDR-tagged.
2) Surgically implanted animals should be returned to the same location from which they were captured.
3) To minimize the chance of mother-pup separation following surgery, only sea otters captured with their pups can be surgically implanted so both the mother and pup can be released simultaneously following the recovery period.
4) Monitoring of instrumented animals should be as extensive as possible. Attempts to locate individual animals should be made at least weekly, for approximately four weeks following surgery if possible, weather permitting.
5) Every feasible effort should be made to recover and treat instrumented otters that show signs of stress or aberrant behavior or are orphaned as a result of the permitted activities. The animals must be fully recovered prior to release to ensure that there is no post-operative bleeding. A qualified veterinarian must be consulted any time animals being held are observed shivering or otherwise appear stressed, and action shall be taken based on the veterinarian's advice.
6) The number of animals which are recaptured for subsequent surgical replacement of implanted radio transmitters is as described in the permit application file. Replacement surgery can be performed no more than one time on any given animal without additional approval from DMA, in consultation with the Marine Mammal Commission.
7) Animals which are re-captured for subsequent surgical removal of implanted radio transmitters and/or TDRs should be closely monitored as in conditions K.4 and K.5, above.

L. The following are hereby designated as Principle Investigators (PI) under this permit and are authorized to use the permit: **Dr. Patrick Lemons, James MacCracken, Joel Garlich-Miller, Kristen Worman, Michelle St. Martin, Michelle Kissling and William Beaty**. All research activities authorized under this permit must be performed by the Permittee's institution biologists or individuals extensively trained in the appropriate techniques and possessing adequate proficiency such that they will not cause undue injury or death of sea otters. The Permittee may designate any other personnel as Co-investigator(s), provided the individuals have received appropriate training and possess adequate proficiency to conduct the research activities in accordance with the permit conditions. Upon designation of additional Co-investigator(s), the Permittee must submit the individuals'

CVs to the Division of Management Authority (DMA). The approvals must remain on file at a designated repository at Permittee's institution for a period of 5 years. A list of all authorized individuals must be reported to DMA as in Condition R, below, and, if requested, must be available to DMA at any time. Approved personnel should possess a copy of this permit when performing authorized research activities, and their names must be included in the annual report.

M. The principal investigators must ensure that there is effective coordination between the activities authorized under this permit and other research activities being conducted in or near the study areas to minimize possible adverse impacts on marine mammals in the wild, and to avoid unnecessary duplication of research.

N. In the event that **FOUR** animals die or are injured during or following permitted activities and that mortality or injury can reasonably be attributed to such activities the Permittee must immediately notify DMA (1-800-358-2104 or fax 703-358-2281 or by email) to describe the circumstances that led to the injury or mortality and to provide suggestions for measures to prevent or minimize the chances of future mortalities or injuries. DMA will have the discretion of changing permit conditions.

In the event that ANY ADDITIONAL animals die or are injured during or following permitted activities and the morality and/or injury can reasonably be attributed to such activities:
1) Immediately suspend research activities until re-authorized by DMA;
2) Immediately notify DMA (1-800-358-2104 or fax 703-358-2281) and follow up such verbal notification with a written report detailing the circumstances that led to the injury or mortality and suggesting measures to prevent or minimize the chances of future mortalities or injuries;
3) DMA, in consultation with the Marine Mammal Commission (MMC) may subsequently authorize continuation of the research with any necessary modifications/conditions or initiate revocation procedures.

O. Necropsies must be performed by a qualified veterinarian experienced in sea otter pathology on any animals that die during the project in order to evaluate both the long and short term effects of capture, handling, implants, etc. A copy of the necropsy report must be provided to DMA.

P. If requested by DMA, the applicant must cooperate with any review of scientific research conducted pursuant to this permit and will provide any documents or other information relating to the scientific research

Q. Permittee (and authorized research collaborators) must maintain compliance with all provisions of a Registered Research Facility under the Animal Welfare Act as required by the U.S. Department of Agriculture, Animal and Plant Health Inspection Service. A copy of the Permittee's and co-investigators' Institutional Animal Care and Use Committee (IACUC) approvals of the proposed research should be submitted in the first annual report, as described in R.9 below. Upon expiration of Permittee's Institutional Animal Care and Use Committee (IACUC) approval, documentation of an extension of this approval must be provided to DMA.

R. Report of Activities: Copies of an Annual Report of the previous year's activities must be submitted by January 31 each year to DMA at the following email: permits@fws.gov <mailto:permits@fws.gov> with reference to the permit number in the subject line. The Annual Report shall include, at a minimum, the following:

1) A summary of research activities conducted.
2) *Captures of individuals*: tabulation of sea otters captured indicating age, sex, weight, type of mark (i.e. tags), tissue samples taken, dates of capture and release and date last observed (if observed since release date).

3) *Captures of mother/pup pairs*: tabulation of mother/pup pairs captured indicating a) age and weight of mother, b) estimated age, sex, and weight of pup, type of mark (i.e., tag/transponder/radio implant), tissue samples taken, dates of capture, release, re-capture and release; date last observed; incidence and date of any mother/pup separation.
4) Results of necropsies performed on animals that died before or after release.
5) Tabulation of carcasses collected during beach surveys including gender, age class, and necropsy results.
6) Discussion of any problems or complications encountered during the research, including any injury or mortality referenced in Condition N.
7) Discussion of study results, including the progress made in meeting the objectives of the research as described in the application, the nature of and rationale for additional studies for upcoming year, and steps that have been or will be taken to coordinate the research activities with other sea otter researchers.
8) List of approved personnel.
9) Copy of IACUC proposal and approvals of the proposed research (for first annual report or extension of approval).
10) The final report should include a summary of data analyses, results, conclusions, and copies of any published research findings.

S. If permittee desires to change study procedures from that previously described in the Permittee's file, then a letter must be submitted to DMA describing the proposed changes, and confirmation that the proposed changes fall within the authorized TAKES in the permit must be received from DMA prior to undertaking the procedural modifications.

T. The authorized permit activities may be extended beyond the expiration date **only** if the renewal request is received by the DMA **at least 30 days prior to the expiration of the permit** [50 CFR 13.22(c)] available at: <http://go.usa.gov/xYDUk> (case sensitive).

APPENDIX A: TAKE TABLES

Table 1. Level A takes of live northern sea otters (*Enhydra lutris kenyoni*) from the wild per year

Total Take	Drug/Teeth/Tag/Blood	Surgically Implant/Transport	TDR Implant
100	100	50	50

Table 2. Level B harassment of live northern sea otters (*Enhydra lutris kenyoni*) from the wild per year

Total Take	Aerial (300ft and above)	Boat	Radio tracking & observations
25,000	24,000	1,000	100

Table 3. Collection and necropsy of carcasses of stranded northern sea otters (*Enhydra lutris kenyoni*) from the wild per year

Total Take
100

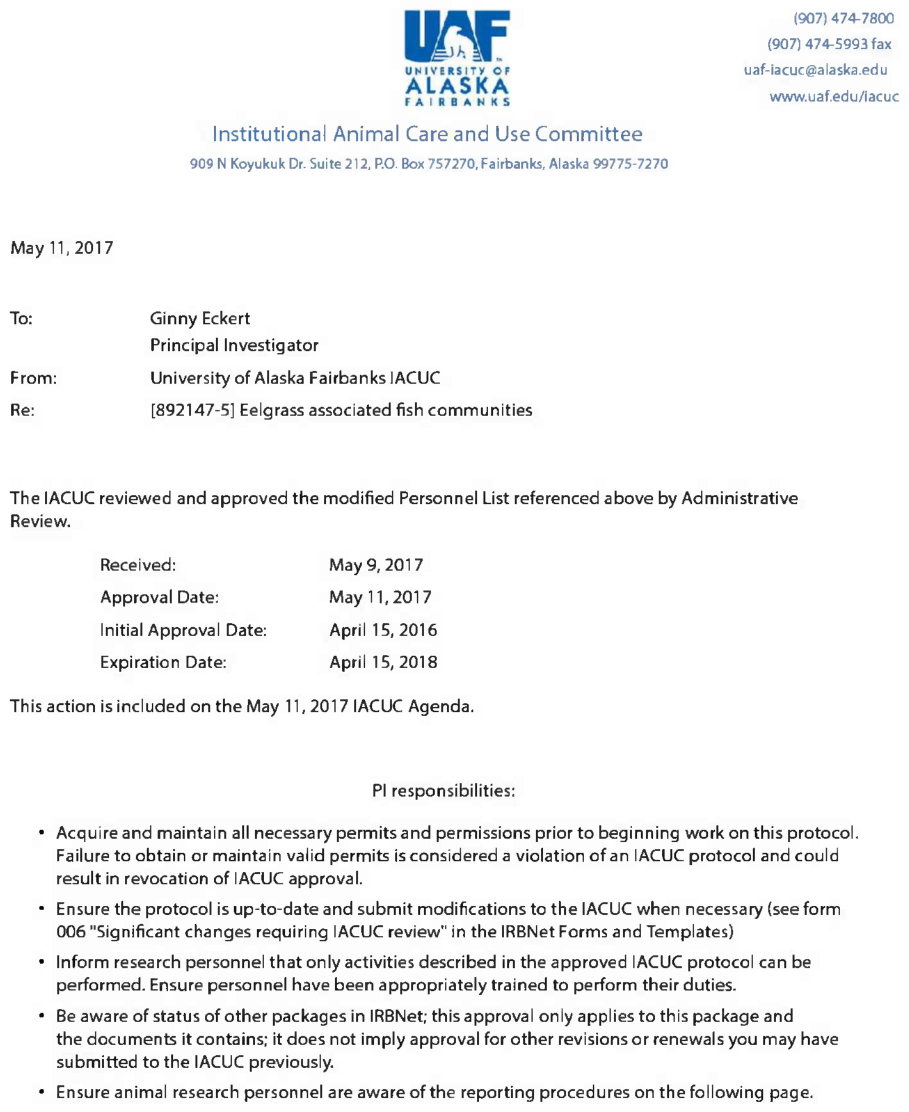
Table 4. Samples authorized for collection from captured sea otters or beachcast remains

Sample Type	Live/ Carcass	Amount Collected	Storage Container	Sample Treatment	Use
Blood & serum	Both	<3% (50cc ad, 10cc juv)	Blood tubes & cryovials	Immediate analysis & frozen	Hematology, clinical chemistry, parasitology, virology, disease archive, microbiology
External swabs	Both	NA	Culture tubes or vials	Refrigerated, frozen, or other	Microbiology, parasitology, virology
Oral & rectal cavity swabs	Both	NA	Cryovials	Frozen or refrigerated	Microbiology
Skin Plugs from flipper tags	Live	2	Cryovials	Fixed in tissue buffer & frozen	Genetic studies
Fecal matter	Both	<100 grams	Plastic tubes & whirlpaks	Frozen or slurried with formalin	Diet assessment, microbiology
Milk	Both	<10cc	Cryovials	Frozen or preserved with BHT	Composition, contaminants, HABs
Urine	Both	<10cc	Cryovials	Frozen	HABs
Lesions	Both	<0.5 grams	Specimen jar	Fixed in formalin	Histopathology
Premolar Tooth	Both	1	Paper envelope	Immediate analysis	Cementum aging

Sample Type	Live/ Carcass	Amount Collected	Storage Container	Sample Treatment	Use
Vibrissae	Both	Up to 2	Paper envelope	Climate controlled	Stable isotopes
Baculum	Carcass	1	Plastic bag/paper box	Climate controlled	Morphometrics, stable isotopes
Tooth	Carcass	All found	Paper envelope	Climate controlled	Cementum aging
Skull	Carcass	1 or portions	Zip lock bag	Climate controlled	Morphometrics
Femur	Carcass	Right	Zip lock bag	Climate controlled	Morphometrics, stable isotopes
Adipose	Carcass	10 grams	Whirlpack	Frozen	Disease archive, histopathology
Lymph nodes	Carcass	1 each	Whirlpack	Frozen	Disease archive, histopathology
Bile	Carcass	4 ml	Amber vial	Frozen	Disease archive, toxicology
Liver	Carcass	1	Cryovials & specimen jar	Frozen & fixed in formalin	Histopathology , toxicology, disease archive
Heart	Carcass	1	Whirlpack	Frozen & fixed in formalin	Histopathology, disease archive, microbiology
Intestines	Carcass	4 inches	Whirlpack	Frozen & fixed in formalin	Histopathology, disease archive, microbiology
Brain	Carcass	1	Whirlpack	Frozen & fixed in formalin	Histopathology, disease archive, microbiology, parasitology
Pancreas	Carcass	1	Whirlpack	Fixed in formalin	Histopathology
Gall bladder	Carcass	1	Whirlpack	Fixed in formalin	Histopathology
Kidney	Carcass	1	Whirlpack	Frozen & fixed in formalin	Histopathology, disease archive, toxicology
Lung	Carcass	1	Whirlpack	Frozen & fixed in formalin	Histopathology, virology, disease archive
Muscle	Carcass	10 grams	Whirlpack	Frozen & fixed in formalin	Histopathology, genetics, disease archive
Pelt	Carcass	1	Zip lock bag	Tanned	Education and outreach
Pericardial fluid	Carcass	4 ml	Cryovial	Frozen	Disease archive, microbiology, HABs
Spleen	Carcass	5 ml	Cryovial	Frozen	Disease archive, histopathology
Testicle	Carcass	1	Specimen jar	Frozen & fixed in formalin	Histopathology, life history studies
Female reproductive tract	Carcass	1	Specimen jar	Frozen & fixed in formalin	Histopathology, life history studies
Bladder	Carcass	1	Specimen jar	Fixed in formalin	Histopathology
Stomach	Carcass	1	Specimen jar	Fixed in formalin, cryovial	Histopathology, microbiology
Amniotic fluid	Carcass	4 ml	Cryovial	Frozen	Disease archive, toxicology
Eye	Carcass	1	Specimen jar	Fixed in formalin	Histopathology
Skin	Carcass	10 grams	Specimen jar	Fixed in formalin, Teflon/foil	Histopathology, toxicology

Appendix B

UAF IACUC approval - 2017



UNIVERSITY OF
ALASKA
FAIRBANKS

(907) 474-7800
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www.uaf.edu/iacuc

Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

May 11, 2017

To:	Ginny Eckert Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[892147-5] Eelgrass associated fish communities

The IACUC reviewed and approved the modified Personnel List referenced above by Administrative Review.

Received:	May 9, 2017
Approval Date:	May 11, 2017
Initial Approval Date:	April 15, 2016
Expiration Date:	April 15, 2018

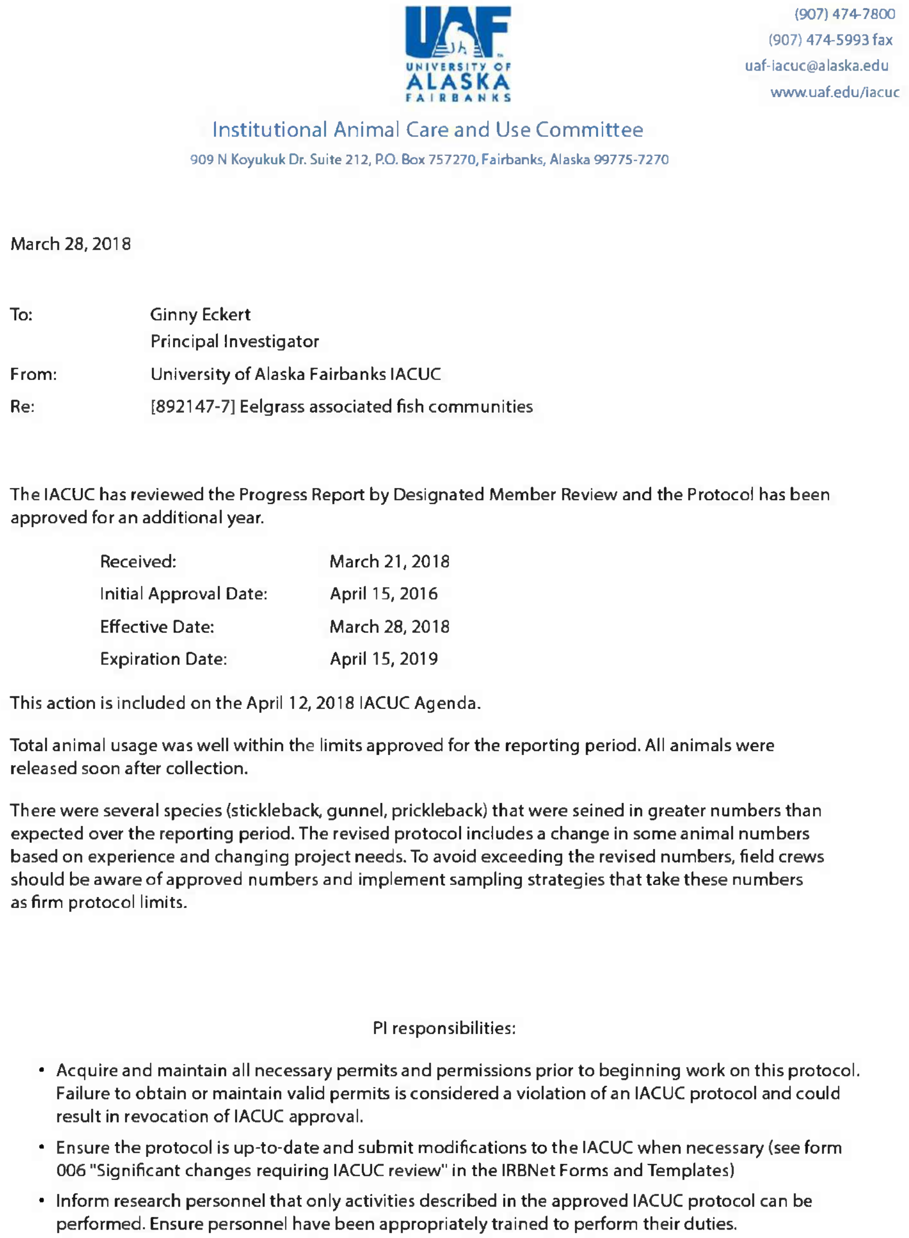
This action is included on the May 11, 2017 IACUC Agenda.

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 C

UAF IACUC approval - 2018



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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

March 28, 2018

To:	Ginny Eckert Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[892147-7] Eelgrass associated fish communities

The IACUC has reviewed the Progress Report by Designated Member Review and the Protocol has been approved for an additional year.

Received:	March 21, 2018
Initial Approval Date:	April 15, 2016
Effective Date:	March 28, 2018
Expiration Date:	April 15, 2019

This action is included on the April 12, 2018 IACUC Agenda.

Total animal usage was well within the limits approved for the reporting period. All animals were released soon after collection.

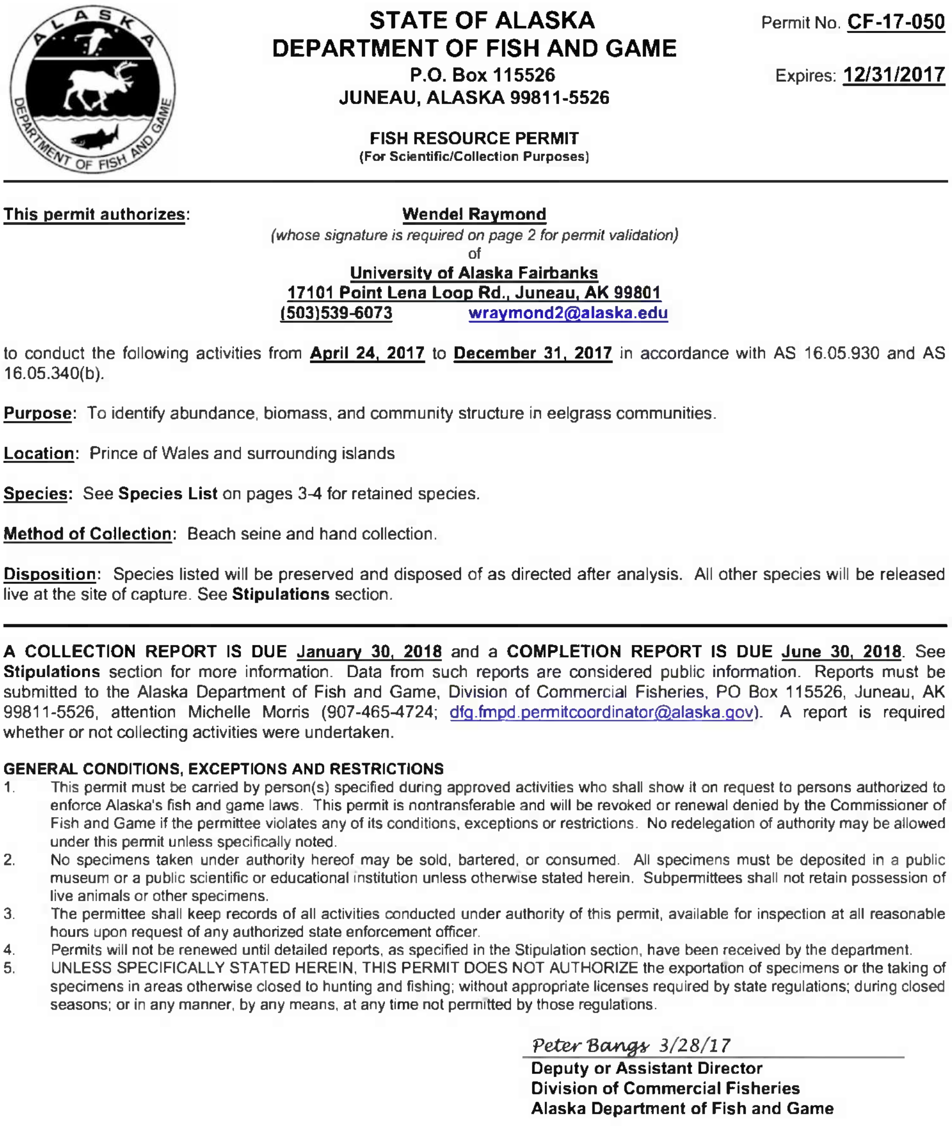
There were several species (stickleback, gunnel, prickleback) that were seined in greater numbers than expected over the reporting period. The revised protocol includes a change in some animal numbers based on experience and changing project needs. To avoid exceeding the revised numbers, field crews should be aware of approved numbers and implement sampling strategies that take these numbers as firm protocol limits.

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.

Appendix D

Alaska Department of Fish and 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; 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 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

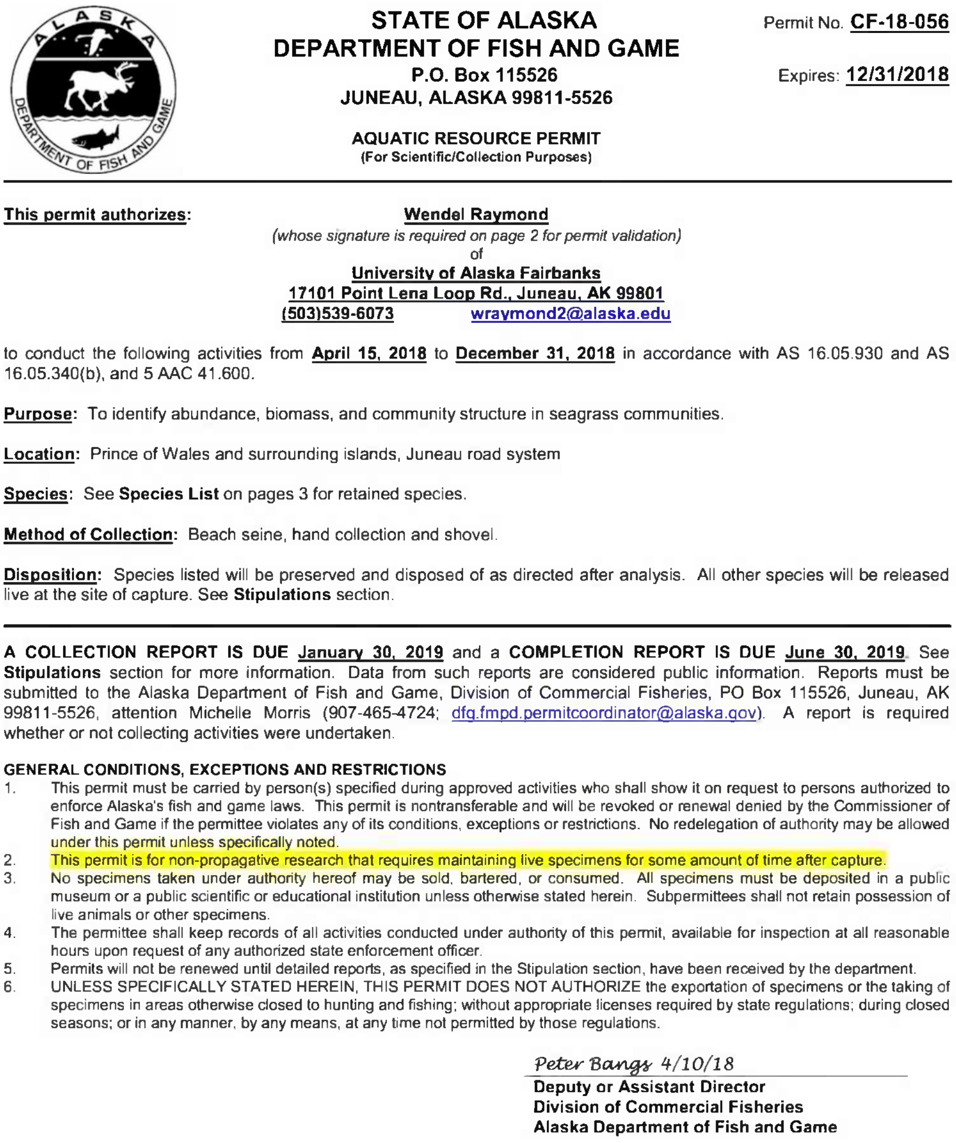
Common Name	Scientific Name	Total retained (size)
Eelgrass (blade only)	*Zostera marina*	3,000 (5-300cm)
Shiner perch	*Cymatogaster aggregata*	180 (10-15cm)
Pink salmon	*Oncorhynchus gorbuscha*	180 (~10cm)
Coho salmon	*Oncorhynchus kisutch*	180 (~10cm)
Sockeye salmon	*Oncorhynchus nerka*	180 (10-15cm)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

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

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

Appendix E

Alaska Department of Fish and Game Permit – 2018



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

Permit No. **CF-18-056**

Expires: **12/31/2018**

AQUATIC 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 15, 2018** to **December 31, 2018** in accordance with AS 16.05.930 and AS 16.05.340(b), and 5 AAC 41.600.

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

Location: Prince of Wales and surrounding islands, Juneau road system

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

Method of Collection: Beach seine, hand collection and shovel.

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, 2019 and a **COMPLETION REPORT IS DUE June 30, 2019**. 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. This permit is for non-propagative research that requires maintaining live specimens for some amount of time after capture.
3. 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.
4. 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.
5. Permits will not be renewed until detailed reports, as specified in the Stipulation section, have been received by the department.
6. 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 4/10/18
Deputy or Assistant Director
Division of Commercial Fisheries
Alaska Department of Fish and Game

CF-18-056 ***continued (page 2 of 3)***

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

Wendel Raymond, Tiffany Stephens, Ann Thomson, Ginny Eckert, Ashley Bolwerk, Lia Domke, Brent Hughs, and Nicole LaRoche.

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 39.145, *Escape Mechanisms for Shellfish and Bottomfish Pots*.
5. Gloves, boots, and collecting gear should be cleaned to remove sediment, vegetation, and seeds and disinfected between streams to reduce the potential of pathogen and invasive species transmission. A wash/rinse in 1/100 Betadyne solution or soak 10% bleach solution for 10 minutes is adequate. Felt or absorbent soles on waders and wading boots are prohibited.
6. Invertebrates, especially sessile invertebrates, should be collected over a broad geographical area to avoid local depletion and disruption of local ecosystems.
7. Upon disposition, specimens must be double-bagged and placed in 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 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.
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. A report is required whether or not research activities were undertaken.
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: Flip Pryor, Judy Lum, Dan Teske, Craig Schwanke
CF Division Files
Alaska Wildlife Troopers–Craig, Juneau

CF-18-056 ***continued (page 3 of 3)***

Species List

Common Name	**Scientific Name**	**Total number**
Threespine stickleback	*Gasterosteus aculeatus*	100 (4 - 18 cm)
Pacific Herring	*Clupea pallasi*	100 (4 - 18 cm)
Shiner perch	*Cymatogaster aggregata*	100 (4 - 18 cm)
Pacific staghorn sculpin	*Leptocottus armatus*	100 (4 - 18 cm)
Chum salmon	*O. keta*	100 (4 - 18 cm)
Coho salmon	*O. kisutch*	100 (4 - 18 cm)
Pink salmon	*Oncorhynchus gorbuscha*	100 (4 - 18 cm)
Great sculpin	*Myoxocephalus polyacanthocephalus*	100 (4 - 18 cm)
Crecent gunnel	*Pholis laeta*	100 (4 - 18 cm)
Pacific sand lance	*Ammodytes hexapteru/personatus*	100 (4 - 18 cm)
Whitespotted greenling	*H. stelleri*	100 (4 - 18 cm)
English sole	*P. vetulus*	100 (4 - 18 cm)
Rock sole	*Pleuronectes bilineatus*	100 (4 - 18 cm)
Padded sculpin	*Artedius fenestralis*	100 (4 - 18 cm)
Smoothhead sculpin	*Artedius lateralis*	100 (4 - 18 cm)
Snake prickleback	*Lumpenus sagitta*	100 (4 - 18 cm)
Speckled sanddab	*C. stigmaeus*	100 (4 - 18 cm)
Pacific sanddab	*Citharichthys sordidus*	100 (4 - 18 cm)
Walleye pollock	*Theragra chalcogramma*	100 (4 - 18 cm)
Eelgrass	*Zostera marina*	5000 (5-300cm)
Surfgrass	*Phyllospadix spp.*	3000 (5-300cm)
Variegated chink snail	*Lacuna variegata*	1500 (5-15mm)
Pacific blue mussel	*Mytilus trossulus*	3000 (5-30mm)
Amphipods	*Family: Gammaridae*	30000 (3-25mm)
Isopod	*Idotea spp.*	3000 (5-35mm)
Polychaete	*Eteone spp.*	300 (10-50mm)
Pile worm	*Nereis vexillosa*	300 (10-50mm)
False white sea cucumber	*Eupentacta pseudoquinquesemita*	300 (10-50mm)
Spot shrimp	*Pandalus platyceras*	300 (10-75mm)
Dock shrimp	*Pandalus danae*	300 (10-75mm)
Opossum mysid	*Neomysis mercedes*	300 (10-75mm)
Alaskan crangon	*Crangon alaskensis*	300 (10-75mm)
Long-clawed crangon	*Crangon franciscorum angustimana*	300 (10-75mm)
Hermit crab	*Pagurus spp.*	300 (10-50mm)
Tuskworm	*Pectinaria granulata*	1500 (10-50mm)
Featherduster worm	*Schizobranchia insignis*	900 (10-75mm)
Burrowing green anemone	*Anthopleura artemisia*	30 (5-25mm)
Littleneck clam	*Protothaca staminea*	300 (5-15mm)
Heart cockle	*Clinocardium nuttalii*	900 (5-50mm)
Green sea urchin	*Strongylocentrotus droebachiensis*	450 (5-30mm)
Broken back shrimp	*Hippolytidae*	300 (10-75mm)
Eelgrass Limpet	*Lotia pelta*	1000 (2-12mm)
Snail	*Margarites sp*	1000 (2-12mm)
Skeleton shrimp	*Caprella sp*	1000 (2-12mm)
Snail	*Littorina sp*	1000 (2-12mm)
Leptocheliidae	*Leptochelia savignyi*	500 (2-12mm)
Sea lettuce	*Ulva sp.*	3000 (1-20cm)
	Monostroma sp.	3000 (1-20cm)
	Scytosiphon sp.	3000 (1-20cm)
	Cladophora sp.	3000 (1-20cm)
	Enteromorpha sp. (Ulva sp)	3000 (1-20cm)
	Smithora sp.	3000 (1-20cm)
	Gracilaria spp.	3000 (1-20cm)
	Saccharina latissima	3000 (1-20cm)

Appendix F

Approval from M.T. Tinker for use of manuscript in dissertation presented as Chapter 1

5/20/2020

To whom it may concern,

Wendel Raymond has my permission to use the following manuscripts as part of his dissertation: Location-specific factors influence patterns and effects of subsistence sea otter harvest in Southeast Alaska

Raymond, W. W., M. T. Tinker, B. Benter, M. Kissling, V. A. Gill, and G. L. Eckert. 2019. Location-specific factors influence patterns and effects of subsistence sea otter harvest in Southeast Alaska. Ecosphere. e02874.

Sincerely,

Dr. M. Tim Tinker
Associate Adjunct Professor, EEB Dept., University of California Santa Cruz
& Nhydra Ecological Research
11 Parklea Dr., Head of St Margaret's Bay, Nova Scotia, Canada
+1-902-222-1378
ttinker@nhydra.com

Appendix G

Approval from M. L. Kissling for use of manuscript in dissertation presented as Chapter 1

April 30, 2020

To whom it may concern,

Wendel Raymond has my permission to use the following manuscripts as part of his dissertation:

Location-specific factors influence patterns and effects of subsistence sea otter harvest in Southeast Alaska

Raymond, W. W., M. T. Tinker, B. Benter, M. Kissling, V. A. Gill, and G. L. Eckert. 2019. Location-specific factors influence patterns and effects of subsistence sea otter harvest in Southeast Alaska. Ecosphere. e02874.

Michelle Kissling
US Fish and Wildlife Service*
3000 Vintage Blvd., Suite 201
Juneau, Alaska 99801
907-723-4139
kissling.michelle@gmail.com
*Current affiliation: University of Montana, Missoula

Appendix H

Approval from B. Benter for use of manuscripts in dissertation presented as Chapter 1

4/30/20

To whom it may concern,

Wendel Raymond has my permission to use the following manuscripts as part of his dissertation:

Location-specific factors influence patterns and effects of subsistence sea otter harvest in Southeast Alaska

Raymond, W. W., M. T. Tinker, B. Benter, M. Kissling, V. A. Gill, and G. L. Eckert. 2019. Location-specific factors influence patterns and effects of subsistence sea otter harvest in Southeast Alaska. Ecosphere. e02874.

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Appendix I

Approval from V. A. Gill for use of manuscript in dissertation presented as Chapter 1

May1, 2020

To whom it may concern,

Wendel Raymond has my permission to use the following manuscripts as part of his dissertation:

Location-specific factors influence patterns and effects of subsistence sea otter harvest in Southeast Alaska

Raymond, W. W., M. T. Tinker, B. Benter, M. Kissling, V. A. Gill, and G. L. Eckert. 2019. Location-specific factors influence patterns and effects of subsistence sea otter harvest in Southeast Alaska. Ecosphere. e02874.

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Appendix J

Approval from B.B. Hughes for use of manuscript in dissertation presented as Chapter 2

April 29, 2020

To whom it may concern,

Wendel Raymond has my permission to use the following manuscripts as part of his dissertation:

Testing the generality of apex predator-mediated trophic cascades in seagrass meadows

Raymond, W. W., B. B. Hughes, T. A. Stephens, C. R. Mattson, A. T. Bolwerk, and G. L. Eckert. Testing the generality of a sea otter meditated trophic cascade in seagrass meadows. Prepared for submission to Proceedings of the National Academy of Sciences of the United States of America

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Appendix K

Approval from T.A. Stephens for use of manuscript in dissertation presented as Chapter 2

30 April 2020

To whom it may concern,

Wendel Raymond has my permission to use the following manuscripts as part of his dissertation:
Testing the generality of apex predator-mediated trophic cascades in seagrass meadows
Raymond, W. W., B. B. Hughes, T. A. Stephens, C. R. Mattson, A. T. Bolwerk, and G. L. Eckert. Testing the generality of a sea otter meditated trophic cascade in seagrass meadows. Prepared for submission to Proceedings of the National Academy of Sciences of the United States of America

Sincerely,

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Appendix L

Approval from C. R. Mattson for use of manuscript in dissertation presented as Chapter 2

4/29/2020

To whom it may concern,

Wendel Raymond has my permission to use the following manuscripts as part of his dissertation:

Testing the generality of apex predator-mediated trophic cascades in seagrass meadows

Raymond, W. W., B. B. Hughes, T. A. Stephens, C. R. Mattson, A. T. Bolwerk, and G. L. Eckert. Testing the generality of a sea otter meditated trophic cascade in seagrass meadows. Prepared for submission to Proceedings of the National Academy of Sciences of the United States of America

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Appendix M

Approval from A. T. Bolwerk for use of manuscripts in dissertation presented as Chapter 2

29 April 2020

To whom it may concern,

Wendel Raymond has my permission to use the following manuscripts as part of his dissertation:
Testing the generality of apex predator-mediated trophic cascades in seagrass meadows
Raymond, W. W., B. B. Hughes, T. A. Stephens, C. R. Mattson, A. T. Bolwerk, and G. L. Eckert. Testing the generality of a sea otter meditated trophic cascade in seagrass meadows. Prepared for submission to Proceedings of the National Academy of Sciences of the United States of America

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Appendix N

Approval from J. B. Schram for use of manuscripts in dissertation presented as Chapter 2

19 May 2020

To whom it may concern,

Wendel Raymond has my permission to use the following manuscripts as part of his dissertation:

Sea otter effects on trophic structure of seagrass communities in Southeast Alaska

Raymond, W. W., J. B. Schram, G. L. Eckert., and A. W. E. Galloway. Sea otter effects on trophic structure of seagrass communities in Southeast Alaska. Prepared for submission to Oikos.

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