

OTTERS, SEA STARS, AND GLACIAL MELT: TOP-DOWN AND BOTTOM-UP FACTORS
THAT INFLUENCE KELP COMMUNITIES

By

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ABSTRACT

Kelp beds are important features of the Alaska coastline and provide habitat, protect coastlines, and support commercial and subsistence harvests. Kelp beds are affected by top-down and bottom-up factors, which are changing due to human and climate-related impacts. The influences of these top-down and bottom-up factors on kelp beds are investigated in three chapters. My first chapter investigated the influence of glacial discharge on recruitment and early community development in subtidal kelp communities by monitoring benthic sessile algae and invertebrates on cleared rocks across a glacial gradient along with various physical and biological parameters in the summers of 2013-2014. It has been predicted that Alaska's glaciers will lose 30-60% of their volume by 2100. The melt from glaciers increases sedimentation and lowers salinity, impacting important habitat-providing kelp. I found that sites upstream from glacial discharge had higher kelp recruitment than downstream sites, and that up to 72% of the variation in community development was related to mobile invertebrates and kelp in the surrounding community. Glacially-influenced environmental factors did not explain any variation that was not already explained by biological factors. My second chapter explored whether patterns in the recruitment of the dominant canopy kelp, *Nereocystis luetkeana* and the subcanopy kelp, *Saccharina latissima* were a result of dispersal limitation or failure to grow to macroscopic size. My goals were to determine 1) whether glacial melt conditions affect adult fecundity (spore production) of either species, 2) how sedimentation affects early gametophyte growth and survival in each species, and 3) whether competitive interaction between species at the gametophyte stage is altered by sediments. I found that glacial melt conditions did not affect the fecundity of either species, but sedimentation affected survival and competition. *Saccharina latissima* was the superior competitor under high sediment conditions. Because glacially-

influenced coastal areas often have little exposed hard substrate and predation by sea otters and sea stars on clams can provide hard substrate for kelp colonization, my third chapter examined methods for determining predation on clams by these predators without direct observation. I found that foraging pits of sea otters and sea stars could not be distinguished using quantitative measurements. In contrast, shell litter proved useful in quantifying relative foraging rates. Clam consumption by sea otters and sea stars was equal at all but one site. Collectively, my thesis chapters provide information on the effects of glacial discharge on microscopic and early kelp life stages in Alaska which can be incorporated into management practices.

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GENERAL INTRODUCTION

The burning of fossil fuels and emission of carbon dioxide into the atmosphere since the industrial revolution has contributed to global climate change (IPCC 2014). Atmospheric and ocean temperatures have increased since the 1950s and are predicted to continue to rise (IPCC 2014). In high latitudes, warming atmospheric temperatures are also expected to affect precipitation with a switch from winter snow to rain (Kundzewicz et al. 2008). Changes in the type and amount of precipitation will affect river discharge into the ocean (Scavia et al. 2002; Kundzewicz et al. 2008; Maloney et al. 2014). Glacial retreat has already been observed and is expected to continue under predicted climate change scenarios. In Alaska, more than half of the tidewater glaciers are currently retreating (McNabb and Hock 2014). The annual runoff of freshwater into the Gulf of Alaska is expected to increase due to loss of glacier volume (Hill et al. 2015). Increases in river and glacial discharge will also affect sedimentation in nearshore areas. Glacial melt delivers large amounts of fine sediment to coastal habitats and can spread tens of kilometers beyond the point source of discharge (Gatto 1982; Svendsen et al. 2002). Increased concentration of carbon dioxide in the atmosphere is also contributing to lowering the pH of the oceans (IPCC 2014). These changes in abiotic conditions have already altered the distribution and abundance of some species, and further changes to ecosystems are predicted with continued climate change (Harley et al. 2006). Kelp beds are coastal ecosystems that are vulnerable to changes in environmental conditions and are likely to be impacted by climate change and increased glacial melt.

Kelp beds are nearshore communities dominated by macroalgae of the family Laminariales in temperate regions throughout the world (Dayton 1985). They extend from the low intertidal to ~ 20 m depth and the term 'kelp bed' generally refers to subtidal communities.

Kelp beds can be highly productive, producing up to $1900 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Dayton 1985). Primary production from kelp forms the base of kelp bed food webs, providing food for grazers and particulate and dissolved organic matter for detrital food webs (Mann 1973). Kelp beds can subsidize low productivity habitats hundreds of kilometers away through kelp detritus as a food source, and are thus important on spatial scales beyond the kelp beds themselves (Kelly et al. 2012). Floating debris from kelp beds provide a dispersal mechanism to fish and invertebrates over long distances and may be important for offshore nutrient cycling (Hinojosa et al. 2011). Many fish and invertebrates utilize biogenic habitat provided by kelp (Teagle et al. 2017). Interstitial spaces in the kelp holdfast provide habitat to infauna (Anderson et al. 2005) and the stipes and blades attract fish (Siddon et al. 2008). The diversity of kelp bed communities is high compared to areas without kelp (Graham 2004). Kelp also alter the physical environment by reducing light (Watanabe et al. 1992) and damping currents and waves (Türker et al. 2006). The potential loss of these important foundation species has consequences for coastal food webs and commercially and recreationally important species.

The abundance, distribution, and composition of kelp beds are controlled by complex interactions of top-down and bottom-up forces. In most kelp bed systems, one or more predators exert top-down control on sea urchins or other grazers, preventing overgrazing and deforestation (e.g., sea otters in the northeast Pacific, Estes et al. 1998, and lobsters in south Africa, Blamey and Branch 2012). Kelp beds can undergo regime shifts to urchin barrens when predators are removed (Ling et al. 2015). Physical environmental factors can also control the abundance and distribution of kelp beds on large and small scales. On a global scale, kelp typically occur in temperate regions near upwelling that supplies cold and relatively high nutrient water (Dayton 1985). At local scales, wave exposure can affect kelp bed composition and depth distribution

(Graham 1997). River discharge can also affect kelp abundance and composition as kelps vary in their tolerance to low salinity and sedimentation (Roleda et al. 2008; Spurkland and Iken 2011; Pirtle et al. 2012).

The overarching goal of my thesis was to explore biological and environmental factors that affect the abundance, distribution, and species composition of glacially-influenced kelp bed communities. I used Kachemak Bay, Alaska as a model system because there are distinct regions within the bay that are influenced by oceanic and glacially-influenced water masses (Gatto 1982; Schoch and Chenelot 2004). The dynamics of abiotic factors such as salinity and sedimentation are likely to be affected by climate change in the 21st century as sea and air temperatures increase and glaciers continue to melt at faster rates. Biological factors, such as the abundance of grazers and predators, fluctuate over time due to natural and anthropogenic causes. The motivation for this thesis was to understand natural variability in drivers of kelp communities in order to anticipate future community changes. Accordingly, I described early community development across a glacial gradient and identified strongly correlated biotic and abiotic factors; I determined the effect of glacial melt and sedimentation on the supply of kelp propagules and kelp early life stage survival and competition; and I examined the roles of sea otters and sea stars in supplying shell litter substrate for kelp colonization.

The first chapter of my thesis explored relationships between recruitment and early community development of kelp beds, glacial melt conditions, and biological factors, including the abundance of mobile invertebrates and adult kelp. Studying recruitment and early community development can give clues to ecological processes controlling community composition such as settlement processes (Sousa 1984), competition (Benedetti-Cecchi and Cinelli 1996), and disturbance (Sousa 1979). Recruitment and early community development patterns are likely to

be affected by changes in abiotic conditions due to climate change (Harley et al. 2012). I described patterns of recruitment and early development of the sessile community in relation to glacial discharge; and I determined which environmental variables and members of the community (adult kelp, invertebrate grazers and predators) best explain these patterns.

The goal of chapter two was to determine how glacial melt affects the microscopic stages of two dominant kelps, the canopy-forming kelp *Nereocystis luetkeana* (hereafter *Nereocystis*) and the prostrate understory kelp *Saccharina latissima* (hereafter *Saccharina*). Reproductive output can vary with environmental conditions (Edwards and Konar 2012; Bartsch et al. 2013), so the supply of spores may vary with glacial melt influence. Based on the distribution of adult individuals, I hypothesized that *Nereocystis* fecundity would be lower at sites downstream of glacial discharge, while *Saccharina* fecundity would be unaffected by glacial discharge. Changing abiotic conditions can also affect competitive interactions among foundation species (Dayton et al. 1999). I conducted a lab experiment to test two hypotheses: 1) *Nereocystis* gametophytes would have lower survival and growth rates than *Saccharina* under sedimentation conditions, and 2) *Saccharina* gametophytes are competitively superior to *Nereocystis* gametophytes with sedimentation.

In Alaska, kelp beds may occur in or near areas of mixed sediment grain sizes that are important habitat for kelps, with mobile predators moving among the different grain size habitats. The goal of my third chapter was to improve my ability to determine relative predation by sea otters and sea stars on clams using remains from their predation, including foraging pits and shell litter, which is an important source of hard substrate for kelp. Clams make up a large portion of the diet of both sea otters and some sea stars such as *Pycnopodia helianthoides* (Smith 1961; Calkins 1978; Kvitek et al. 1992). Declines in clam abundance have been associated with

sea otter recolonization into certain areas (Doroff and DeGange 1994); however, the role of sea stars in these declines is unknown. Foraging pits have been used to determine locations and clam consumption rates by sea otters (Kvitek et al. 1992; Boehm et al. 2007; Bodkin et al. 2012), but there is some uncertainty around this method because it is unknown how long foraging pits last and if they are truly sea otter pits, as opposed to sea star pits. It is important to accurately assess relative clam predation by each predator in order to manage clam populations and predict impacts on clams based on changes in predator abundance. Clam shell litter can be important substrate for kelp (Kvitek et al. 1992), so clam predation rates can affect kelp abundance. I hypothesized that 1) after two weeks, sea otter and sea star foraging pits can be distinguished, 2) recent (two weeks old or less) foraging pits can be distinguished based on measureable characteristics, and 3) shell litter can be used to assign relative clam predation by sea otters and sea stars.

This research helped to advance our understanding of how kelp beds in Alaska and other high latitude systems may respond to climate change. I observed effects of glacial melt conditions, including sedimentation on the early life stages of kelp (sporophyte recruitment and gametophyte survival), and my findings emphasize the importance of investigating organisms at multiple stages of their life cycle. The timing of key processes such as reproduction and disturbance is critical to ecosystem stability and can be affected by human activities in many ways, including fishing and climate change. Shell litter provided by sea otters and sea stars may be critical substrate for kelp attachment, but the persistence and seasonality of shell litter are not well understood. Seasonal shifts in glacial melt and associated sedimentation could increase exposure of settling spores and early gametophytes to sedimentation and decrease kelp bed

resilience. Changes to kelp phenology in response to climate change will also affect kelp bed stability and interactions.

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CHAPTER 1: INITIAL RECRUITMENT AND EARLY COLONIZATION OF KELP-ASSOCIATED BENTHIC COMMUNITIES VARIES IN RELATION TO GLACIAL DISCHARGE¹

1.1 ABSTRACT

The assembly and maintenance of biological communities is influenced by environmental factors, which are predicted to shift with climate change. Glaciers in Alaska are melting at increasing rates, delivering sediment and freshwater to coastal habitats. I hypothesized that environmental factors related to glacial discharge would be correlated to initial recruitment and community development in kelp-associated benthic communities. To test this hypothesis, I placed cleared rocks at six sites at 10-m depth across a gradient of glacial-influence in Kachemak Bay, Alaska and monitored the initial recruitment and community development of sessile benthic communities on the rocks for 18 months. I concurrently monitored environmental (sedimentation rates, salinity, temperature, irradiance, and nutrient concentration) and biological factors (density of mobile invertebrates and kelp) in the surrounding community at each site. At glacially-influenced sites with higher sedimentation rates, the developing sessile community was dominated by barnacles with little or no kelp and high temporal variation in availability of bare space. At more oceanic sites in outer Kachemak Bay, sessile communities were characterized by a slow increase in cover of encrusting and upright macroalgae, with high variability among sites. Using distance-based linear models, up to 72% of the variation in community development was related to mobile invertebrates and kelp in the surrounding community. Glacially-influenced environmental factors did not explain any variation that was not already explained by biological

¹ Traiger, S.B., Konar, B. Initial recruitment and early colonization of kelp-associated benthic communities varies in relation to glacial discharge. *Journal of Experimental Marine Biology and Ecology*. *In Review*

factors. This research indicates that glacial melt may influence recruitment and community development indirectly through effects on the surrounding community.

1.2 INTRODUCTION

Recruitment and early community development is affected by larval or propagule supply, environmental conditions, and biotic interactions. Differences in upwelling can result in different larval supply and the species that can recruit to an area (Menge, 2000). Environmental conditions may prevent certain organisms from establishing or surviving to maturity (Balata et al., 2007). Early community development can also be structured by competition, grazing, or predation (Schiel and Foster, 2015). As environmental regimes are altered with global climate change, it is critical to understand the effects of these changes on recruitment and early community development in habitats that provide important ecosystem services.

Glaciers are important features of the Alaska coastline with direct connections to the nearshore environment (tidewater glaciers) or indirect connections through rivers fed by glaciers. These glaciers are melting at accelerating rates (Neal et al., 2010), resulting in increased glacial discharge that reduce water temperatures and salinities, increase sedimentation rates, reduce light availability (Wiencke et al., 2007), and degrade substrate quality (Spurkland and Iken, 2011). These environmental changes have been observed to diminish benthic biodiversity and macroalgal abundance (Wlodarska-Kowalczyk and Weslawski, 2001; Spurkland and Iken, 2011); however, it is not yet understood whether these declines are due to differences in survival of initial recruits or drivers impacting subsequent community development. This study investigated the relative roles of environmental and biological factors in structuring kelp communities in a glacial estuary by determining the timing and rate of macroalgal and sessile

invertebrate initial recruitment and community development upstream and downstream of glacial discharge point sources.

Kelp beds are important ecosystems in Alaska that are affected by glacial melt. Kelp beds support a wide range of commercial, recreational and subsistence fish and invertebrate species. Many fish use kelp beds as habitat during adult and juvenile life stages (Hamilton & Konar, 2007, Hayden-Spear and Gunderson, 2007). Kelp canopies provide important microhabitat for juvenile rockfish (Nelson, 2001) and Pacific cod (Hamilton and Konar, 2007). The primary productivity in kelp beds is great and as such, feed nearshore communities via detritus and through kelp drift (Dayton, 1985). Kelp beds can subsidize low productivity habitats hundreds of kilometers away through kelp detritus as a food source, and are thus important on spatial scales beyond the kelp beds themselves (Kelly et al., 2012). Floating debris from kelp beds provide a dispersal mechanism to fish and invertebrates over long distances and may be important for offshore nutrient cycling (Hinojosa et al., 2011). In addition to providing habitat and food, kelp beds also serve coastal communities. As upright structures in the water column, kelp alter current speed and directions, protecting coastal areas by damping waves and reducing coastal erosion (Turker et al., 2006). Hence kelp beds are important to terrestrial, nearshore and offshore ecosystems and to human communities.

Kelp beds naturally experience environmental or biological disturbance; however, kelp beds can also be highly resilient to disturbance. It is critical to understand how kelp beds recover from disturbance in order to predict their response to climate change. In California, kelp beds can be greatly thinned or eliminated by El Nino conditions of high temperature and low nutrients, but kelp can quickly recover when conditions return to normal (Dayton et al., 1992). Other environmental disturbances may result in phase shifts with more permanent effects. In Australia,

coastal development led to reduced water quality (eutrophic and high sedimentation), causing a phase shift from kelp to turf algal dominated (Connell and Irving, 2008). Biological disturbance such as destructive sea urchin grazing can also lead to phase shifts from kelp beds to urchin barrens (Ling et al., 2015). Understanding climate change impacts on kelp bed communities is important because changes in kelp beds provide ecosystem services.

Changes in environmental and biological factors in estuaries due to human activities have been observed (Husa et al., 2014) and further changes are also expected with global climate change (Neal et al., 2010). The study of initial recruitment and community development can give clues to ecological processes such as propagule supply (Sousa, 1984), competition (Benedetti-Cecchi and Cinelli, 1996), and disturbance (Sousa, 1979). My objectives were to 1) describe patterns of recruitment and early development of the sessile community in relation to glacial discharge; and 2) determine which environmental variables and members of the community (adult kelp, invertebrate grazers and predators) best explain these patterns.

1.3 METHODS

1.3.1 Study Site

Kachemak Bay, Alaska, is a high latitude estuary whose kelp beds are exposed to an environmental gradient influenced by glaciers. It is divided into an inner and outer bay at the Homer spit, which extends several kilometers into the bay (Figure 1). Oceanic water from the Alaska Coastal Current enters the outer bay along the southern shore and flows counter-clockwise to then exit along the northern shore (Schoch and Chenelot, 2004). The outer, southern bay is free of glacial sediments while the inner bay has a sedimentation gradient along the coast with lower light and salinity and greater inorganic sedimentation at the head of the bay

(Abookire et al., 2000; Spurkland and Iken, 2011). The counter-clockwise circulation carries some glacial freshwater and sediment westward along the bay's north shore toward the mouth (Gatto, 1982). Six sites at 10-m water depth were established to encompass the range of glacial exposure in Kachemak Bay (Figure 1). Three sites were in the more oceanic outer bay (O1, O2, and O3) and three were in the glacially fed inner bay (I1, I2, and I3). These sites were chosen to standardize bottom topography and substrate composition (boulders, shell hash, and sediments) as much as possible.

1.3.2 Environmental factors

At each site, environmental factors directly related to glacial discharge were monitored, including sedimentation rate, bottom water temperature, irradiance, salinity, and nutrient concentrations [nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^{3-}), and silicate (SiO_4^{2-})]. Sediment traps were used to determine sedimentation rates at each site from March to September 2013 and April to September 2014. These traps consisted of three polyvinyl chloride pipes with a height: diameter ratio of 5:1 to prevent resuspension (Hargrave and Burns, 1979) and were placed with the mouth of the trap approximately 0.7 m above the bottom. Once per month, traps were retrieved and replaced with new ones. Particulate mass flux was quantified by filtering the trap samples onto pre-weighed Whatman GF/F glass microfiber filters (0.7 μm). Filters were dried for 24 h at 60°C to obtain dry weight. Filters were then burned for 6 h at 500°C and re-weighed to determine organic content as the ash-free dry weight. Inorganic content was estimated as the remaining content after the organic content was burned off.

Bottom temperature and irradiance (photon intensity per area) were recorded hourly at each site using Honest Observer by Onset (HOBO) Pendant data loggers (Onset Computers,

Bourne, Massachusetts), fixed to cinderblocks on the sea floor. Two-week averages of temperature and irradiance were calculated from daily averages of the hourly data. For irradiance, data points between sunset and sunrise were excluded. The maximum and minimum temperature and maximum irradiance value within each two-week period were also included as variables in my analysis. Minimum irradiance was not used because the minimum irradiance was always zero. Due to loss of data loggers, no data are available for some of the outer sites (O1 in 2013 and O2 and O3 from July to September 2013).

Bottom salinity was measured with a hand-held multiparameter instrument (Yellow Springs Instruments ProPlus, Yellow Springs Instrument Company, Yellow Springs, Ohio) at each site and each sampling event in 2013. In 2014, salinity was monitored hourly with HOBO conductivity U24 data loggers (Onset Computers, Bourne, Massachusetts) fixed to cinderblocks next to the light and temperature loggers at each site. Two-week averages of the daily average salinity data from 2014 were used in the analysis. Maximum and minimum salinity in each two week period was compared to long-term succession (2014 data, see “2.4. Patterns of initial recruitment and early community development”). I only compared mean salinity to 1 – 6 month community development because maximum and minimum salinities were not available; only one salinity measurement was taken at each site and each sampling event in 2013.

For nutrient analysis, water samples were collected from less than one meter above the bottom at each site on each visit. Water samples were filtered with Nalgene syringe filters (0.45 μm) within one hour of collection and transported back to the lab in a cooler with ice. Water samples were then frozen until nutrient analysis. Nitrate, ammonium, phosphate, and silicate were measured with a Technicon AutoAnalyzer II (SEAL Analytical Inc., Mequon, Wisconsin).

1.3.3 Biological factors

At each site, I monitored densities of mobile invertebrate grazers, predators, and adult kelp in the surrounding community. Small, more abundant invertebrate abundances (such as limpets and chitons) were determined by counting all individuals present on each experimentally cleared rock (see below). Larger invertebrates (e.g., sea stars such as *Pycnopodia helianthoides*) and adult kelp were counted along two haphazardly-placed replicate 2 x 10-m transects at each site. Transects started 1 m from each end of the permanent transect where cleared rocks were placed (see below) and the direction of each transect was chosen haphazardly. All invertebrates and kelp were identified to the lowest taxonomic level possible.

1.3.4 Patterns of initial recruitment and early community development

To monitor initial recruitment and early community development, percent cover and counts of sessile individuals that recruited onto cleared rocks were monitored at all sites. Thirty-six slate rocks were collected from two intertidal sites located mid-bay (Kasitsna Bay and Jakolof Bay), scraped clean with a wire brush, placed in the sun for 48 hours to eliminate any spore bank, and individually tagged with white-out paint. All rocks were approximately 5 cm thick, 25 cm wide and 35 cm long with two flat surfaces, one facing down to ensure that the rock did not roll and one facing up for settlement. Each of the six sites was assigned six randomly-chosen rocks. The first set of rocks was deployed in March 2013. A subsequent set was deployed in April 2014 to examine temporal variability in recruitment and succession. Rocks were haphazardly placed along a 10-m permanent transect along the 10-m isobath at mean lower-low water. After deployment, all rocks were surveyed in April of both years, and biweekly from May to September in 2013 and 2014 using SCUBA. No surveys were conducted from October to

March due to inclement weather. Percent cover was estimated for all algae and sessile invertebrates. Mobile invertebrates were counted (see above in 1.3.3 Biological factors) and pictures were taken of the rocks so that rock area could be calculated using Image J. Counts were standardized to rock surface area by dividing the raw count by the surface area. I examined initial recruitment and community development over the first 1 – 6 months for rocks deployed in 2013 and 2014 and from 12 – 18 months (2014 data) for the rocks deployed in March 2013.

1.3.5 Data Analysis

Multivariate analyses were carried out in Primer, a multivariate statistical software package (v7, Plymouth Marine Laboratories). Before statistical analyses, all predictor variables were examined for univariate correlations using draftsman plots (Clarke et al., 2014). One variable from each pair of variables that covaried ($r \geq 0.95$) was removed from further analysis (Clarke et al., 2014). Abundance of the sea star *Leptasterias hexactis* was deleted because of high correlations with other biological factors. Biological data were 4th-root transformed to prevent the most abundant organisms from dominating the analysis (McCune et al., 2002). Environmental data (sedimentation rates, minimum and maximum temperature, mean and maximum light, salinity, nitrate, ammonium, phosphate, and silicate) were normalized.

I used PERMANOVA performed on a Bray-Curtis similarity matrix generated from the multivariate percent-cover data from rocks deployed in March 2013 (except for site O2 where rocks were deployed in May) through September 2014 to examine spatial and temporal variation in recruitment and early community development. Percent cover data among replicate rocks were averaged at each site for each sampling event. The PERMANOVA design included Region (fixed, 2 levels: Outer Bay, Inner Bay), Site (random, nested in Region, 6 levels: O1, O2, O3, I1,

I2, I3), Month (random, 6 levels: April, May, June, July, August, September), and Year (random, 2 levels: 2013, 2014). To account for the repeated measures aspect of the study design, “Months-deployed” was included as a covariate. I used SIMPER analysis to determine species that contributed to similarity within each site and constructed time series plots to visualize changes in percent cover over time for the most important species.

To meet my objective of determining spatial and temporal variation in environmental conditions, permutational multivariate analysis of variance (PERMANOVA) was performed on a Euclidean distance similarity matrix. Three-factor tests were used with site (fixed, six levels: sites 1 - 6), month (fixed, six levels: April, May, June, July, August, and September), and year (fixed, two levels: 2013 and 2014). Pairwise tests were performed for differences among sites. SIMPER analysis was used to describe the most important similarities in the surrounding community within regions and principal component analysis (PCA) was used to show spatial and temporal variation in environmental variables.

Distance-based linear models (DistLM) were used to determine the importance of environmental (sedimentation, temperature, salinity, light and nutrients) and biological (density of mobile invertebrate grazers and predators, kelp in the surrounding area) factors for affecting first year (1 – 6 months) and second year (12 – 18 months) algal and sessile invertebrate community development. I also included “months-deployed” as an ordinal variable available for the model to select. Step-wise selection procedure and adjusted R^2 selection criteria were used. Distance-based redundancy analysis (dbRDA) plots were used to visualize the fit of the DistLM models. I also performed DistLM analyses on individual variables of interest (density of some kelp species) to determine relationships with environmental factors and the surrounding community.

1.4 RESULTS

1.4.1 Environmental factors

Glacially influenced environmental factors were significantly different between monthly and annual temporal scales and differed among some sites (Table 1, Table 2). The largest variation in environmental factors was across months, followed by year, and lastly, the interaction of month and year (Table 1). The PCO reflects the PERMANOVA by showing clear separation of data points among months (Figure 2A). In contrast, sites were not clearly distinguished by environmental factors (Figure 2B). Maximum temperature and mean salinity showed strong seasonal changes in both summers at all sites (Figure 3). Maximum temperature increased from May to September and salinity declined markedly in late summer (Figure 3). There was high variability in inorganic and organic sedimentation rates, though rates were highest in late summer for most sites (Figure 3).

There was high similarity in environmental conditions among most sites, as shown by the proximity of points from different sites in the PCO (Figure 2B). There were significant differences in environmental conditions between the most upstream site, site O1, and all inner bay sites (Table 2). Site O2, on the southern side of the outer bay was only significantly different from site I3, a downstream site (Table 2). The seasonal decline in salinity was most apparent and consistent between years at site O1 and site O3 (Figure 3). Inorganic sedimentation rates were almost always higher at sites downstream from glacial discharge (sites I1, I2, I3, and O3) than at upstream sites (site O1 and O2; Figure 3). Correspondingly, irradiance was almost always lower at site I3 than at sites O1 and O2 (Figure 3). Although concentration of nutrients was highly variable within sites, ammonium, nitrate, and silicate were sometimes different between site 1, the most upstream site, and the remaining sites. Ammonium increased from 2.7 to 5.5 μM from

July to early September in both years at site 5 and site 4, while levels remained $\sim 1 - 3 \mu\text{M}$ during that time at site 1 and site 2 (Appendix Figure 1). Nitrate and silicate were usually higher at site O1 than at site I3 and site I2 (Figure 3, Appendix Figure 1). Organic sedimentation rates were similar among sites (Appendix Figure 1). In general, inorganic sedimentation rates were lower and irradiance and nitrate were higher at sites upstream of glacial discharge than those downstream.

1.4.2 Biological factors

Abundance of kelp and mobile invertebrates was generally higher in the outer bay. Unidentified limpets contributed 23% to similarity within the outer bay and were the most abundant herbivores (Table 3A). The understory kelps, *Agarum clathratum* and *Saccharina latissima* contributed to similarity within both regions and were more abundant in the outer bay (Table 3). The canopy-forming kelps, *Nereocystis luetkeana* and *Eualaria fistulosa* were never observed in the inner bay or at site O3.

1.4.3 Patterns of community development

There were clear differences in initial recruitment and early community development over the first six months between the inner bay and outer bay regions (Figure 4). The two regions differed in the composition of early colonizers (Table 4). Species that contributed to similarity within the outer bay included spirorbid worms, encrusting brown and red algae, and filamentous brown algae (Table 4A). Bare space was abundant at outer bay sites for the first six months rocks were deployed, while percent cover of encrusting brown and red algae and filamentous brown algae gradually increased in the early summer (Figure 5A). In the inner bay, barnacles

quickly colonized rocks, resulting in a decline in availability of bare space (Figure 5B). Barnacles and hydroids contributed to similarity within the inner bay (Table 4B), while these were largely absent from the outer bay. Kelp recruits appeared at site O1 in June and O2 in July, while no kelp recruits appeared at O3 (Table 5). Kelp recruits appeared in July at I1, in May at I2, and no kelp recruits appeared at I3 (Table 5). Juvenile *Saccharina latissima* occurred at O1, O2, and I1. Juvenile *A. clathratum* occurred at O1 and O2. Juvenile *Laminaria yeozoensis* occurred at O1. Even after variability due to months-deployed was partitioned, there were still significant effects of region (PERMANOVA, $Pseudo-F = 3.923$, $P = 0.003$), and site nested within region ($Pseudo-F = 3.372$, $P = 0.005$). Community development over time differed between regions and among sites, as indicated by the significant interaction between months-deployed and these factors (Table 6).

In the second summer of community development (12 – 18 months after rocks were deployed) differences in community structure among sites became more apparent with less distinction between regions (Figure 6). This can be seen from the tight clustering of data points by site on the MDS (Figure 6) and the larger $Pseudo-F$ value associated with site(region) than region (Table 7). During this time period, there was no longer a significant effect of the months-deployed covariate (Table 7). However, some sites were more variable over time than others, which is reflected by the spread of points within sites in Figure 6 and the significant interaction of months-deployed and sites (region) (Table 7). The number of species contributing to similarity was higher in both regions over the 12 – 18 month time period than the 1 – 6 month period. In the outer bay, encrusting brown algae and spirorbid worms were again among the most important contributors to similarity (Table 8A). Percent cover of these groups remained similar through this time in the outer bay (Figure 7A). O3 in the outer bay, located on the northern side of Kachemak

Bay, varied from the other two outer bay sites in the high availability space during this period. This can be seen by the placement of the O3 data points near the top of the plot where the vector for bare space indicates high availability of bare space (Figure 6). As in the 1 – 6 month period, barnacles and hydroids were among the most important contributors to similarity within the inner bay (Table 8B). I1 in the inner bay had lower cover of barnacles, and this can be seen in Figure 6 by the placement of these data points closer to the outer bay sites where barnacles were absent or very rare (Figure 6). Kelp were more abundant at the outer bay than inner bay (Table 9). *Saccharina latissima* and *A. clathratum* grew to adult size at sites where they occurred. In contrast to sites O1 and O2, only one kelp recruit occurred at O3, which became identifiable as a juvenile *A. clathratum* in late summer. Only two *N. luetkeana* appeared at site O1 and these only survived for one month.

1.4.4 Correlations with environment and surrounding community

Community development in the first summer that rocks were deployed (1-6 months) was most strongly correlated to abundance of limpets and maximum temperature. These two variables together explained 42.6% of the variation in the rock communities (Table 10). Other variables correlated to rock community structure included the anemone *Metridium* spp., kelps in the surrounding community *S. latissima*, and *A. clathratum*, the grazing gastropod *Lacuna vineta*, the limpet *Acmaea mitra*, and mean temperature (Table 10). The dbRDA plot illustrates the fit of the model to the rock community data (Figure 8). The data points from early in the summer are in the top left of the plot and the data points move toward the bottom of the plots on the left side for outer bay points and on the right side for inner bay points, as the rock communities developed (Figure 8). The vectors for mean and maximum temperature are oriented

in the direction of this change, reflecting the correlation between maximum temperature and the development of the rock communities (Figure 8). The differences in surrounding community and rock communities between the outer and inner bay are reflected by orientations of the vectors. *Agarum clathratum*, limpets (including *A. mitra*), and the gastropod *Lacuna vincta* were more abundant in the outer bay and the vectors for these variables point toward the left side of the plot (Figure 8). *Metridium* spp. was more abundant in the inner bay and this vector points toward the inner bay points on the right side of the plot (Figure 8).

DistLM analysis was additionally performed with kelp recruit density in the first summer (1-6 months) to determine what environmental and surrounding community factors were correlated with this variable. Variation in kelp recruit density was related to the abundance of *Lacuna vincta* (*Pseudo-F* = 9.111, *P* = 0.015, variation explained = 18.6%), the red urchin *Strongylocentrotus franciscanus* (*Pseudo-F* = 9.5549, *P* = 0.020, variation explained = 16.0%), and concentration of NO₃ (*Pseudo-F* = 4.6882, *P* = 0.036, variation explained 7.2%) for a total of 41.8% of variation related to these variables. The pattern of highest density of kelp recruits at site O2 at the end of the summer (Table 5) is reflected by the increased abundance of *L. vincta* toward the end of the summer at this site. Concentration of NO₃ was higher at outer bay sites at the end of the summer, when density of kelp recruits was highest at site O2.

Variation in rock community development in the second summer (12-18 months) was related to the chiton *Tonicella* spp., *A. mitra*, the omnivorous snail *Calliostoma* spp., *S. latissima*, and *Pycnopodia helianthoides* for a total of 72.7% of variation related to these variables (Table 11). These variables are correlated to the differences in community development between the outer and inner bay. *Tonicella* spp., *A. mitra*, *Calliostoma* spp., and *S. latissima* were more abundant at outer bay sites than at inner bay sites (Table 3). The first axis of the dbRDA plot

reflects the differences between the outer and inner bay sites, while the second axis separates the three outer bay sites (Figure 9). None of the environmental variables were related to variation in the rock community that was not already related to surrounding community variables.

DistLM analysis was also conducted on density of kelp that occurred on deployed rocks during the 12 – 18 month period. This included unidentified kelp recruits (< 2 cm in length), *S. latissima*, *A. clathratum*, *L. yezoensis*, *Cymathaere triplicata*, and *N. luetkeana*. Variation in kelp density on rocks was best related to density of *S. latissima* in the surrounding community ($Pseudo-F = 15.181$, $P = 0.0001$, variation explained = 37.8%), *Calliostoma* spp. ($Pseudo-F = 7.501$, $P = 0.0001$, variation explained = 14.8%), and *A. mitra* ($Pseudo-F = 4.7301$, $P = 0.0043$, variation explained = 8.1%) for a total of 60.7% of variation related to these factors.

1.5 DISCUSSION

Patterns of recruitment and early community development on the rocks differed between the oceanic-influenced outer region and the glacially-influenced inner region of Kachemak Bay, with the most abundant members of the communities being spirorbid worms and macroalgae in the outer bay and barnacles in the inner bay. Many environmental factors were similar among sites, but inorganic sedimentation was the most different, with the highest rates at sites downstream of glacial discharge point sources. Community development in the first summer (1-6 months) was driven by temperature, grazers, the anemone *Metridium* spp., and the understory kelp *Saccharina latissima* while community development in the second summer (12-18 months) was driven by *S. latissima*, grazers, and the sea star *Pycnopodia helianthoides* (Table 10-11). After temperature and the surrounding community were included, environmental factors associated with glacial discharge did not increase the percentage of variation explained. The

effects of environmental factors related to glacial melt on community development at our study sites may be masked by indirect effects on the surrounding community.

1.5.1 Patterns of early community development

The effect of early colonists on later recruits of the same or different species is an important aspect determining the mode of succession (Connell and Slatyer, 1977). Early colonists may inhibit, facilitate, or have no effect on later colonists (Connell and Slatyer, 1977). While barnacles in the inner bay may have had negative effects on later recruits through preemptive competition, it is unclear whether the same can be said for early colonizers (spirorbid worms and encrusting algae) in the outer bay. Competition for space may not have been important in the early stages of community development in the outer bay where bare space was abundant during the first summer of the study. Preemptive competition among macroalgae has been shown to be an important structuring mechanism of communities in other systems. In littoral rock pools in Italy, turf forming algae and *Cystoseira* spp. have nonhierarchical competitive interactions such that the most abundant taxon can exclude recruitment of the other group (Benedetti-Cecchi and Cinelli, 1996). When turf algae and *Cystoseira* spp. recruit at the same time, they can coexist (Benedetti-Cecchi and Cinelli, 1996). Similarly, dense mats of filamentous algae preempt kelp recruitment in subtidal kelp beds in Australia, (Connell and Russell, 2010). Spatial extent and distribution of bare space can be crucial to the coexistence of species. Encrusting algae can inhibit kelp recruitment; however, kelp canopies can persist despite high cover of encrusting algae because kelp produce very high numbers of spores, which can settle in minute bare patches or on top of encrusting invertebrates (Okamoto et al., 2013).

Recruitment rates varied among my sites, with barnacles quickly colonizing bare space in the inner bay and recruitment by spirorbid worms and macroalgae occurring much more slowly in the outer bay. Although most kelp and red macroalgal species are reproductive during early summer in Kachemak Bay (personal observation), recruits of these groups were not observed on the experimental rocks for many months after their initial placement in March or April (2013 and 2014, respectively). This may be because kelp gametophytes can delay reproduction and production of macroscopic sporophytes until they are triggered by changing environmental factors such as light or nutrients (Carney and Edwards, 2006). Slow substrate colonization in high latitude systems compared to temperate systems has been reported previously (Barnes and Conlan, 2007). For example, in an Arctic boulder field, experimentally cleared boulders still had over 90% cover of bare space after 3 years (Konar, 2007). In contrast, rapid recovery of kelp cover was observed in experimental and natural clearings in kelp forests in California (Dayton et al., 1992). In many systems, following a disturbance, typical succession process includes early opportunists followed by slower growing species. In the intertidal, early opportunists include *Ulva* spp., which are later replaced by slower growing red macroalgae (Sousa, 1984). In my system, the early opportunists were spirorbid worms and barnacles. Spirorbid worms are also abundant early colonizers in highly disturbed subtidal habitats in Antarctica (Barnes and Conlan, 2007).

1.5.2 Factors correlated with community development

I expected to see some similarities in early colonizers between upstream and downstream sites due to the common water mass that passes through the study area (Figure 1), possibly resulting in a somewhat similar propagule pool reaching multiple sites; however, there were few

early colonizers in common between sites upstream and downstream of glacial discharge. Spirorbid polychaetes were among the earliest colonizers at sites upstream of discharge while barnacles were early colonizers downstream of glacial discharge. Several processes could be responsible for this pattern. A hydrodynamic front located at the boundary of the inner and outer bay at Homer spit may concentrate larvae, leading to higher transport into the inner bay, as was observed for the decorator crab, *Oregonia gracilis* (Murphy and Iken, 2014). Concentration and net transport into the inner bay may explain the much higher abundance of species with longer larval duration such as barnacles in the inner bay than was observed in the outer bay. Another explanation for the differences in early recruits between upstream and downstream sites is that some species may have shorter dispersal distances, and their propagules may not reach the downstream sites during the pelagic larval period. Spirorbid worms, which were common upstream but not downstream of glacial discharge, brood their larvae (Knight-Jones et al., 1991), and presumably have shorter dispersal distance than species with pelagic larvae such as barnacles. Encrusting algae such as crustose corallines also have short dispersal distances (Opazo and Otaiza, 2007), so populations upstream of glacial discharge may not supply propagules to glacially-influenced sites. Lastly, settlement and early post-settlement processes may prevent recruitment. Inorganic sedimentation could be limiting encrusting macroalgal recruitment by preventing spore attachment or contributing to post-settlement mortality (Deiman et al., 2012; Maughan, 2001).

Environmental conditions were also more spatially homogeneous than expected, which indicates that currents are important in spreading glacially-influenced water throughout Kachemak Bay. However, my findings contrast with previous work in Kachemak Bay, which found large differences in surface salinity, halocline depth, temperature, irradiance, and nitrate

concentrations between sites upstream and downstream of glacial discharge (Abookire et al., 2000; Spurkland and Iken, 2011). Conductivity temperature depth (CTD) profiles conducted at Halibut Cove, a downstream site, near my site I1, showed that there is a halocline at 4-m depth, below which salinities are similar to those found in the outer bay (Schoch and Chenelot, 2004). In Kachemak Bay, Spurkland and Iken (2011) observed differences in salinity and irradiance at 5-m depth, but my sites were at 10-m depth, so the low salinity, low temperature, low nitrate, and high silt-containing water from glacial discharge, though present, may have reached my loggers or experimental rocks at the deeper depth only occasionally. Stratification may therefore partially protect subtidal kelp beds from glacial meltwater-related effects. Similarly, flooding of the Orange River in Africa caused high mortality of algae and invertebrates in the intertidal zone while the subtidal zone was not affected (Branch et al., 1990). Rates of inorganic sedimentation did follow spatial patterns similar to previous findings in this and other systems (Spurkland and Iken, 2011; Svendsen et al., 2002). Similar to the Kongsfjorden glacial fjord system in Svalbard, I observed a gradient in inorganic sedimentation with rates declining toward the mouth of the bay (Svendsen et al., 2002). Some of my sites (site I1 & O3) may be located at regions representing transitions between the outer bay oceanic conditions and the inner bay glacially-influenced conditions. Circulation patterns may help homogenize conditions around the bay by spreading glacial freshwater and sediment to the north shore of the outer bay. The incoming current from Cook Inlet on the southern side of the inner bay may mix with the fresher and more turbid waters of the inner bay, decreasing the glacial influence along the southern side of inner Kachemak Bay (i.e., site I1, Figure 1). As glacial discharge increases with warming temperatures in the future, the extent of glacial influence, including sedimentation, will determine which

locations will be affected by changing conditions, and may include sites tens of kilometers past point sources of glacial discharge (Svendsen et al., 2002; this study).

Grazers, including unidentified limpets, *Calliostoma* spp., *Strongylocentrotus droebachiensis*, *Acmaea mitra*, and *Tonicella* spp., explained variation in the development of the sessile community on cleared rocks among sites; however, it is unclear whether these grazers truly exert control on recruitment and abundance of sessile organisms, or whether they were statistically significant drivers of recruitment because their patterns of abundance closely matched spatial patterns of the rock communities. Grazers exert top-down control on kelp through grazing on gametophytes and sporophytes (Henriquez et al., 2011). Limpets and *Tonicella* spp. also graze on crustose corallines (Demopolos, 1975; Steneck et al., 1991). Thus, grazers may have a direct role in algal recruitment and abundance at the two sites upstream from glacial discharge (sites O1 & O2), where I observed differences in macroalgal recruitment and increases in percent cover over time that were inversely related to grazer abundance. However, it seems unlikely that the absence or very low abundance of these grazers truly drives patterns of recruitment at the inner bay, glacially-influenced sites.

The lack of grazers in the inner bay did not result in greater macroalgal growth, probably because macroalgae themselves were negatively affected by the glacial discharge conditions like high sedimentation. The strength of top-down interactions, including grazing, often decreases with increasing environmental stress (Menge, 2000). For example, sedimentation has been shown to directly affect the spatial distribution, survival, and grazing of limpets (Airoldi and Hawkins, 2007; Branch et al., 1990). Limpet movement reduces recruitment and survival of *Balanus* spp. barnacles (Dayton, 1971). The absence of limpets at the downstream sites in the inner bay may be one factor contributing to the high recruitment and percent cover of barnacles

at these sites. In contrast, at the outer bay sites where limpets and other grazers were abundant, barnacles were very rare or totally absent. However, I cannot exclude the possibility that grazers are simply responding to the same environmental conditions as the algae and invertebrates recruiting to the cleared rocks, rather than exerting direct control on recruitment.

The low grazer abundances I observed were associated with high rates of inorganic sedimentation at the glacially-influenced, inner bay sites. Grazers may be more abundant upstream of glacial discharge due to lower sedimentation rates (Airoldi and Hawkins, 2007), or due to the higher abundance of kelp in the surrounding community that grazers feed on (Bustamante et al., 1995). *Tonicella* spp. also graze benthic diatoms (Latyshev et al., 2004), which may be more abundant at sites with low glacial influence. In my study, even in the outer bay where grazers are abundant, they did not have obvious effects on development of the sessile rock communities. Grazers can reset successional progressions by reopening bare space and can mediate competitive interactions among macroalgae (Dayton, 1971; Scheibling et al., 2009; Sousa, 1984). For example, in subtidal cobble fields in Nova Scotia, molluscan mesograzers (periwinkles, limpets, and chitons) graze early successional filamentous algae, allowing later successional algae to colonize (Scheibling et al., 2009). In Kachemak Bay, grazers may play a more important role as communities age and availability of bare space decreases.

Glacially-influenced environmental factors are expected to have direct impacts on benthic sessile community succession through impacts on recruitment, growth, and survival of members of the community. Kelp recruitment is negatively correlated to sedimentation rates (Devinny and Volse, 1978; Spurkland and Iken, 2011; Valentine and Johnson, 2005) and sedimentation and low salinity decrease the success of *Nereocystis luetkeana* spore settlement and attachment (Deiman et al., 2012), and gametophyte survival and growth (Lind, 2016). Sediments can kill

early macroalgal life stages through burial or smothering, scour, and changes in substrate stability (Airoldi, 2003). In southeastern Tasmania, kelp recruits transplanted to urchin barrens, where thick sediment layers accumulate, experienced high mortality, even when urchins were excluded (Valentine and Johnson, 2005). Sedimentation also inhibits recruitment of spirorbid polychaetes (Connell, 2003). Low salinity can cause osmotic stress in recruiting barnacles, causing latent effects on growth and survival (Qiu and Qian, 1999). While I didn't observe community shifts that coincided with seasonal shifts in glacially-influenced environmental factors, these factors may be having direct effects on the species available to form these communities through effects on recruitment and early post-settlement survival.

1.5.3 Implications

Examining sessile community development under glacial influence provides an opportunity for natural experiments to determine what changes may occur in other kelp beds if the spatial extent or intensity of glacial influence changes. Increased sedimentation rates have already been associated with decreased diversity and dominance of a few opportunistic species (Balata et al., 2007; Connell, 2007; Pratt et al., 2014). In Alaska, I can expect kelp beds to be negatively impacted by the spread of glacial sediment. Climate change may also result in the peak in glacial discharge to shift from late summer and early fall to earlier in the summer. Both environmental variables and biological communities should be monitored to understand the effects of changes in glacial melt dynamics on developing communities.

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1.7 TABLES AND FIGURES

Table 1. Results of a three-way PERMANOVA comparing environmental variables among sites (fixed, six levels), months (fixed, five levels: May, June, July, August, and September), and years (fixed, two levels: 2013 and 2014). Significant p values are in boldface. High values of pseudo-F indicate the magnitude of variance explained by that factor.

Source	<i>df</i>	SS	MS	Pseudo-F	<i>P(perm)</i>	Unique perms
Site	5	75.762	15.352	3.3725	0.0024	9929
Month	5	201.8	40.361	8.8661	0.0001	9936
Year	1	27.604	27.604	6.0638	0.0009	9943
Site x Month	22	104.68	4.7583	1.0453	0.4645	9923
Site x Year	5	32.452	6.4904	1.4258	0.189	9923
Month x Year	3	55.771	18.59	4.0837	0.0011	9935
Site x Month x Year	10	40.505	4.0505	0.88978	0.6436	9922
Res	5	22.761	4.5522			
Total	56	728				

Table 2. Pairwise PERMANOVA comparison of environmental variables among sites.
Significant p values are in boldface.

		Outer			Inner		
		O1	O2	O3	I1	I2	I3
Outer	O1						
	O2	0.2144					
	O3	0.071	0.3489				
Inner	I1	0.0426	0.219	0.3392			
	I2	0.0268	0.1615	0.3257	0.3966		
	I3	0.0006	0.0028	0.0477	0.0292	0.0059	

Table 3. Percent contribution of discriminating species for surrounding community from May to September in 2013 and April to September in 2014 in A) outer bay and B) inner bay using SIMPER analysis.

A) Outer Bay

	Average \pm SE			
	Abundance (x/m ²)	Average \pm SD Similarity	% Contribution	Cumulative
Unidentified Limpet	12.6 \pm 0.2	12.29 \pm 4.09	23.24	23.24
<i>Agarum clathratum</i>	10.2 \pm 0.2	10.95 \pm 1.67	20.71	43.95
<i>Saccharina latissima</i>	11.6 \pm 0.3	6.95 \pm 1.15	13.14	57.09
<i>Tonicella</i> spp	0.7 \pm 0.01	5.82 \pm 1.67	11.00	68.08
<i>Pagurus</i> spp	0.7 \pm 0.03	3.24 \pm 0.99	6.12	74.20
<i>Calliostoma</i> spp	1.4 \pm 0.04	2.39 \pm 0.73	4.52	78.72
<i>Pycnopodia helianthoides</i>	0.4 \pm 0.02	2.21 \pm 0.81	4.17	82.90
<i>Nereocystis luetkeana</i>	0.5 \pm 0.01	1.27 \pm 0.48	2.41	85.30
<i>Strongylocentrotus droebachiensis</i>	2.2 \pm 0.1	1.18 \pm 0.32	2.23	87.53
<i>Eualaria fistulosa</i>	1.7 \pm 0.09	0.99 \pm 0.40	1.87	89.41
<i>Acmaea mitra</i>	0.1 \pm 0.004	0.94 \pm 0.42	1.78	91.19

B) Inner Bay

	Average \pm SE			
	Abundance (x/m ²)	Average \pm SD Similarity	% Contribution	Cumulative
<i>Saccharina latissima</i>	4.0 \pm 0.07	17.87 \pm 2.12	39.24	39.24
<i>Agarum clathratum</i>	1.4 \pm 0.03	9.98 \pm 1.23	21.92	61.17
<i>Pycnopodia helianthoides</i>	0.4 \pm 0.008	5.00 \pm 0.77	10.97	72.14
<i>Pagurus</i> spp	0.2 \pm 0.005	3.38 \pm 0.58	7.43	79.56
<i>Metridium</i> spp	0.3 \pm 0.01	3.00 \pm 0.55	6.59	86.15
Unidentified Limpet	0.7 \pm 0.02	2.39 \pm 0.41	5.24	91.39

Table 4. Percent contribution of discriminating species for community structure over 1-6 months in each region (A: Outer Bay, B: Inner Bay) using SIMPER analysis.

A) Outer Bay

	Average \pm Similarity	% Contribution	Cumulative
Bare space	44.67 \pm 2.58	72.96	72.96
Spirorbid	5.39 \pm 0.81	8.80	81.76
Encrusting brown algae	2.71 \pm 0.60	4.43	86.19
Encrusting red algae	1.46 \pm 0.45	2.38	88.57
Filamentous brown algae	1.25 \pm 0.40	2.04	90.60

B) Inner Bay

	Average \pm Similarity	% Contribution	Cumulative
Bare space	35.68 \pm 2.40	60.00	60.00
Barnacle	14.34 \pm 0.99	24.11	84.11
Hydroid	5.29 \pm 0.80	8.90	93.01

Table 5. Average +/- standard error density (x/900 cm²) of kelp recruits in each month in the first summer rocks were deployed at each site. Surface area of rocks was approximately 900 cm².

Month	O1	O2	O3	I1	I2	I3
April	0 ± 0	No data	0 ± 0	0 ± 0	0 ± 0	0 ± 0
May	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0
June	2.4 ± 1.4	0 ± 0	0 ± 0	0 ± 0	0.03 ± 0.03	0 ± 0
July	3.5 ± 1.5	1.3 ± 1.0	0 ± 0	2.9 ± 1.8	0.3 ± 0.1	0 ± 0
August	1.5 ± 1.3	4.5 ± 4.5	0 ± 0	2.0 ± 1.6	0 ± 0	0 ± 0
September	1.2 ± 0.8	13.9 ± 4.8	0 ± 0	1.2 ± 0.5	0.1 ± 0.1	0 ± 0

Table 6. Results of a PERMANOVA comparing community development over 1-6 months between regions (fixed, two levels), among sites nested within regions (random, six levels), months (random, five levels: May, June, July, August, and September), and years (random, two levels: 2013 and 2014). Months-deployed was included as a covariate. Significant p values are in boldface. High values of pseudo-F indicate the magnitude of variance explained by that factor.

Source	<i>df</i>	SS	MS	Pseudo-F	<i>P(perm)</i>
Months-deployed	1	25156	25156	14.405	0.0021
Region	1	35464	35464	3.9234	0.0027
Month	5	7675.7	1535.1	1.3829	0.2047
Year	1	3878.2	3878.2	2.294	0.0861
Site(Region)	4	18596	4649	3.372	0.0048
Months-deployed x Region	1	6899.8	6899.8	6.4239	0.0119
Months-deployed x Site(Region)	4	4057.3	1014.3	3.1206	0.0021
Region x Month	5	4403.5	880.7	1.0115	0.4915
Region x Year	1	1720.9	1720.9	1.458	0.2532
Site(Region) x Year	4	1944.2	486.05	1.8956	0.0747
Res	26	5246.7	201.8		
Total	117	0.00001			

Table 7. Results of a PERMANOVA comparing community development over 12-18 months between regions (fixed, two levels), among sites nested within regions (random, six levels), and months (random, five levels: May, June, July, August, and September). Months-deployed was included as a covariate. Significant p values are in boldface. High values of pseudo-F indicate the magnitude of variance explained by that factor.

Source	<i>df</i>	SS	MS	Pseudo-F	<i>P(perm)</i>
Months-deployed	1	6200.6	6200.6	2.9578	0.1912
Region	1	34233	34233	3.4634	0.0059
Month	5	9703	1940.6	1.006	0.4769
Site(Region)	4	31697	7924.3	23.247	0.0001
Months-deployed x Region	1	483.7	483.7	4.1022	0.0962
Months-deployed x Site(Region)	4	3026.9	756.72	2.595	0.0291
Region x Month	5	493.81	98.763	0.29901	0.978
Total	63	93448			

Table 8. Percent contribution of discriminating species for community structure over 12-18 months in A) outer bay and B) inner bay using SIMPER analysis.

A) Outer Bay

	Average \pm Similarity	% Contribution	Cumulative
Bare space	16.78 \pm 4.18	27.08	27.08
Encrusting brown algae	9.53 \pm 6.96	15.38	42.46
Spirorbid	7.49 \pm 5.09	12.09	54.55
Crustose Coralline	5.95 \pm 1.55	9.61	64.16
Unidentified Polychaetes	5.58 \pm 4.97	9.01	73.17
<i>Saccharina latissima</i>	2.67 \pm 0.88	4.31	77.48
Kelp Recruits	2.24 \pm 0.90	3.62	81.10
Unidentified Sand-tube Polychaete	2.20 \pm 0.78	3.54	84.64
Encrusting red algae	1.44 \pm 0.43	2.32	86.97
<i>Agarum clathratum</i>	1.42 \pm 0.72	2.29	89.25
Filamentous red algae	0.80 \pm 0.42	1.30	90.55

B) Inner Bay

	Average \pm Similarity	% Contribution	Cumulative
Bare space	22.81 \pm 6.18	39.49	39.49
Barnacle	7.76 \pm 1.20	13.43	52.92
Hydroid	5.64 \pm 1.31	9.77	62.70
Filamentous red algae	4.20 \pm 1.26	7.28	69.98
<i>Saccharina latissima</i>	3.59 \pm 0.89	6.21	76.19
Kelp Recruits	2.67 \pm 1.00	4.63	80.81
Filamentous brown algae	1.78 \pm 0.59	3.08	83.89
<i>Metridium</i> spp	1.53 \pm 0.50	2.65	86.54
Brown tube polychaete	1.00 \pm 0.41	1.74	88.27
Peach bryozoan	0.87 \pm 0.43	1.50	89.77
Red blades	0.85 \pm 0.43	1.47	91.24

Table 9. Density ($\times/900 \text{ cm}^2$) of kelp on rocks at A) outer bay and B) inner bay over 12-18 months.

A) Outer Bay						
	April	May	June	July	August	September
<i>Saccharina latissima</i>	0.3 ± 0.4	1.3 ± 1.2	1.5 ± 1.4	1.8 ± 2.1	3.2 ± 3.2	2.4 ± 3.1
<i>Agarum clathratum</i>	0.3 ± 0.5	0.3 ± 0.4	0.3 ± 0.5	0.4 ± 0.5	0.7 ± 0.7	0.6 ± 0.8
Kelp Recruits	5.9 ± 9.9	4.0 ± 5.9	1.7 ± 2.3	1.2 ± 1.4	0.6 ± 0.9	0.5 ± 0.9

B) Inner Bay						
	April	May	June	July	August	September
<i>Saccharina latissima</i>	0.6 ± 0.9	1.3 ± 1.2	0.9 ± 0.8	0.9 ± 0.8	0.7 ± 0.6	0.8 ± 0.8
<i>Agarum clathratum</i>	0 ± 0	0 ± 0	0 ± 0	0.03 ± 0.07	0 ± 0	0 ± 0
Kelp Recruits	0.5 ± 0.3	0.5 ± 0.5	0.5 ± 0.2	0.3 ± 0.4	0.1 ± 0.1	0.1 ± 0.1

Table 10. Results of sequential DistLM tests on first year (1-6 months) of community development showing significant variables, their contribution to explained variation (Contrib.), the cumulative contribution of the explained variation (Cum.) and p values.

	Pseudo-F	Contrib.	Cum.	p-value
Limpets	12.55	23.9	23.9	0.0001
Maximum temperature	12.708	18.7	42.6	0.0001
<i>Metridium</i> spp.	6.7606	8.7	51.3	0.0002
<i>Saccharina latissima</i>	4.5809	5.4	56.6	0.0009
<i>Lacuna vincta</i>	3.4153	3.8	60.4	0.0079
<i>Acmaea mitra</i>	3.4325	3.5	63.9	0.0064
<i>Agarum clathratum</i>	2.9943	2.9	66.8	0.0175
Mean temperature	3.5939	3.3	70.1	0.0082

Table 11. Results of sequential DistLM tests on second year (12-18 months) of community development showing significant variables, their contribution to explained variation (Contrib.), the cumulative contribution of the explained variation (Cum.) and p values.

	Pseudo-F	Contrib.	Cum.	p-value
<i>Tonicella</i> spp.	17.68	41.4	41.4	0.0001
<i>Saccharina latissima</i>	7.7925	14.4	55.8	0.0001
<i>Calliostoma</i> spp.	4.3024	7.0	62.8	0.0006
<i>Acmaea mitra</i>	4.5314	6.4	69.1	0.0013
<i>Pycnopodia helianthoides</i>	2.7878	3.6	72.7	0.0254

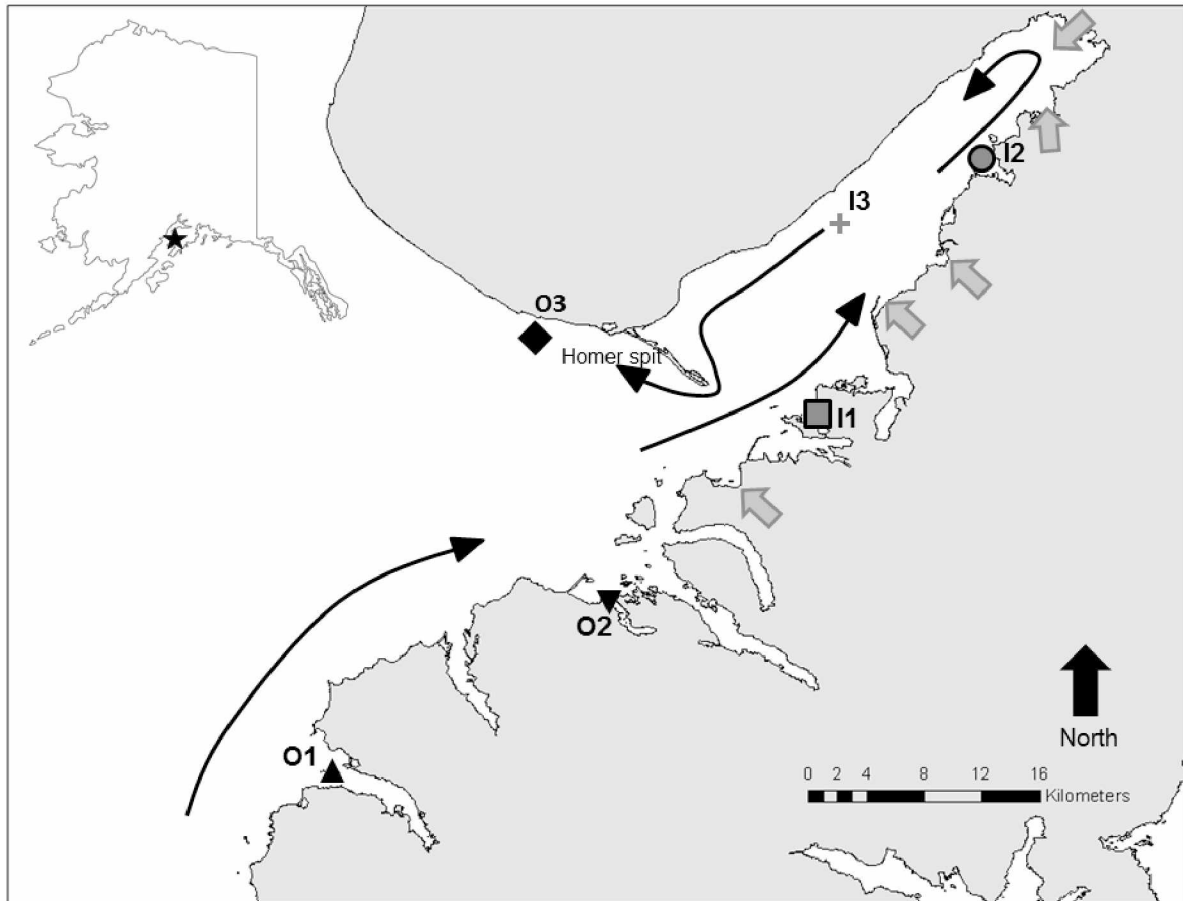


Figure 1. Map of Kachemak Bay showing study sites. The black star on the inset map shows the location of the study area within Alaska. The Homer spit divides the bay into the outer (black symbols) and inner (grey symbols) regions. Study sites are Port Graham (O1), Jakolof Bay (O2), Bishop's Beach (O3), Peterson Bay (I1), Bear Cove (I2), and McNeil Canyon (I3). Black arrows show circulation patterns. Gray arrows show freshwater and glacial point discharges.

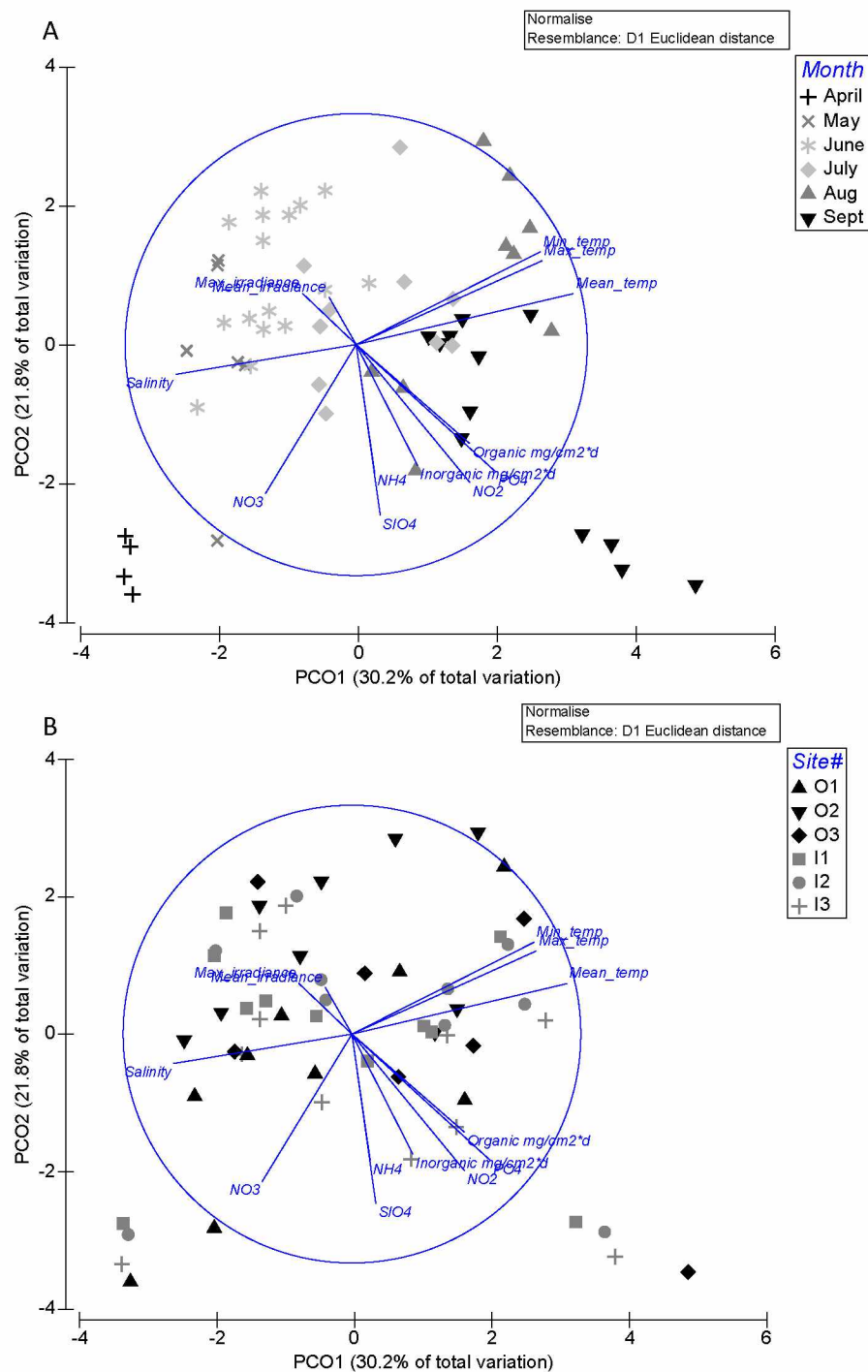


Figure 2. Principal Coordinates Analysis (PCO) of the physical variables. Each point represents physical conditions at one site at one sampling event. A) Seasonal changes are represented by color coding by month. B) Data points color coded by site to illustrate spatial patterns. Solid lines represent vectors of environmental variables. The length of the vector indicates the strength of the correlation with each PCO axis and direction indicates the direction of change along the axes. The first two PCO axes explained 52.1% of the variation in environmental variables

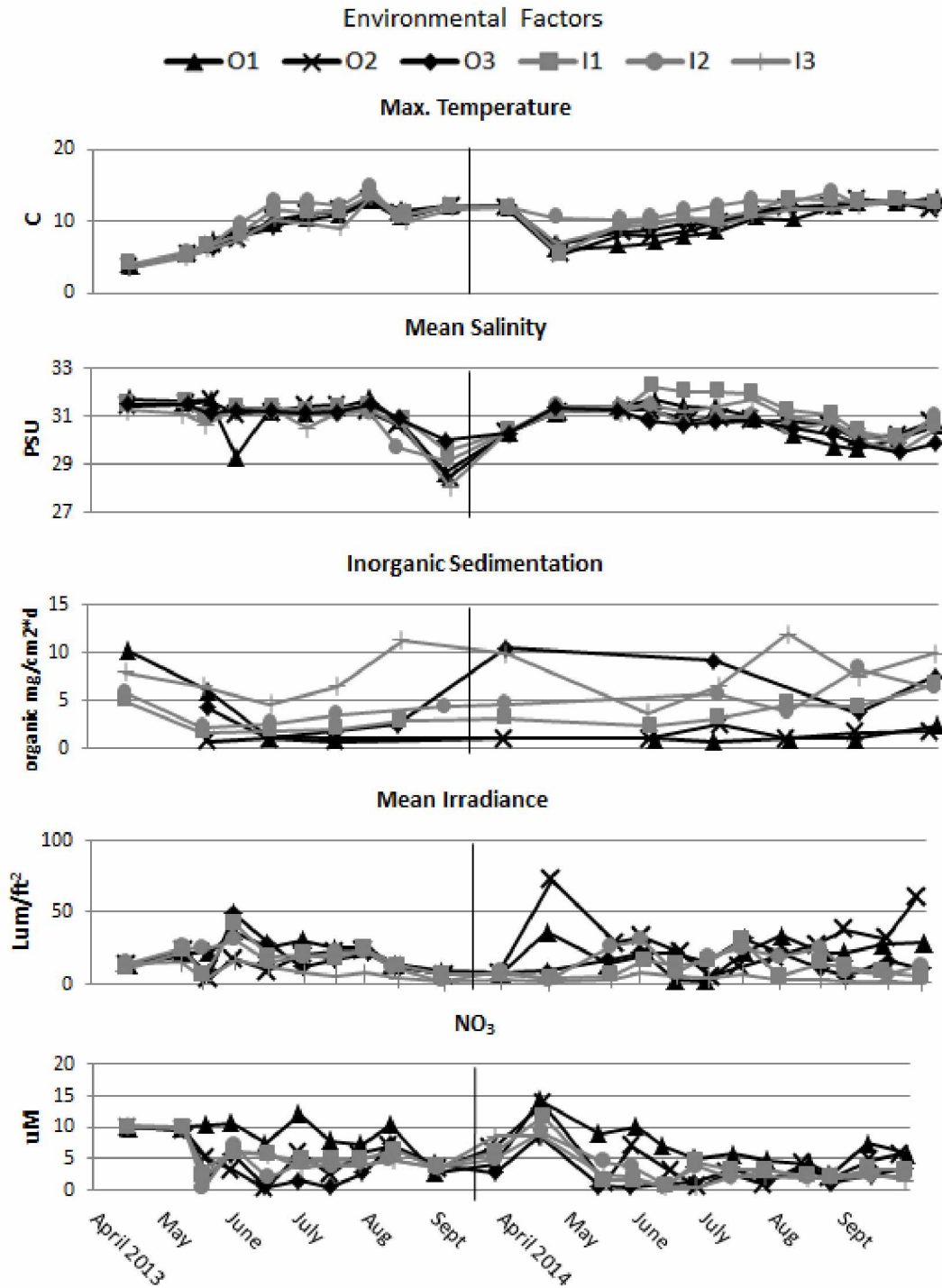


Figure 3. Temporal variations in environmental variables (maximum daily temperature, mean salinity, inorganic sedimentation, maximum daily irradiance, and NO₃). For sedimentation rate panel, data represent sedimentation rate over period traps were deployed. For all other panels, each data point is the average of the daily average (or maximum in the case of temperature) over the previous two weeks. Vertical bar distinguishes 2013 from 2014 data

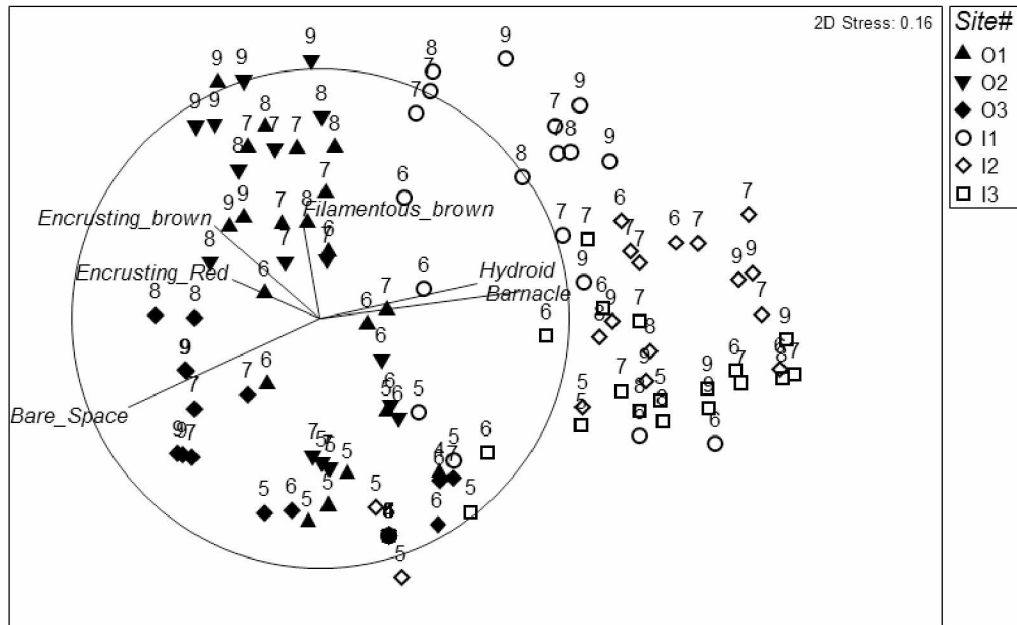


Figure 4. Community structure developing on rocks 1-6 months after deployment represented in non-metric multidimensional scaling plot using bray Curtis similarity matrix. Numbers above the data points are months (5: May, 6: June, 7: July, 8: August, 9: September). Vectors are shown for species that contributed to similarity within regions (Table 4).

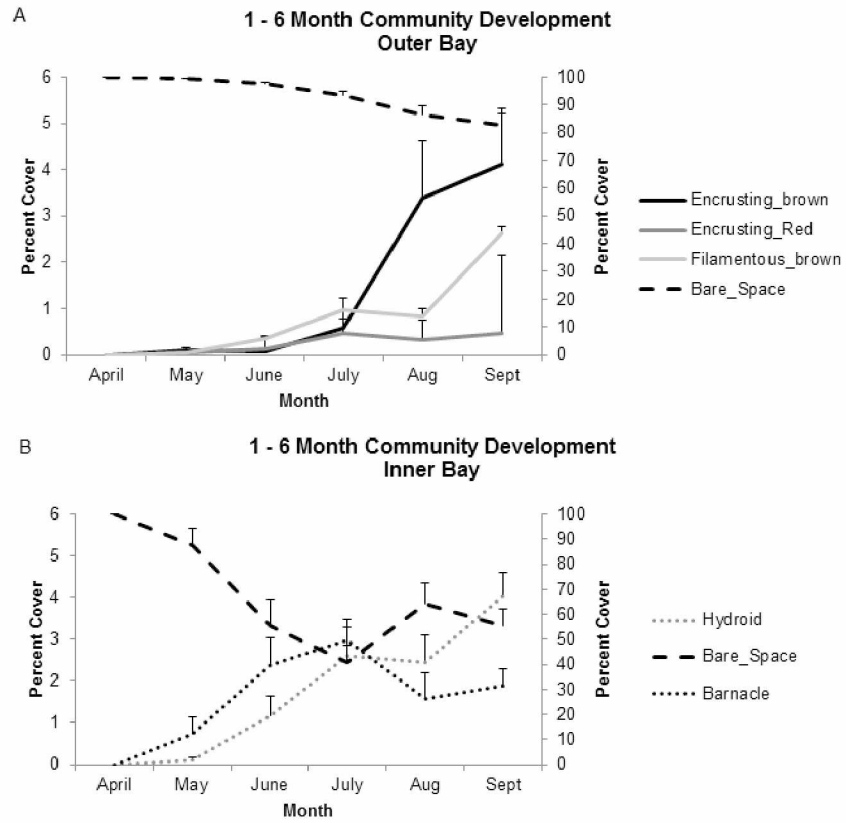


Figure 5. Percent cover of selected species that contributed to similarity within the A) outer bay, and B) inner bay on rocks up to six months (Table 4). Bare space and barnacles are shown on the secondary axis.

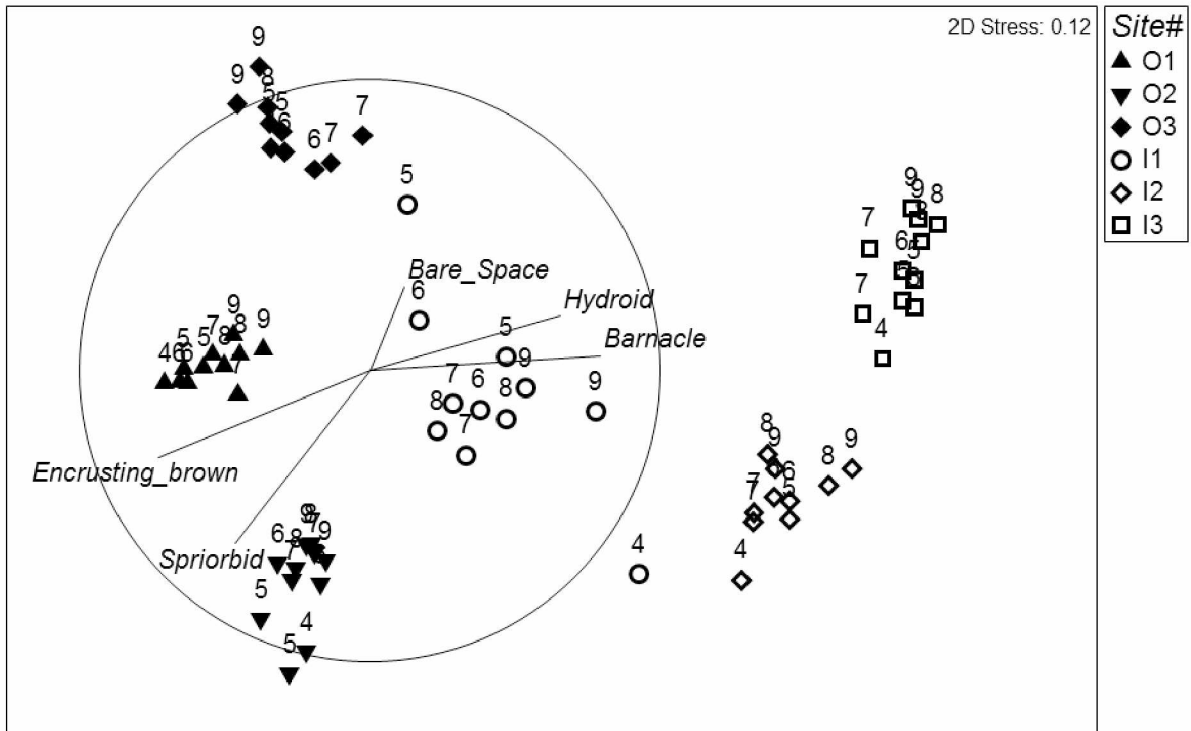


Figure 6. Community structure developing on rocks 12-18 months after deployment represented in non-metric multidimensional scaling plot using bray Curtis similarity matrix. Numbers above the data points are months (5: May, 6: June, 7: July, 8: August, 9: September). Vectors show species that contributed to similarity within regions (Table 8).

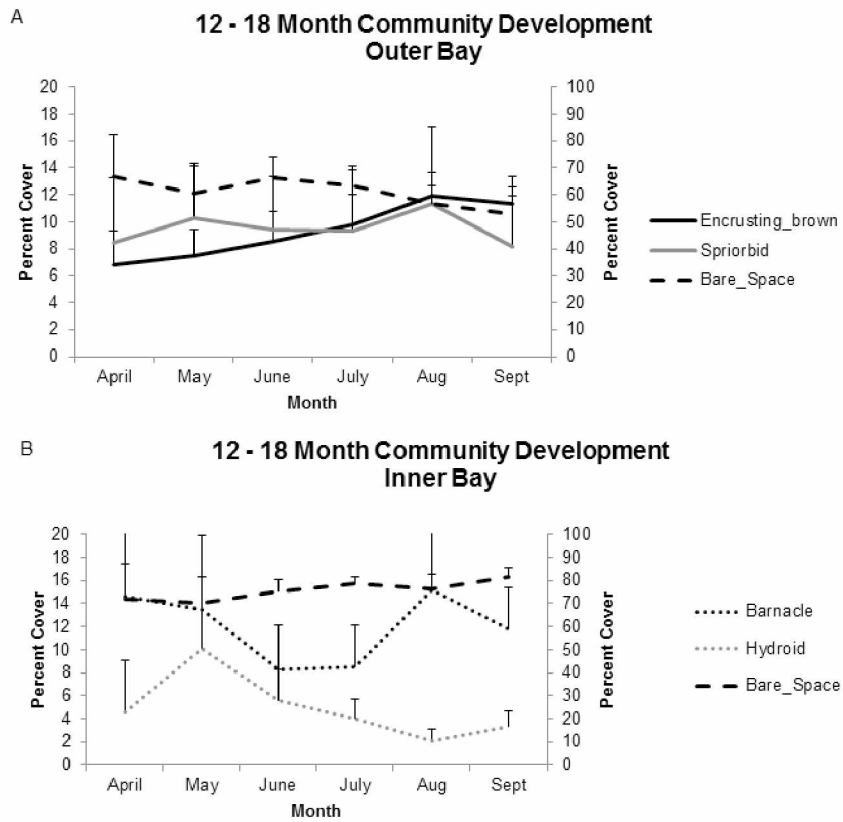


Figure 7. Percent cover of selected species that contributed to similarity within the A) outer bay, and B) inner bay on rocks from 12 to 18 months (Table 8). Bare space is shown on the secondary axis. Barnacles are shown on the primary axis.

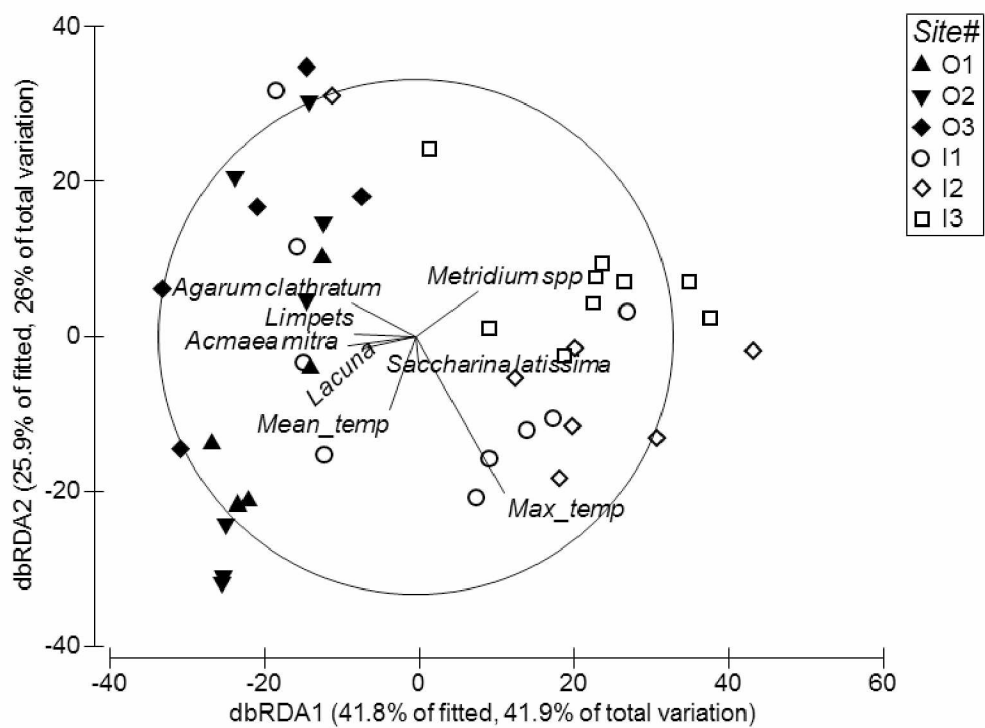


Figure 8. DistLM analysis of 1-6 month rock community. Vectors show variables that explained variation in the community. Numbers above points show months.

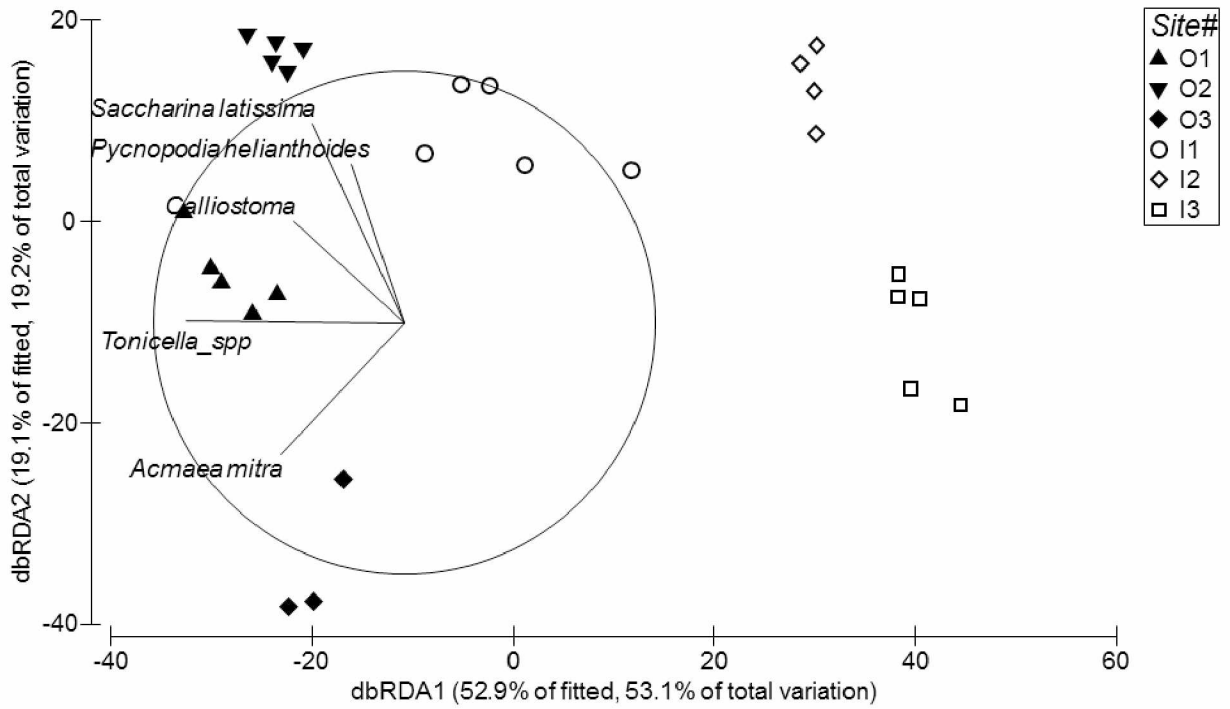


Figure 9. DistLM analysis of 12-18 month rock community. Vectors show variables that explained variation in the community. Numbers above points show months.

1.8 APPENDIX A

Table 1. Correlations between environmental variables and the first and second principal component axes from principal component analysis. Monthly mean values for variables in bold are shown in Table 1.

Variables	PC1	PC2
Inorganic sedimentation	0.223	0.443
Organic sedimentation	0.239	0.197
PO ₄	0.393	0.052
SIO ₄	0.273	-0.087
NH ₄	0.119	0.289
NO ₃	-0.024	-0.141
Bottom Salinity	-0.384	0.021
Mean Temperature	0.471	-0.106
Maximum Temperature	0.380	-0.114
Minimum Temperature	0.366	-0.168
Mean Irradiance	0.042	-0.554
Maximum Irradiance	-0.011	-0.540
Total Variance explained	32.9%	21.1%

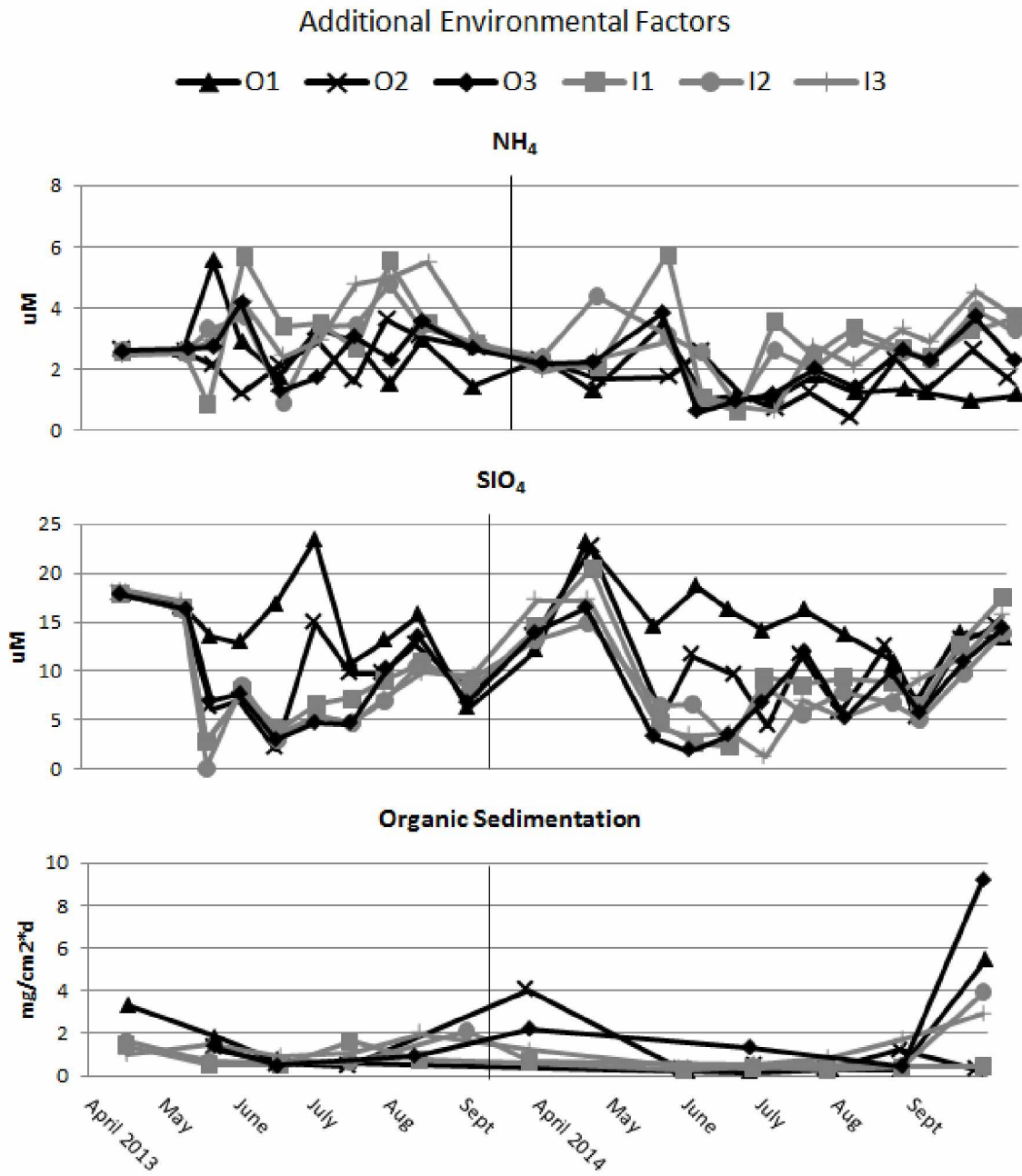


Figure 1. Temporal variations in ammonium, silicate, and organic sedimentation rate. Vertical bar distinguishes 2013 from 2014 data

CHAPTER 2: SUPPLY AND SURVIVAL: GLACIAL MELT IMPOSES LIMITATIONS AT THE KELP MICROSCOPIC LIFE STAGE¹

2.1 ABSTRACT

High latitude kelp beds may be at risk from increasing sedimentation rates due to glacial melt. The sporophyte *Nereocystis luetkeana* (canopy-forming) occurs infrequently downstream of glacial melt where thick layers of sediment accumulate, while sporophytes of *Saccharina latissima* (understory) are common in these areas. I examined whether glacial melt conditions affect adult fecundity of either species, how sedimentation affects early gametophyte survival and growth, and whether gametophyte competitive interactions are altered by the presence of sediment. Fecundity did not differ in relation to glacial discharge for either species. In single species treatments, there was an effect of sediment on gametophyte survival but not growth for both species. In mixed species treatments when no sediment was added, *N. luetkeana* had higher survival than *S. latissima* when *N. luetkeana* was settled first. When sediment was added, *S. latissima* had higher survival than *N. luetkeana* when *S. latissima* was settled first. There was no difference in gametophyte growth between the two species for any treatment. Settlement timing may explain *Nereocystis*' ability to coexist with *Saccharina* and to occur in some locations downstream of glacial discharge. Climate change could result in the loss of *N. luetkeana* by favoring *S. latissima* gametophytes in competitive interactions.

¹ Traiger, S.B., Konar, B. Supply and survival: Glacial melt imposes limitations at the kelp microscopic life stage *In Review*, Journal of Experimental Marine Biology and Ecology

2.2 INTRODUCTION

Understanding biotic and abiotic constraints to species distributions is a central goal in ecology, and is particularly important for foundation species such as kelp, which may be vulnerable to climate change. Kelp beds are productive and diverse habitats that occur in temperate regions globally. At broad geographic scales, kelp distribution is typically limited by temperature and light (Gattuso et al. 2006, James et al. 2015) while at local scales, kelp abundance and species composition varies with spatially heterogeneous abiotic variables such as salinity, sedimentation, substrate, and wave exposure (Balata et al. 2007, Wernberg and Connell 2008, Spurkland and Iken 2011a). Biotic interactions such as competition with weedy macroalgae (Connell 2007) and urchin grazing (Ling et al. 2015) can also limit the abundance and distribution of kelp beds. At both broad and local scales, climate change is expected to alter environmental drivers (IPCC 2014), such as sea surface temperature, salinity, turbidity, and sedimentation (Harley et al. 2006). Changes in these drivers may affect biological processes in kelp beds, such as reproduction and species interactions (Harley et al. 2012).

Competition for space or other resources, in particular, can be an important structuring force in kelp bed communities. Competition and resource use vary over the kelp life cycle, which consists of two distinct phases. The large, dominant sporophyte (2N) produces microscopic spores that disperse, settle to the benthos, and form microscopic, filamentous gametophytes. Those gametophytes (1N) produce sperm and eggs that upon fertilization give rise to sporophytes (Schiel and Foster 2006). As the macroscopic and microscopic life stages are exposed to different physical conditions (i.e., light and hydrodynamics), their interspecific competitive interactions also likely differ. Much is known about kelp competition at the macroscopic stage. For example, competition for hard substrate and light can limit abundance of

some kelp species (Watanabe et al. 1992, Konar 2007, Benes and Carpenter 2015). Interspecific competition can also be important when one species overgrows another (Konar and Iken 2005, Yorke and Metaxas 2011). In late successional stages of kelp community development, perennial kelp sporophytes can achieve competitive dominance over annual species, forming patches that are stable over time (Vadas 1968, Duggins 1980, Dayton et al. 1984). Although competition exists among kelps at the early life stages, it is unclear whether it is occurring at the gametophyte stage or early sporophyte stage (Reed 1990). Competition at the gametophyte stage may occur through space preemption, differential uptake of nutrients and growth rates, or allelopathy (Reed 1990). Environmental stress can affect competitive interactions by removing competitive dominants (Sousa 1979) or reducing their growth rates (Wootton et al. 2008). The morphological variation among kelp species provides structurally diverse habitat to other kelp bed inhabitants. The species composition of a kelp bed can thus affect the diversity and abundance of associated organisms (Hamilton and Konar 2007, Siddon et al. 2008). Changes in interspecific competition among habitat-forming species that alter the composition of the kelp assemblage may then have consequences for other species.

Effects of climate change on reproduction in marine organisms have been less studied than effects on survival and growth, but have important consequences for population dynamics. Kelp sporophytes are highly fecund and can release tens of millions of spores per year (Schiel and Foster 2006), although changes in physical factors (such as temperature and light) can affect sporophyte fecundity. For example, increased temperature can result in increased sporulation and spore release (Bartsch et al. 2013). Additionally, fecundity can differ between isolated individuals and those within a bed, presumably due to differences in light and hydrodynamics (Edwards and Konar 2012). Shading by canopy kelp can also reduce fecundity of subcanopy

kelps (Dayton et al. 1999). While warming temperatures may increase fecundity, environmental changes that reduce light, such as sedimentation, could decrease fecundity, and the interaction of these factors is unknown.

Climate change is expected to cause continued loss of glacial volume and increased discharge (Neal et al. 2010, Huss and Hock 2015), elevated precipitation and extreme rainfall events (Scavia et al. 2002), and accelerated soil erosion (Nearing et al. 2004). These factors are likely to increase sediment input to the nearshore environment, which may affect kelp fecundity, recruitment, and interspecific competition. Field studies have shown high sedimentation rates lower community diversity and kelp recruitment (Balata et al. 2007, Spurkland and Iken 2011a). Melting glaciers discharge large amounts of fine sediments to coastal habitats with peak discharge occurring in late summer or early fall (Gatto 1982, Cowan 1992). Suspended sediment can reduce light available to benthic organisms and settled sediment can scour or bury sessile organisms (Airoldi 2003).

Although glacial melt and sedimentation have negative effects on many species, some macroalgae persist downstream of glacial discharge and in areas of high sedimentation (Balata et al. 2007, Kawamata et al. 2012). *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl et G.W. Saunders (hereafter *Saccharina*) is a perennial understory kelp that commonly thrives downstream of glacial discharge in Alaska (Spurkland and Iken 2011a). This species is resistant to the low salinity and irradiance conditions associated with glacial melt (Spurkland and Iken 2011b) but does have a shorter growing season at glacially-influenced sites (Spurkland and Iken 2012). *Nereocystis luetkeana* (Mertens) A.P. Postels and F.J. Ruprecht (hereafter *Nereocystis*) is a surface canopy-forming annual or biannual kelp that co-occurs with *Saccharina* upstream of glacial discharge and on outer coasts (Spurkland and Iken 2011a, Pirtle et al. 2012). Only rarely

does *Nereocystis* co-occur downstream with *Saccharina*. In addition to environmental conditions, competitive interactions may also contribute to the distributions of these species. *Nereocystis* is generally considered competitively inferior to perennial species during the sporophyte phase (Vadas 1968, Duggins 1980, Dayton et al. 1984). Interactions between these two species during the gametophyte stage are unknown but may affect abundance of sporophytes growing out from these gametophytes. Given their adult distribution, it is likely that sporophyte fecundity or gametophyte survival of the two species is differently affected by the level of glacial melt sedimentation.

To investigate this possibility, I compared kelp fecundity between areas with oceanic and glacial influence and exposed kelp gametophytes to sediment in a lab experiment to test three hypotheses: 1) *Nereocystis* fecundity is lower at sites downstream of glacial discharge, while *Saccharina* fecundity is unaffected by glacial discharge, 2) *Nereocystis* gametophytes have lower survival and growth rates than *Saccharina* in the presence of sediment, and 3) *Saccharina* gametophytes are competitively superior to *Nereocystis* gametophytes with sedimentation.

2.3 MATERIALS AND METHODS

2.3.1 Study site

Kachemak Bay is a large high-latitude estuary in southcentral Alaska that can be divided into oceanic and glacially-influenced regions. Currents enter the bay from the Gulf of Alaska, flow along the southern coast toward the head of the bay, and exit the bay along the northern coast (black arrows, Figure 1) (Schoch and Chenelot 2004). The Homer spit extends several kilometers into the bay and divides it into an inner and outer bay. Several rivers discharge glacial melt water into the inner bay (grey arrows, Figure 1). In Chapter 1 (August-September 2013-

2014), at sites upstream of glacial discharge point sources in the outer bay, average rates of inorganic sedimentation ranged from 1.4 ± 0.3 to 1.7 ± 1.0 $\text{mg}/\text{cm}^2 \cdot \text{d}$ (average \pm s. d.). In the inner bay, monthly average sedimentation rates ranged from 4.2 ± 1.7 to 9.6 ± 1.6 $\text{mg}/\text{cm}^2 \cdot \text{d}$ (average \pm s. d.). Mean irradiance at depth (10 m below mean lower-low water (MLLW)) was 6.420 ± 1.959 $\mu\text{mol m}^{-2}\text{s}^{-1}$ and 1.511 ± 0.940 $\mu\text{mol m}^{-2}\text{s}^{-1}$ in the outer and inner bays, respectively (average \pm s. d.). Nitrate concentrations at 10 m MLLW were 4.8 ± 0.3 μM and 3.2 ± 1.0 μM in the outer and inner bays, respectively (average \pm s. d.). Similar contrasts in irradiance and nitrate concentration between sites upstream and downstream of glacial discharge were observed at 5 m depth MLLW in July and August 2006 (Spurkland and Iken 2011a). Bottom temperature was similar between regions at $11.7 \pm 0.2^\circ\text{C}$ and $11.0 \pm 0.1^\circ\text{C}$ in the outer and inner bays, respectively (average \pm s. d., Chapter 1). Salinity at depth (10 m MLLW) was similar between regions at 30.1 ± 0.5 and 30.2 ± 0.4 in the outer and inner bays, respectively (average \pm s. d., Chapter 1); however, surface salinity can be different between regions with haloclines forming deeper in the water column in the inner bay where surface salinity can decline from values at depth by approximately 21% (Schoch and Chenelot 2004).

2.3.2 Fecundity Comparison

I quantified *Nereocystis* and *Saccharina* fecundity at four sites in Kachemak Bay (Figure 1). Outside Beach and Hesketh Island are located upstream of glacial discharge (Figure 1) while Peterson Bay and Gull Island are downstream (Figure 1). Both *Nereocystis* and *Saccharina* occurred at all sites. Three times from mid-August to mid-September 2016 (8/10-12, 8/21-23, 9/8-10), three 10 x 2-m transects were randomly placed at 5-m depth MLLW within the *Nereocystis* bed at each site. At each sampling event, sites were visited within 2 hours of low

tide. Reproductive and non-reproductive *Saccharina* were counted and all stipes of *Nereocystis* were counted. The sori, i.e., the patch on the blade where sporophytes produce and release spores, of all reproductive *Saccharina* encountered were collected from each transect. At the surface, reproductive and non-reproductive *Nereocystis* were counted in a straight line until the same number of individuals that was seen on the benthic transects was reached. *Nereocystis* were counted in this way because their buoyant pneumatocyst holds the blades bearing sori at the surface. All ripe sori of each reproductive *Nereocystis* encountered were collected in separate plastic bags.

Nereocystis can be annual or biannual, while *Saccharina* are perennial. *Nereocystis* sporophytes typically recruit from spring to summer and their stipe elongates until individuals reach the surface, at which time they develop sori. Annual plants will senesce in the fall, while biannual plants will continue producing spores through the winter and into a second summer (personal observation). I conducted counts separately for first and second year individuals to determine whether these demographic patterns varied between regions.

Reproductive *Saccharina* and *Nereocystis* were transported to the Kasitsna Bay Laboratory in coolers of chilled seawater. At the lab, sori for each individual were photographed and the area of ripe sori was measured using ImageJ. A single 19.63 cm² disc of ripe sorus was randomly collected from one of the sori on each individual. Each disk was wrapped in moist paper towels and placed in a cold room chilled to 10 °C for 1 hour. This was done to synchronize spore release across replicates (Deiman et al. 2012). Each sorus disc was then placed in a separate petri dish with 100 ml of sterile seawater (Redmond et al. 2014) at 10 °C under 3.375 μmol m⁻²s⁻¹. This light condition was chosen as an intermediate level between upstream and downstream sites. After 1 hour, the spore solution was gently stirred and released spores were

counted once using a hemocytometer. Spore release for the total sori area of the entire plant was extrapolated based on the spores released from the single 19.63 cm² disc. Fecundity was calculated for each species at each site as the average spores released/cm² sori (Buschmann et al. 2006, Edwards and Konar 2012).

2.3.3 Competition-sedimentation experiments

Fertile sori of *Saccharina* were collected from Kasitsna Bay and ripe sori of *Nereocystis* were collected from the adjacent Jakolof Bay (Figure 1). For these experiments, sori were collected from different sites than the fecundity survey sites so as to not remove individuals that could be later recorded in transects. Sori of *Nereocystis* were collected from the surface from populations growing at approximately 5 – 10 m MLLW depth and transported to the lab in a dark cooler with chilled seawater and placed in running seawater until use. For logistical reasons, *Saccharina* sori were collected at ~2 m MLLW depth at Kasitsna Bay where they could be reached by wading at low tide or snorkeling. Sori were carried from the beach to the Kasitsna Bay Laboratory in mesh bags and immediately placed in running seawater until use. Sori of each species were held in running seawater for up to 24 hours before use. For each species, sori from 3-5 individuals were randomly selected from the site. Sori were gently scraped with razor blades to remove diatoms, after which they were desiccated in the dark at 10 °C for up to 1 hour. Spores were then released in 1-L beakers of sterile sea water under 3.375 μmol m⁻²s⁻¹. Spore solution density was calculated using a hemocytometer. Spores from three to five different individuals were combined and then diluted with sterile seawater to 100,000 spores/ml for single species treatments (see below) and 50,000 spores/ml for mixed species treatments (see below) to facilitate settlement densities of approximately 450 and 225 germlings/mm², respectively.

Sediment was collected from the shallow subtidal (~2 m MLLW) in Kasitsna Bay and filtered to < 63 μm (defined as fine silt by the Wentworth scale), after which it was sterilized by heating in a microwave oven for 15 seconds (Wentworth 1922; Deiman et al. 2012). Six separate runs of the single and mixed species treatments (see below) were conducted, with three replicates per treatment within each run. All treatments were exposed to $3.375 \mu\text{mol m}^{-2}\text{s}^{-1}$ in a 12:6 light:dark cycle at 10 °C for the duration of the experiment.

2.3.4 Single Species Response to Sedimentation

To examine how sedimentation affected gametophyte growth and survival, four single species treatments were completed: 1) *Saccharina* with no sediment, 2) *Nereocystis* with no sediment, 3) *Saccharina* with sediment, and 4) *Nereocystis* with sediment. For this, a microscope slide was placed at the bottom of each plastic container and 250 ml of 100,000 spores/ml spore solution was gently poured into the container. To compare results of these treatments to the mixed-species treatments described below, I mimicked the handling and dying procedure employed during the mixed-species treatments. After 12 hours, slides were removed and 12 drops of sterile sea water were placed on the surface of the slides and allowed to stand for 2 minutes, after which slides were replaced in plastic containers with 100 ml of sterile seawater. During this procedure, the slides were removed from the cold room and handled in a room with windows covered in black plastic to avoid high light levels stressing the germlings. The door of the room was left open to provide enough light to see the slides and containers, but to prevent light from shining on the slides.

Thirty-six hours after the original settlement, gametophytes were counted in five haphazardly chosen replicate fields of view at 400 x magnification on each slide and then placed

in new containers with 250 ml of sterile seawater. New containers and new sterile seawater were used so that these treatments were again handled in the same way as the mixed species treatments. For the treatments with sediment, 105 mg of sediment were added to each replicate at this time, achieving a sediment density of 5.38 mg/cm^2 (Deiman et al. 2012). This sediment density is similar to those observed near glacial melt in Kachemak Bay and to what has been used in previous lab experiments on spore settlement (Deiman et al. 2012; Spurkland and Iken 2011a). For each replicate, sediment was suspended in 50 ml of seawater and gently poured into the containers containing 200 ml of seawater so that the sediment settled evenly onto the slide. To capture early gametophyte survival and growth, slides were removed from containers six days later, gently rinsed with sterile seawater, and photos of the slides were taken through the microscope eyepiece in five replicate fields of view at 400 x magnification. In Image J, all gametophytes were counted and the germtube length of the first 100 gametophytes was measured. Germtubes were measured from the outside of the original spore cell to the end of the germtube using the reticle as a size reference. Gametophytes were counted and measured in the same room and under the same conditions as the staining procedure described below.

2.3.5 Mixed Species Response to Sedimentation

To examine how sedimentation affected the competitive interaction of gametophytes of the two species, four mixed species treatments were completed: 1) *Saccharina* settled first and *Nereocystis* settled second with no sediment, 2) *Nereocystis* settled first and *Saccharina* settled second with no sediment, 3) *Saccharina* settled first and *Nereocystis* settled second with sediment, and 4) *Nereocystis* settled first and *Saccharina* settled second with sediment. A microscope slide was placed at the bottom of each plastic container and 250 ml of a 50,000

spores/ml solution of the first species was gently poured into the container. After 12 hours, germlings of the first species were stained with Fungifluor dye (Edwards 1999) so that the first species could be distinguished from the second. Dye was added after 12 hours so that most of the spores would have settled to the bottom and spores would have time to form germtubes to which the dye could adhere. For this, slides were removed from containers, gently rinsed with sterile seawater and 12 drops of dye were placed on the slide surface and allowed to stand for 2 minutes, as per the staining kit instructions, then replaced in containers with 100 ml of sterile seawater. A smaller volume of seawater was used at this time to maintain a higher concentration of dye in the containers. As with the single species treatments, the slides were removed from the cold room and handled in a room with windows covered in black plastic to avoid high light levels stressing the germlings. Twenty-four hours later, slides were removed from containers, gently rinsed with sterile seawater to remove any remaining dye, and then placed in new containers with 250 ml of a 50,000 spores/ml solution of the second species. The second species was allowed to settle and grow for 24 hours before sediment was added, using the same procedure described above for single species treatments. At this time, slides were removed and gently rinsed with seawater and gametophytes of each species were then counted for three fields of view at 400 x magnification and replaced in new containers of 250 ml of seawater. Because the process of counting and measuring gametophytes for these treatments was slower than for the single species treatments, fewer fields of view were used to prevent these slides from being out of the water for longer than the single species treatments. A black light was used to identify dyed gametophytes. Six days later the counts were repeated and germtube lengths were measured. For the mixed species treatments, counts and size estimates were conducted visually instead of in

Image J as was done for the single species treatments. Gametophytes were counted and measured in the same room and under the same conditions as the staining procedure.

2.3.6 Data analysis

Fecundity (spore release/cm² sori), proportion of reproductive individuals, proportion of first year *Nereocystis*, and density (individuals/m²) were tested for normality using the Shapiro-Wilk tests and for homogeneity of variances using Fligner tests in R (R Development Core Team 2008). Spore release data were log transformed. Normal distributions were not achieved with any transformation for the other variables, so no transformations were applied. Variance was equal between regions for all variables. Differences among sites (random factor), between regions (upstream or downstream of glacial discharge, fixed factor), and among the three sampling events (random block) were tested using a three-way PERMANOVA with site nested within region. Separate PERMANOVAs were performed on each variable for each species on Euclidian distance matrices for spore release and proportion variables and Bray-Curtis resemblance matrices for density. PERMANOVA was used for these analyses because it uses permutations and is distribution free.

Gametophyte survival and growth data were square root transformed. A two-factor PERMANOVA test was performed on gametophyte survival and growth separately. The factors were species (fixed, two levels: *Nereocystis* and *Saccharina*) and treatment (fixed, six levels: single species, single species with sediment, *Nereocystis* settled then *S. latissima*, *Saccharina* settled then *Nereocystis*, *Nereocystis* settled then *Saccharina* with sediment, and *Saccharina* settled then *Nereocystis* with sediment). PERMANOVA was used so that variability could be

partitioned between the species and treatment factors. All PERMANOVA analyses were performed in Primer, a statistical software package (v7, Plymouth Marine Laboratories).

2.4 RESULTS

2.4.1 Fecundity did not differ between sites upstream and downstream of glacial discharge

Fecundity was highly variable among individuals for both species in each region and did vary between region for either species. For *Nereocystis*, spore release (Figure 2), proportion of reproductive individuals (Figure 3), proportion of first year individuals, and density were similar among sampling events, between regions, and among sites nested within region (PERMANOVA, $p > 0.05$ for all factors for each test). Spore release by *Nereocystis* ranged from a minimum of $910,975 \text{ spores/cm}^2 \pm 1,373,340$ at Hesketh Island, an upstream site, to a maximum of $27,011,641 \text{ spores/cm}^2 \pm 29,932,617$ (average \pm s. d.) at Outside Beach, also an upstream site (Figure 2). The proportion of reproductive *Nereocystis* ranged from a minimum of $2.0\% \pm 4.5$ at Peterson Bay, a downstream site, and a maximum of $24.6\% \pm 20.9$ at Outside Beach (average \pm s. d.; Figure 3). Within sites, the proportion of reproductive *Nereocystis* varied over time, as indicated by the significant interaction of site and sampling event ($Pseudo-F = 7.645$, $P = 0.002$). Average densities of *Nereocystis* by site ranged from $0.1/\text{m}^2 \pm 0.165$ to $0.2/\text{m}^2 \pm 0.246$ (average \pm s. d.).

I did not test for spatial differences in spore release by *Saccharina* because very few reproductive individuals were encountered during the study (four individuals upstream and two downstream). Spore release by *Saccharina* ranged from a minimum of $190,532 \text{ spores/cm}^2 \pm 152,172$ at Outside Beach, an upstream site, to a maximum of $881,538 \text{ spores/cm}^2 \pm 159,241$ (average \pm s. d.) at Gull Island, a downstream site (Figure 2). The proportion of reproductive

Saccharina was much lower than *Nereocystis* and ranged from 0% at Peterson Bay, a downstream site, to a mean of $0.2\% \pm 0.5$ (average \pm s. d.) at Gull Island (Figure 3). Average site densities of *Saccharina* ranged from 2.0 ± 1.4 to 3.2 ± 1.3 /m² (average \pm s. d.).

2.4.2 Competition-sedimentation experiment

2.4.2.1 *Nereocystis* and *Saccharina* gametophyte survival and growth are similar under sedimentation conditions

To determine whether sediment affects gametophytes of the two study species differently, gametophyte survival was compared between the two species in the single species treatment where sediment was added. In the global test of gametophyte survival by treatment and species, there was a significant interaction of treatment and species (Table 1). *Nereocystis* gametophyte survival was similar to that of *Saccharina* with and without sediment (Figure 4A). Both species had lower survival with sediment than in the no sediment control. *Nereocystis* and *Saccharina* survival declined to $83\% \pm 8.8$ (average \pm s. e.) and $70\% \pm 5.1$ (average \pm s. e.), respectively. *Nereocystis* and *Saccharina* growth did not differ from each other or between control and sediment single species treatments (Table 2, Figure 4B).

2.4.2.2 Competition outcomes depend on sedimentation conditions and order settled

Saccharina gametophytes had higher survival than *Nereocystis* gametophytes in the presence of sediment when *Saccharina* was settled first (Figure 5, Table 3). In this treatment, *Saccharina* survival was $57\% \pm 9.0$ (average \pm s. e.) and *Nereocystis* survival was $27\% \pm 3.4$ (average \pm s. e.). In the sediment treatments where *Nereocystis* was settled before *Saccharina*, survival of each species was approximately 40% with no difference in the survival between the

two species. *Nereocystis* gametophyte survival was higher than *Saccharina* survival in the treatment without sediment where *Nereocystis* was settled first. There were no significant differences in growth between *Nereocystis* and *Saccharina* in any of the mixed species treatments.

2.5 DISCUSSION

Climate change has a strong potential to influence marine communities not only by affecting organism survival, but also by altering reproduction and interspecific interactions. I showed that glacial melt conditions do not affect the fecundity of two Alaskan kelps, but competitive interactions at the gametophyte stage are affected by sedimentation. Since the spore settlement order was important to the outcome of these competitive interactions, the timing of naturally occurring spore settlement could be an important factor determining these species ability to persist in high seasonal sedimentation areas and to coexist with each other. As climate change alters the physical environment, I expect direct effects on kelp recruitment and interactions among competitors.

While few *Saccharina* were reproductive, there was no difference in the fecundity of *Nereocystis* in relation to glacial discharge at the time of sampling in August and September, when glacial discharge rates are typically at their peak in Alaska (Chikita et al. 2002) and environmental conditions vary between regions upstream and downstream of glacial discharge (Schoch and Chenelot 2004, Spurkland and Iken 2011a, Traiger 2017). *Nereocystis* may be similar to some other kelp that are rigid in their reproductive strategies and do not increase spore release in response to changing environmental conditions (Reed et al. 1996). These findings indicate that glacial melt conditions may not reduce the local supply of spores within *Nereocystis*

beds. It should be noted, however, that the light conditions during spore release in the laboratory may have affected *Nereocystis* spore release. Individuals collected from sites upstream of glacial discharge may be adapted to higher light levels than those downstream of glacial discharge. In previous studies, observed differences in kelp fecundity may have been due to differences in light conditions caused by varying density in kelp canopy (Reed 1987, Edwards and Konar 2012). Inducing sori collected from different regions to release spores under the same light conditions may have masked an effect of adaptation to local light levels. However, the differences in irradiance noted in my methods section (see 2.3.1 Study site) are values at depth, while *Nereocystis* reaching the surface likely experience similar light conditions between regions upstream and downstream of glacial melt. Therefore, it is unlikely that their spore release is adapted to different light levels. While *Saccharina* do release spores near the substrate and are exposed to the different light conditions upstream and downstream of glacial discharge throughout their sporophyte phase, insufficient reproductive individuals were observed to allow a regional comparison of fecundity.

Although the individuals that were reproductive did not differ in their fecundity between regions upstream and downstream of glacial discharge, the timing of reproduction for either species may be affected by glacial melt. Seasonal timing of sporogenesis is under environmental control and may correspond with seasonal changes in photoperiod, irradiance, temperature, and nutrient concentration (Santelices 1990). *Saccharina* patterns of sporogenesis vary widely among locations, with many perennial populations reproducing in autumn and winter and some annual populations in the western Atlantic producing spores in the summer (Lee and Brinkhuis 1986). Initiation of sporogenesis of annual species such as *Nereocystis* may be related to individual size or age (Maxell and Miller 1996, McConnico and Foster 2005). *Nereocystis* may grow more

slowly downstream of glacial discharge than populations upstream, as is the case for *Saccharina* (Spurkland and Iken 2012), and thus may reach their reproductive peak later in the fall or early winter. Reproducing later in the year may benefit kelp because they release spores during periods of lower sedimentation rates.

The outcome of competitive interactions, with and without sediment, was dependent on the settlement order of competing species' spores. In the field, settling first may offer an advantage by allowing spores to occupy the best microhabitats, such as small depressions in rocks that may protect them from sediment; however, in my lab experiment I used smooth microscope slides, which presumably had uniform physical characteristics across the entire surface. The lower gametophyte survival in the mixed-species treatments relative to the single-species treatments may be due to competition for resources such as nutrients or CO₂ in the closed containers. In the mixed-species treatments, the species settled first were 1.5 days older than the second species, and these older germlings may have an advantage in taking up resources.

The outcomes observed may have been due to differential mortality between the two species in response to the combined stressors of sedimentation and competition for resources. Density dependent gametophyte mortality and inhibition of reproduction has been observed previously and was best explained by nutrient limitation (Reed et al. 1991). Target settlement densities were equal between single-species and mixed-species treatments, but a difference in the rate at which species take up nutrients could have caused nutrient limitation to occur sooner in mixed-species treatments.

Differences in spore release timing may facilitate coexistence of kelp species by allowing spores of early-release species to settle when more open space is available (Santelices 1990). Fecundity surveys showed that at least some proportion of *Nereocystis* are reproductive when

few *Saccharina* are reproductive. This may give *Nereocystis* the opportunity to settle before spores of *Saccharina* and avoid competition, or gain a competitive advantage. Kelp gametophytes typically delay development until the spring when available light increases and conditions are favorable for sporophyte recruitment (Carney and Edwards 2006). Even though there may be little overlap in the timing of spore release, gametophytes of later species may compete with already established gametophytes. Annual plants, such as *Nereocystis*, are often poor competitors with perennial species (Grime 1977) and can be considered “fugitives” if they only persist in areas where disturbance removes perennials. While some annual kelps such as *Alaria marginata* have been demonstrated to be non-fugitive (McConnico and Foster 2005), there are some observations that support labelling *Nereocystis* as a fugitive species. *Nereocystis* can be opportunistic and occupy open spaces when other kelp are removed by storms (Dayton et al. 1984). In the absence of disturbance, stands of *Nereocystis* may be replaced by perennial species (Vadas 1968). My finding that *Nereocystis* gametophytes gain a competitive advantage over *Saccharina* when *Nereocystis* spores are settled first supports descriptions of *Nereocystis* at the sporophyte stage as an opportunistic or fugitive species.

Kelp spore settlement densities in the field are not well understood, but could indicate whether gametophytes are likely to compete. It is unclear how settlement densities of *Nereocystis* and *Saccharina* in the field compare. Spore settlement densities near reproducing adult kelp (e.g., 50 germlings/mm² for understory kelp *Pterygophora californica*, 25 germlings/mm² for canopy-forming kelp *Macrocystis pyrifera*) are typically much higher than those even a few meters away (Reed et al. 1988). *Nereocystis* release a greater magnitude of spores than *Saccharina* (Figure 2), so it may be expected that *Nereocystis* gametophytes would occur at higher densities. However, *Nereocystis* release spores from their sori at the top of the water

column and continue releasing as sori detach from the blades and sink to the benthos (Amsler and Neushul 1989), so *Nereocystis* spores may disperse farther, resulting in lower gametophyte densities near the parent plant. Although molecular methods have been used to identify species-specific presence/absence of kelp gametophytes (Fox and Swanson 2007), no method has yet been developed to identify individual gametophytes in the field by species.

To better predict the effects of climate-induced abiotic changes on marine ecosystems, we need to identify which life stages of foundation species like kelp are most impacted, how important species interactions are affected, and how multiple environmental factors interact (Harley et al. 2012). In species with complex life cycles, different stages can vary in their responses to environmental conditions. For example, the gametophyte and embryonic sporophyte stages of the giant kelp *M. pyrifera* respond differently to simulated El Niño conditions (Ladah and Zertuche-González 2007). Although gametophytes survived, they were unable to reproduce and form sporophytes, while the embryonic sporophytes were able to survive and recover after exposure to warmer, lower-nutrient El Niño conditions (Ladah and Zertuche-González 2007). Similarly, the effects of sedimentation appear to vary among different stages of the kelp microscopic life phase. I observed relatively high rates of gametophyte survival in the presence of sediment, whereas several studies of *Nereocystis* and other species have found severe reductions in spore attachment to substrate in the presence of sediment (Devinny and Volshe 1978, Deiman et al. 2012, Geange et al. 2014). Established gametophytes seem to be more tolerant of fine sediments than settling spores. Therefore, spore release and germination before the seasonal increase in sedimentation from river or glacial discharge may be required for persistence in areas of seasonally high sedimentation.

Terrestrial runoff and glacial melt appear to be affected by global climate change. Over the course of the 20th century, peak streamflow shifted earlier by 1-2 weeks in western North America (Bates et al. 2008) and in Europe peak glacier runoff has shifted from August to earlier in summer (Huss 2011). It may become more difficult for *Nereocystis* gametophytes to establish in glacially-influenced areas if seasonal peaks in glacial discharge shift to earlier in the summer (Kundzewicz et al. 2008). Increased amount of discharge in the future could also lead to higher rates of sedimentation than currently observed, with impacts on spore settlement and gametophyte survival. Although overall glacial runoff in Alaska is predicted to be stable for several decades and then decline, approximately 19% of glaciers in Alaska are predicted to have increasing runoff (Bliss et al. 2014). Precipitation is also predicted to increase over the 21st century in response to climate change (Royer and Grosch 2006, Kundzewicz et al. 2008, Maloney et al. 2014) and where precipitation increases, soil erosion and runoff to the marine environment is also likely to increase (Nearing et al. 2004) and impact kelp beds.

Species interactions within kelp beds may also shift due to climate change. While grazers often have structuring influences on kelp abundance and community composition (Ling et al. 2015), kelp grazers such as urchins tend to be less abundant in areas of high sedimentation (Branch et al. 1990, Airoidi and Hawkins 2007, Traiger 2017). Interactions among macroalgal species may thus be relatively more important than grazer effects in more heavily sedimented areas. This study demonstrated that competition between *Nereocystis* and *Saccharina* does occur, and that the outcome is in part dependent on sedimentation conditions. While this study only examined interactions between two abundant kelps, interactions with turf algae may also be important as this functional group can be highly tolerant of sedimentation (Airoidi and Virgilio 1998), and can outcompete kelp under certain conditions (Connell and Russell 2010).

Competition between kelp and turf algae has only been examined at the macroscopic stage (e.g., Benedetti-Cecchi and Cinelli 1996), but interactions at the early microscopic stages may actually be responsible for the outcomes observed in macroscopic stages.

Synergistic effects of multiple stressors can affect survival, growth, and interspecific interactions. For example, in human-dominated coastlines in southern Australia, the combined stressors of sediment accumulation and elevated nutrient concentration allow turf algae to outcompete kelp (Gorman and Connell 2009). In high-latitude systems, increased sedimentation combined with other environmental factors may lead to different effects on survival, growth, and competitive outcomes at the gametophyte stage. The seasonal increase in glacially-influenced sedimentation coincides with changes in salinity and temperature (Etherington et al. 2007). *Saccharina* may thus have an even greater competitive advantage over *Nereocystis* because sporophytes and gametophytes of *Saccharina* are relatively tolerant to low salinity conditions (Spurkland and Iken 2011b, Lind 2016).

Changes to glacial discharge dynamics could affect the species composition of kelp beds through direct effects on survival and competitive interactions in microscopic life stages of kelps. If changes in glacial discharge dynamics or coastal erosion increase sediment loads to kelp beds, *Nereocystis* could be stressed by both sedimentation and competition with *Saccharina*. Changes to the composition of foundation species could also affect overall productivity, physical characteristics such as light and hydrodynamics, and biogenic habitat structure, which could influence the composition of associated species and the biodiversity of coastal marine communities. In Alaska, kelp beds with both surface and subsurface canopies support different fish species than kelp beds with only subsurface canopies (Hamilton and Konar 2007). Kelp beds can provide detritus to other nearshore habitats (Hyndes et al. 2012), and variation in dominant

kelp species may affect the timing and quality of these subsidies. Thus, shifts in the abundance of these two kelps may have far reaching effects.

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2.7 TABLES AND FIGURES

Table 1. Two-way PERMANOVA on gametophyte survival. The factors are the six treatments (Alone, Alone with sediment, *Nereocystis* settled before *Saccharina*, *Saccharina* settled before *Nereocystis*, *Nereocystis* settled before *Saccharina* with sediment, and *Saccharina* settled before *Nereocystis* with sediment) and Species (*Nereocystis* and *Saccharina*).

	df	Sum Sq	Mean Sq	Psuedo-F	P value
Treatment	7	120.37	17.195	11.273	0.0001
Species	1	0.16924	0.16924	0.11096	0.7487
Treatment x Species	3	31.968	10.656	6.986	0.0004
Residuals	59	89.994	1.5253		
Total	70	244.07			

Table 2. Two-way PERMANOVA on gametophyte growth. The factors are the six treatments (Alone, Alone with sediment, *Nereocystis* settled before *Saccharina*, *Saccharina* settled before *Nereocystis*, *Nereocystis* settled before *Saccharina* with sediment, and *Saccharina* settled before *Nereocystis* with sediment) and Species (*Nereocystis* and *Saccharina*).

	df	Sum Sq	Mean Sq	Pseudo-F	P value
Treatment	5	4.2175	0.84349	6.2099	0.002
Species	1	0.0096	0.0096645	0.071152	0.7917
Treatment x Species	5	0.3904	0.07808	0.57484	0.7194
Residuals	51	6.9273	0.13583		
Total	62	11.624			

Table 3. Differences in gametophyte survival between species within treatments.

Treatment	t	P value
Alone	0.514	0.5141
Alone + Sediment	1.1597	0.263
<i>Nereocystis</i> then <i>Saccharina</i>	2.5198	0.0291
<i>Saccharina</i> then <i>Nereocystis</i>	0.7425	0.4779
<i>Nereocystis</i> then <i>Saccharina</i> + Sediment	0.25542	0.7967
<i>Saccharina</i> then <i>Nereocystis</i> + Sediment	3.3466	0.0091

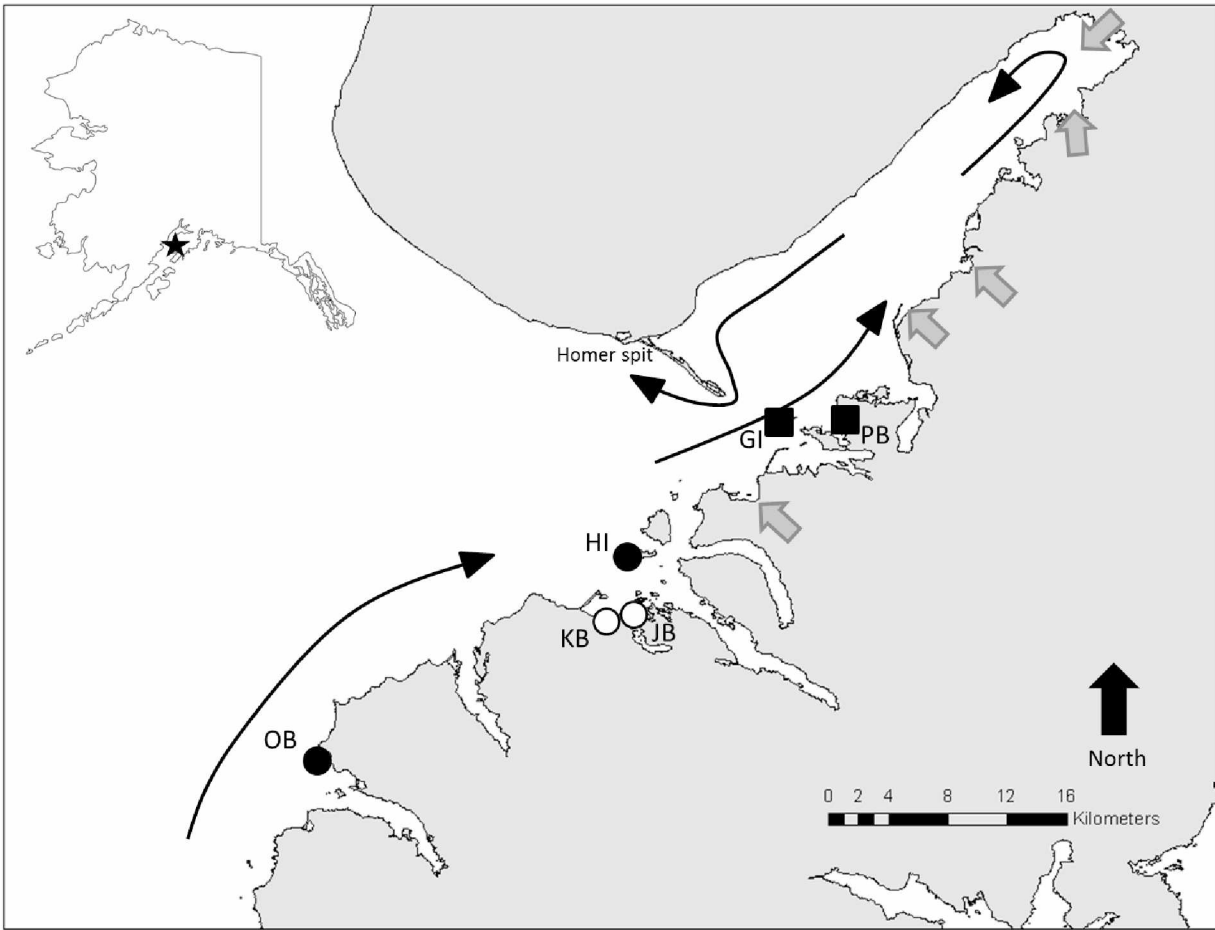


Figure 1. The study sites of kelp fecundity comparisons and sori collections. The black star shows the location of Kachemak Bay in Alaska (<http://www.worldatlas.com>). Black arrows show surface current flow and grey arrows indicate locations of glacial discharge. White markers indicate locations of sori collection for competition-sedimentation experiment. Black circles and black squares show upstream and downstream sites, respectively, for fecundity surveys. Site abbreviations are as follows: Outside Beach (OB), Kasitsna Bay (KB), Jakobof Bay (JB), Hesketh Island (HI), Gull Island (GI), and Peterson Bay (PB).

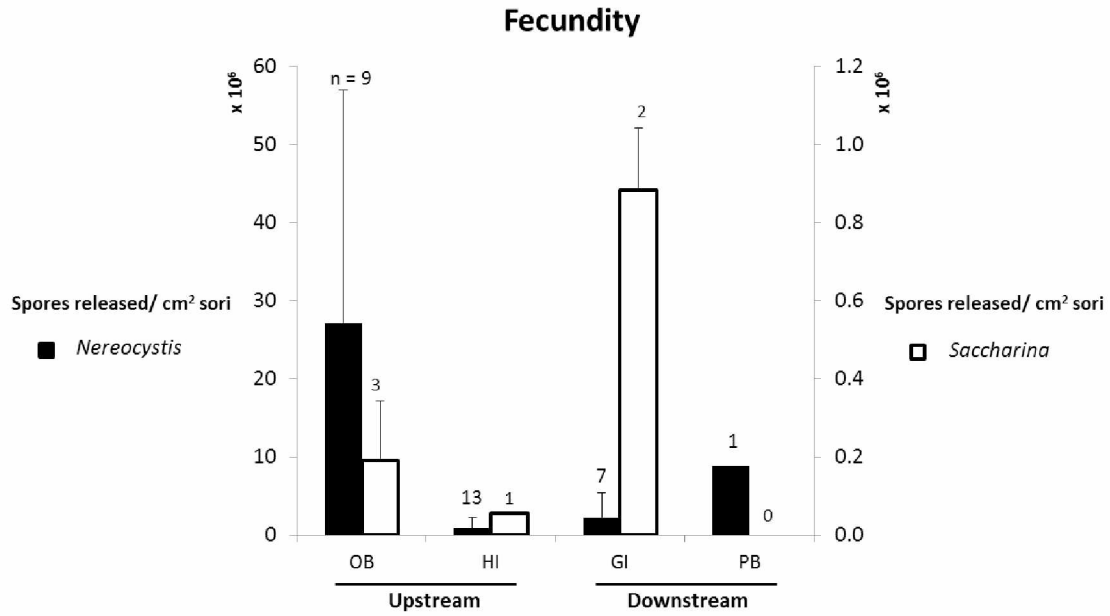


Figure 2. Mean (+ standard deviation) spore release by *Nereocystis* (black, primary axis) and *Saccharina* (white, secondary axis) among sites and between regions. Numbers above bars show the number of reproductive individuals observed. Site abbreviations are as follows: Outside Beach (OB), Kasitsna Bay (KB), Jakolof Bay (JB), Hesketh Island (HI), Gull Island (GI), and Peterson Bay (PB).

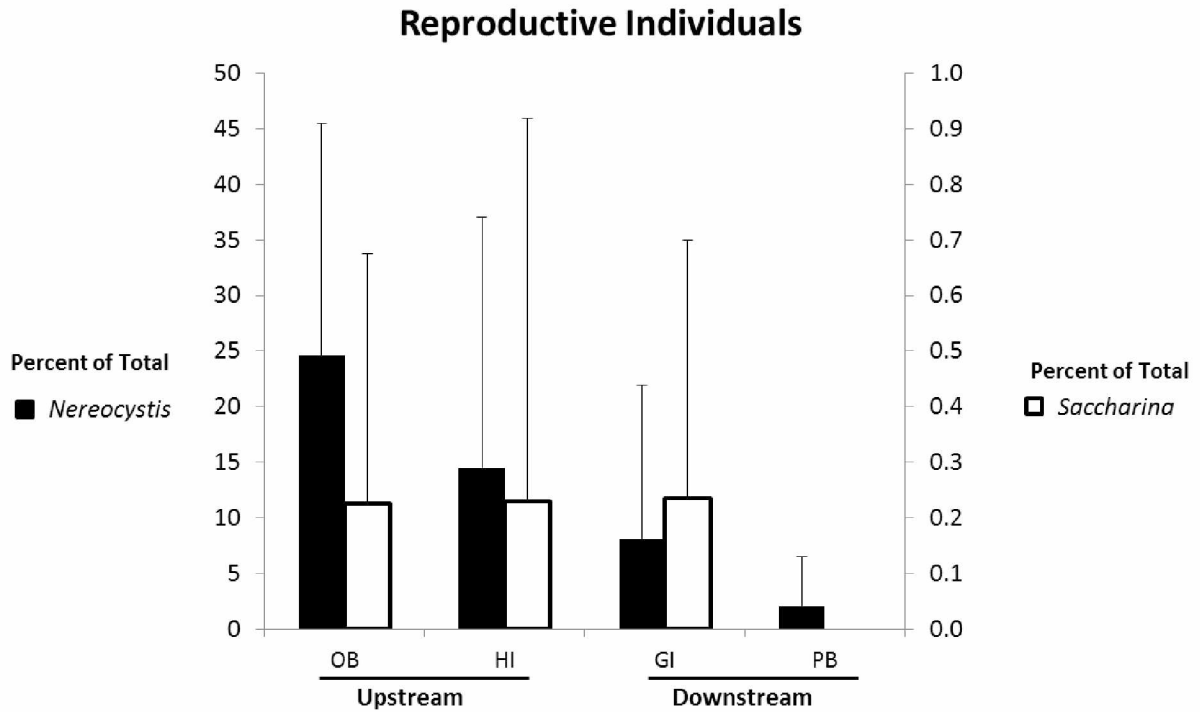


Figure 3. Mean (+standard deviation) proportion of reproductive individuals of *Nereocystis* (black, primary axis) and *Saccharina* (white, secondary axis) among sites and between regions. Site abbreviations are as follows: Outside Beach (OB), Kasitsna Bay (KB), Jakolof Bay (JB), Hesketh Island (HI), Gull Island (GI), and Peterson Bay (PB).

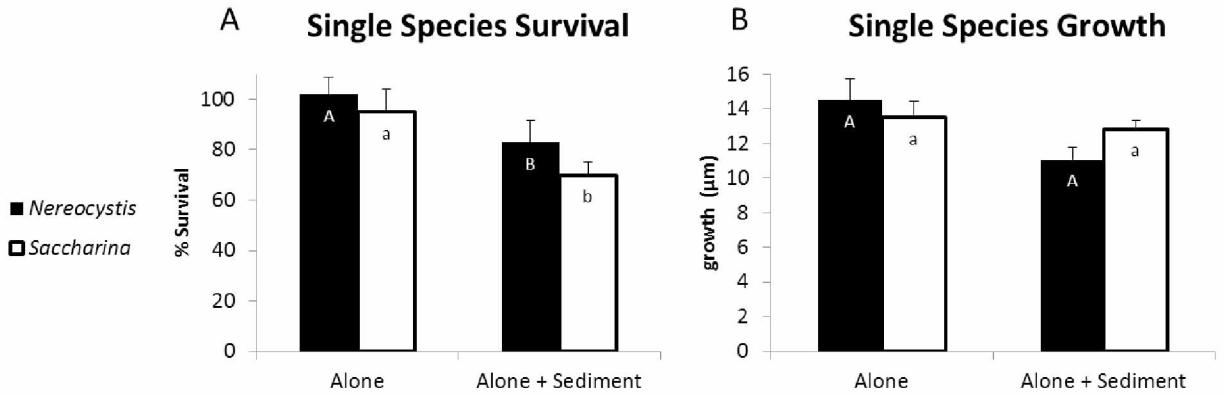


Figure 4. Mean (+ standard error) A) gametophyte survival and B) gametophyte growth in single species treatments. Uppercase and lowercase letters indicate significant differences in *Nereocystis* and *Saccharina*, respectively, among treatments.

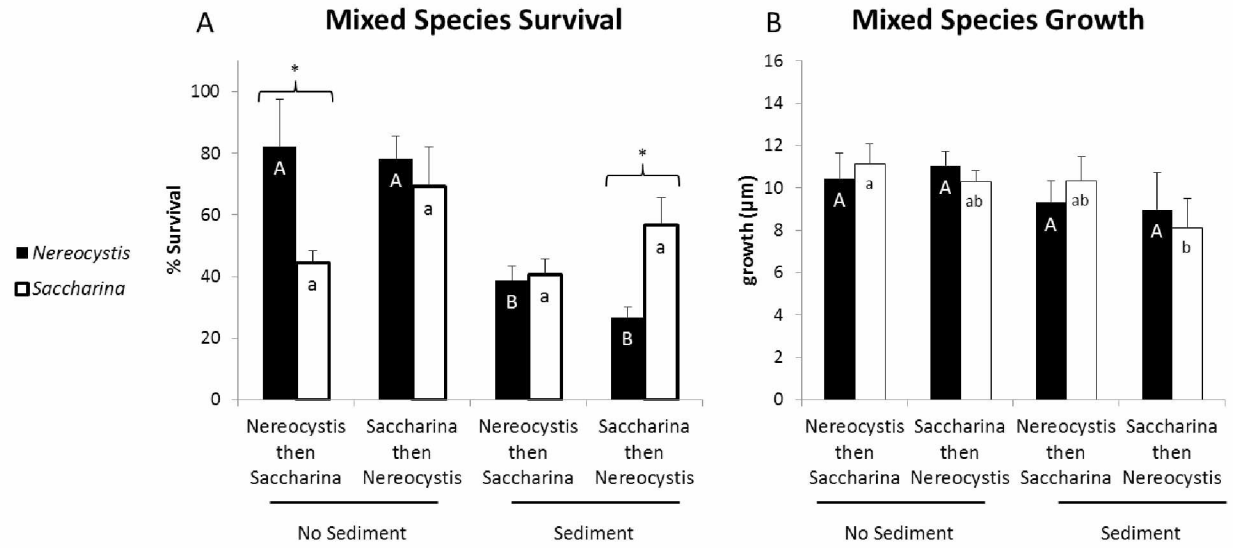


Figure 5. Mean (+ standard error) A) gametophyte survival and B) gametophyte growth in mixed species treatments. Uppercase and lowercase letters indicate significant differences in *Nereocystis* and *Saccharina*, respectively, among treatments. Asterisks indicate significant differences between *N. luetkeana* and *Saccharina* within treatments.

CHAPTER 3: SEA OTTER VERSUS SEA STARS AS MAJOR CLAM PREDATORS: EVIDENCE FROM FORAGING PITS AND SHELL LITTER¹

3.1 ABSTRACT

Sea otters *Enhydra lutris* and sea stars both excavate clams and leave behind foraging pits. If the source of pits can be determined with confidence, they may provide information about benthic foragers without direct foraging observations. My objectives were to determine (1) if pits can be attributed to either predator (sea otters or sea stars) using pit dimensions; (2) how pit shape changes over time; and (3) whether shell litter can be used to distinguish the relative clam predation by sea otters and sea stars. Naturally occurring pits were tagged and measured at 4 subtidal and 2 intertidal sites in Kachemak Bay, Alaska, USA, every 2 wk from May to August 2014. To determine how pit dimensions change over time, experimental sea otter and sea star pits matching published descriptions were dug at each site and measured after 2 wk. Additionally, I collected and analyzed shell litter at each site to determine the source of their mortality. Cluster analysis on pit dimensions showed that none of the measured parameters could identify pit source for the 109 pits measured. Consistent with this finding, the experimental pit types were indistinguishable after 2 wk. In contrast, shell litter proved useful in quantifying predator-specific predation. Consumption of clams by sea otters and sea stars was equal at all but one site. Only 2.4% of overall clam predation was attributed to other predators besides sea otters or sea stars. The significant sea star predation should be taken into account when making policy decisions concerning shellfish harvests and sea otter population management.

¹ Traiger, S. B., Konar, B. 2016. Sea otter versus sea stars as major clam predators: evidence from foraging pits and shell litter. *Marine Ecology Progress Series* 560: 73-86. doi: 10.3354/meps11871

3.2 INTRODUCTION

Sea otters *Enhydra lutris* and sea stars both excavate clams in the low intertidal and shallow subtidal zones (Smith 1961, Calkins 1978, Kvitek et al. 1992), which can impact clam fisheries and soft and mixed substrate habitat dynamics (Kvitek et al. 1992, Ross et al. 2002). In habitats with unconsolidated benthic substrate in Alaska, USA, clams comprise 71 to 100% of sea otter diet (Calkins 1978, Kvitek et al. 1992, Doroff & DeGange 1994, Wolt et al. 2012) and are also important prey for several northeast Pacific coast sea stars including sun stars *Pycnopodia helianthoides*, North Pacific sea stars *Asterias amurensis*, rainbow stars *Orthasterias koehleri*, and short-spined stars *Pisaster brevispinus* (Mauzey et al. 1968, Sloan & Robinson 1983). Where sea otters or sea stars have high predation rates on clams, clam harvest limits may need to be adjusted to maintain healthy clam populations. To better examine the ecological role of sea otters versus sea stars in soft-sediment habitats and to incorporate this predation into ecosystem-based management of clam fisheries, it is important to have accurate methods to determine foraging rates on clams.

Healthy and recovering sea otter populations have often been associated with reductions in the abundance and size of their prey, including clams (Hines & Loughlin 1980, Kvitek et al. 1992, Doroff & DeGange 1994). However, clam populations have also been able to persist and sustain otter populations for many years despite otter-associated mortality. In Prince William Sound, Alaska, sea otters reduced crab populations quickly after recolonizing but continue to be sustained at an equilibrium density in the region where clam populations exist (Garshelis et al. 1986). Sea otters have been perceived as a threat to commercial and recreational clam fisheries. In California, USA, the recolonization of sea otters prevented the opening of a recreational clam fishery (Wendell et al. 1983). In the Czech Republic, fishers' attitudes toward the recovering

Eurasian otters *Lutra lutra* were negative, although damage to fish stocks by the otters was not as severe as perceived (Vaclavikova et al. 2011). Understanding and accounting for primary sources of mortality in native bivalve populations will help resource management agencies inform human harvest levels in coastal Alaska.

Sea stars are diverse and abundant in the intertidal and subtidal in the North Pacific and in Kachemak Bay, Alaska (Chenelot et al. 2007, Iken et al. 2010) and, like sea otters, may be major clam predators. *P. helianthoides* are generalist predators, and burrowing clams are a large component of their diet in soft-substrate habitats (Shivji et al. 1983), contributing up to 72% of their diet in the subtidal zone (Mauzey et al. 1968). *P. brevispinus*, *Evasterias troschelii*, and *O. koehleri* feed on clams in Washington, USA (Mauzey et al. 1968, Smith 1961), and these species also occur in Alaska (Chenelot et al. 2007). *A. amurensis* dig shallow pits for clams and have reduced commercial clam stocks in Tasmania, Australia, where they are invasive (Ross et al. 2002). As one of the most common and active sea stars in Alaska, *P. helianthoides* is the most likely sea star to prey on clams at levels comparable to those of sea otters. Foraging by sea otters can facilitate *P. helianthoides* predation on clams by allowing easier access to remaining small clams excavated and not consumed by the sea otters (Kvitek et al. 1992). However, in habitats with high population densities of both sea stars and sea otters, predation pressure on all clam size-classes may be elevated. Further information on prey competition or facilitation between sea otters and sea stars such as *P. helianthoides* is needed to assess their respective impacts on clam resources.

Foraging pits can provide information about clam consumption by benthic foragers without direct foraging observations. For example, the presence and density of foraging pits has been used to determine sea otter foraging rates and locations (Kvitek et al. 1992) and to assess

their potential exposure to lingering oil in oil spill-impacted areas (Boehm et al. 2007, Bodkin et al. 2012). Substrate disturbance through pit digging has ecological consequences across a range of terrestrial and marine habitats (woodlands: Eldridge & Mensinga 2007; ponds: Adamek & Marsalek 2013; marine soft-sediments: Oliver & Slattery 1985). However, determining the source of foraging pits based on measured dimensions may be difficult. There is a high degree of overlap and a wide range of values in described characteristics of sea otter and sea star pits in the literature. Sea otter pits have been described as oblong with excavated sediment piled on one end of the pit (Kvitek et al. 1992); however, their dimensions have not been consistently reported among studies. Similar to sea otters, *P. helianthoides* also excavate pits while foraging for clams (Mauzey et al. 1968, Sloan & Robinson 1983). *P. helianthoides* push sediment aside with their arms and extend half of their arms into the pit (Sloan & Robinson 1983). Their pits have been described as being rounder and shallower than otter pits, with sediment piled in a ring around the pit (Kvitek et al. 1992). This description has been used by others to distinguish between otter pits and *P. helianthoides* pits (Boehm et al. 2007). In British Columbia, Canada, *P. helianthoides* were observed digging pits 6 to 14 cm deep (Sloan & Robinson 1983). Variation in observed pit dimensions among studies could be due to differences in sea otter foraging behavior, depth of the prey being targeted, or other factors affecting pit persistence such as the physical processes of wave action, currents, and sedimentation.

A major challenge in using foraging pits as a metric of foraging activity is that pit persistence is uncertain. Experimental pits dug around Kodiak Island, Alaska, were present after 6 mo but were gone after 12 mo (Kvitek et al. 1992). However, no detailed measurements or analyses were done on these pits since pit persistence was not the focus of that study. Foraging pits in the northern Knight Islands, Prince William Sound, Alaska, may persist for 1 yr based on

photographs taken 1 yr apart (Boehm et al. 2007), while experimental pits at mean lower low water (MLLW) in western Prince William Sound persisted for approximately 4 to 6 mo (Bodkin et al. 2011). In Elkhorn Slough, California, recently made otter pits had claw marks on the inner walls, which wore away over time (Kvitek et al. 1988), but this characteristic of foraging pits has not been reported elsewhere. If foraging pits actually fill in and are replaced by new pits by the time researchers return to a site, foraging activity could be underestimated. Foraging pit persistence may vary with environmental factors such as water motion or sediment grain size. In mixed grain size gravel beds, smaller particles are sorted through the interstitial spaces between larger particles (Buscombe & Masselink 2006). Foraging pits may fill in more quickly in areas with high amounts of interstitial space in the sediment. High water motion would also likely facilitate sediment movement. In addition, pits may change shape due to *P. helianthoides* foraging activity, as there is clear evidence that *P. helianthoides* are attracted to otter pits (Kvitek et al. 1992). They are chemoreceptive (Brewer & Konar 2005), quickly aggregate at experimentally dug pits, and prey on the smaller clams that sea otters leave behind (Kvitek et al. 1992). While foraging for remaining smaller clams within a sea otter pit, *P. helianthoides* could change the shape of the pit, or how the sediment mounds around the pit. This will make distinguishing between sea otter and *P. helianthoides* pits difficult and may lead to inaccurate designation of predators. Without a better understanding of pit persistence and changes in pit dimensions over time, studies using pit dimensions as a metric of foraging intensity on clams are not able to draw accurate conclusions about their predators. The use of foraging pits for determining otter predation on clams needs to be validated by comparing estimates with other methods, as was done for time–depth recorder data (Tinker et al. 2007).

Shell litter has also been used to determine the source of foraging pits (Kvitek et al. 1992, Boehm et al. 2007). Sea otters break clam shell valves or the hinge when feeding (Calkins 1978), while a laboratory study showed that *P. helianthoides* always leave the shell intact (Kvitek et al. 1992). Previous studies have used the presence of otter-cracked shells next to a pit as an identifying characteristic of otter pits (Kvitek et al. 1992, Boehm et al. 2007). However, sea otters eat their prey on the surface, and in areas with large tidal currents the shell litter may not fall directly next to the foraging pit from which they obtained their prey. For this reason, the use of shell litter for determining individual pit source may be inappropriate; however, these materials may be used for predation source at the site level.

Gaps in my knowledge about the origin and persistence of foraging pits currently limits my ability to quantify the relative contribution of sea otters, sea stars, and other consumers to local clam predation. While previous studies have attempted to draw conclusions on clam predation events based on pit dimensions, questions regarding clam predation still remain: (1) Can sea otter and sea star foraging pits be distinguished using quantitative dimensions? (2) How long do characteristics distinguishing sea otter and sea star foraging pits persist? and (3) Can shell litter be used to determine the relative importance of sea otters and sea stars as clam predators? Here, I hypothesize that recent (2 wk old or less) foraging pits can be distinguished based on measurable characteristics (major axis, minor axis, pit depth, and how sediment is piled) and that after 2 wk sea otter and sea star pits can still be distinguished. Lastly, I hypothesize that shell litter can be used to assign relative clam predation by sea otters and sea stars.

3.3 MATERIALS AND METHODS

3.3.1 Study area

This study was conducted in Kachemak Bay, a large estuary in southcentral Alaska with a tidal range of approximately 9 m. Sea otters were extirpated from this area by 1792 (Lensink 1962), and after the close of the commercial fur trades for sea otter pelts, the region recovered through natural recolonization processes during the late 1960s and 70s (Schneider 1976, Gill et al. 2009). Between 2002 and 2008, the population increased by 26% yr⁻¹, reaching 3.9 otters km⁻² (Newsome et al. 2015). Based on this last estimate, the Kachemak Bay population is below its carrying capacity based on estimated available food sources (Gill et al. 2009, Newsome et al. 2015). Since then, the sea otter population has continued to grow in this region at approximately 13% yr⁻¹ (USFWS and USGS unpubl. data). *Saxidomus gigantea* and *Leukoma staminea* are the most popular clams for recreational fishing in Kachemak Bay (ADFG 2009). Surveys of clam populations in Kachemak Bay in 2007 and 2008 found that *S. gigantea* was abundant (up to 58 m⁻²) and *Macoma balthica*, *Mya truncata*, and *L. staminea* were also observed (Stewart et al. 2014). *Pycnopodia helianthoides* are common in Kachemak Bay and can reach densities of 0.1 to 0.28 m⁻² (Brewer & Konar 2005, S. B. Traiger & B. Konar unpubl.).

Sampling sites in this study were located at 10 m depth (referenced to MLLW) at 4 sites (Port Graham, PG; Peterson Bay, PB; McDonald Spit, MS; and Kasitsna Bay, KB) and at 2 intertidal sites (0 m depth at MLLW) (MS and KB; Fig. 1). These water depths were chosen because sea otters and sea stars often forage there (Mauzey et al. 1968, Calkins 1978, Sloan & Robinson 1983, Kvitek et al. 1992) and clams are common (Stewart et al. 2014). Sites were chosen to standardize substrate as much as possible.

3.3.2 Distinguishing unknown pit sources using quantitative dimensions

Foraging pits that were recently made (within the last 2 wk) were tagged, counted and measured along three 10 × 2 m permanent transects every 2 wk from May to August 2014 at all 6 sites. The center of each pit was marked with a landscaping flag so that it could be revisited and so that new pits could be distinguished from those previously sampled. For each pit, the lengths of the major axis, minor axis and depth in the middle of the pit were recorded. Surface area was calculated using the equation for area of an ellipse. As an indicator of pit shape, I calculated the percent difference between the major axis and the minor axis as $[(\text{major} - \text{minor}) / \text{major}] \times 100$. The size of the sediment pile on the edge of each pit was quantitatively binned by the proportion of the pit edge encircled by sediment mound (0, 1–25, 26–50, 51–75, 76–100%). Approximately every 2 wk, new pits were measured and marked as previously described. Thus, the maximum age of pits surveyed after the initial sampling was known, except for those identified the first time the survey was conducted. Only pits of known maximum age were used in my analysis. If a previously marked pit was totally filled in with sediment and no longer recognizable as a foraging pit, it was recorded as ‘filled in’ and the marker was removed.

To determine whether the natural pits fell into distinct groups representing sea otter and sea star pits, the multivariate data cloud of pit dimensions was analyzed in Primer (PRIMER v. 6, Primer-E, Ltd., 2006). Major axis and minor axis were strongly correlated with surface area ($r = 0.95$ for both) and were excluded from analysis. Variables were normalized before analysis. I used CLUSTER analysis with group averages on Euclidean distance similarity matrix and SIMPROF test to determine whether there were significant subgroups within the data cloud (Clarke et al. 2014). A principal coordinate analysis (PCO) plot was used to visualize the data. A

1-way analysis of similarity (ANOSIM) test was used to detect differences in pit dimensions among sites (random, 5 levels: MS 0 m, KB 10 m, MS 10 m, PB, and PG).

3.3.3 Persistence of characteristics distinguishing experimental sea otter and sea star foraging pits

To test the persistence of pits in Kachemak Bay, experimental pits were constructed on May 28, 30, 31, and June 1, 2014. A total of 6 replicate sea otter and sea star pits were dug at all 6 sites. The dimensions selected for the experimental pits were based on descriptions of naturally occurring sea otter and *P. helianthoides* pits (Kvitek et al. 1992, Boehm et al. 2007). Specifically ‘sea otter’ pits were constructed to be 20 cm deep, with major and minor axes of 26 and 23 cm, respectively. For these pits, sediment was piled on one end of the oval pit, and all clams larger than 20 mm were removed from the excavated sediment to model the removal of clams by otters (Kvitek et al. 1992). Target dimensions for the experimental sea star pits were 10 cm deep and had a 20 cm diameter. For these, sediment was piled evenly around the edge of the round pit and all clams were removed from the excavated sediment to model the clams that would be removed by sea stars (Kvitek et al. 1992). Pairs of experimentally dug sea otter and sea star pits were placed side by side every 2 m along the depth contour. The side of the transect on which a pit was placed was determined randomly. Pits were numbered and marked with flagging tape on stakes in the sediment.

Experimental pit dimensions were measured immediately after digging the pits. Partly because of infill while digging and larger rocks in the substrate, actual dimensions varied from the target dimensions. Actual dimensions were typically within 10 cm of the target but ranged

from 12 cm below and 35 cm above the target dimension. Even with the infill, average starting dimensions for the 2 experimental pit types were significantly different (permutational multivariate ANOVA, PERMANOVA, $p = 0.0007$; Table 2).

To monitor short-term changes in experimental pit dimensions, pits were measured approximately 2 wk after set-up as previously described for naturally occurring pits. If an experimental pit was totally filled in with sediment and the sediment pile was gone, it was recorded as 'filled in'. Presence and activity of sea stars in all experimentally dug pits were noted and classified as described previously. Differences between experimental sea otter and sea star pits at the initial set up and after 2 wk were tested using the PERMANOVA procedure based on a Euclidean distance matrix in Primer. Variables were normalized before analysis. Variables were checked for correlation using Draftsman plots and Spearman correlations and subsequently removed from the analysis if correlations ≥ 0.9 occurred. Differences between experimental sea otter and sea star pits (Type) were tested at set-up and after 2 wk and among sites in a 3 factor design. The factors were Type (fixed, 2 levels: Otter, Star), Sampling event (random, 2 levels: Set-up, After 2 wk), and Site (random, 6 levels: KB 0 m, KB 10 m, MS 0 m, MS 10 m, PB, and PG). To further compare the degree of change among sites, percent change was calculated for each dimension of each pit by dividing the 'After 2 wk' measurement by the 'Set-up' measurement and multiplying by 100. Differences in percent change among sites were tested with a PERMANOVA on a Euclidean distance matrix with Site as a random factor.

The rates at which experimental pits fill in or change dimensions may be influenced by water motion. To assess relative water motion at each site where experimental pits were dug, 3 replicate clod cards were deployed at each site and at each depth contour (Denny 1985). Clod card cubes were made of Plaster of Paris using ice cube trays (plaster to water ratio of 1:1 based

on manufactures instructions), glued to plastic sheets, and attached to bricks. After the cards were assembled, they were cured in seawater for 2 d, then dried for 1 wk and weighed twice to ensure they were fully dried before they were deployed in the field for approximately 2 wk. Handling controls were taken to the sites (either intertidal or subtidal) and then returned to the lab and placed in still sea water for 2 wk. Average weight loss of controls for each site was subtracted from the weight loss of the field-deployed clod cards. Weight loss of clod cards was compared among sites using ANOVA with Tukey's pairwise comparisons to assess relative water motion (Thompson & Glenn 1994) using the R program (R Development Core Team 2008).

The rates at which experimental pits fill in may also be influenced by substrate composition. To assess percent cover of substrate grain size at each site, sediment grain size (sand [<2 mm], gravel [2–6 mm], cobble [6–100 mm], boulder [10 cm–1 m], or bedrock [>1 m]) was determined at 5 to 10 random points in 5 replicate haphazardly placed 625 cm² gridded quadrats. To calculate percent cover of each grain size for each replicate quadrat, the number of points for each grain size was divided by the total number of points and multiplied by 100. Grain size bins were based off the Wentworth scale (Wentworth 1922). Differences in grain size distribution among sites were tested using a 1-way PERMANOVA based on a Euclidean distance matrix with site as a random factor.

3.3.4 Predator importance based on shell litter

To assess if shell litter can be used to determine the relative importance of sea otters and sea stars as clam predators, shells were collected along the permanent transects in mid-June, and

at the end of July and August. Only recently deposited shells (no fouling on the shell) were collected, as these would have the greatest chance of being related to recent foraging activity in the same area. Shells were collected in plastic bags and brought back to the lab where they were recorded as ‘otter-cracked’ if at least 1 valve or the hinge was broken or cracked (Kvitek et al. 1992) and as ‘star-preyed’ if both halves of the shell were intact, open and not drilled. Drilled shells have bore-holes that are indicative of predation by moon snails or octopus (Ambrose et al. 1988). To provide further insight into the species and sizes of clams preyed on by sea otters and sea stars, shells were identified to the lowest taxonomic level possible and shell width was measured. The size frequency distributions of otter-cracked and star-preyed shell widths were compared using a 2-sided Kolmogorov-Smirnov (KS) test. Densities of shells (shells per 10 m²) were calculated by dividing the number of shells collected along a transect by the transect area (20 m²) then multiplying by 10. To determine which predator is responsible for the most clam predation, I compared densities of shell litter by type (otter-cracked, star-preyed, or bore-holed) using 1-way ANOVAs in R (R Development Core Team 2008) for all sites combined and within each site.

To determine whether sea star density is an indication of sea star predation, all sea stars were counted and identified along the transects at the same time that shell litter was collected. Only *P. helianthoides* were used in my analysis because the other 2 stars that were found, *Evasterias troschelii* and *Orthasterias koehlerii*, occurred at very low densities. I tested for Spearman correlations between shell litter (total shell litter and star-preyed shells) and *P. helianthoides* abundance. I also compared density of *P. helianthoides* across sites using ANOVA in R (R Development Core Team 2008). Since surveys of shell litter and *P. helianthoides* abundance at the 0 m sites were performed during low tide, these sites were excluded from the

correlation analysis. *P. helianthoides* can move into the intertidal zone during high tide to feed but typically retreat to the subtidal zone as the tide drops (S. B. Traiger, B. Konar, A. Doroff pers. obs.); hence, surveys of their abundance at low tide probably do not reflect their true use of the habitat.

3.4 RESULTS

3.4.1 Distinguishing unknown pit sources using quantitative dimensions

Foraging pits ($n = 109$) were measured across all four 10 m sites and one of the 0 m sites from May to August 2014. Although sea otters were seen in the area, no pits were observed at the KB 0 m site during the study. There were no significant clusters within the data set of measured pits based on the CLUSTER analysis and SIMPROF test ($p = 0.174$), and no clusters were apparent from the PCO plot either (Fig. 2A) so pit source could not be determined. Most pits were elongate with the major axis on average $18 \pm 13\%$ SD longer than the minor axis. Major axes ranged from 0 to 56% longer than minor axes. Fourteen percent of pits were perfectly round. Although most pits surveyed (53%) had no sediment pile, 26% had up to 25% of the pit edge with piled sediment, which is indicative of sea otters. This contrasts with only 2% of pits having sediment piled on 76–100% of the pit edge, which is indicative of sea stars. Pit depths averaged 11.8 ± 4.7 cm SD and ranged from 3 to 27 cm. Surface area averaged 958 ± 674 cm² SD and ranged from 71 to 3533 cm².

There were some differences in pit dimensions among sites (ANOSIM, $R = 0.095$, $p = 0.006$), so separate CLUSTER analyses and SIMPROF tests were run for each site (excluding MS 0 m due to low sample size). There were no significant clusters within KB 10 m, MS 10 m, or PG (SIMPROF, $p = 0.727$, 0.710 , and 0.430 , respectively). There were 3 significant clusters

within the pits measured at PB (Fig. 2B). There was a wide range of values for each dimension in Cluster a, so I were unable to determine the source of pits in this cluster (Fig. 2C). The pits in Cluster b were deep compared to pits in Cluster a (13.5 ± 2.1 cm SD vs. 7.9 ± 3.0 cm SD), both pits had 26–50% of the rim covered in sediment mound, surface area was large relative to cluster a (834 ± 180 cm² SD vs. 468 ± 369 cm² SD) and both pits were perfectly round (%major axis > minor axis = 0) while pits in cluster a had major axes 11% longer than minor axes on average (7% SD; Fig. 2C). Due to the round shape of the pits and the presence of sediment on more than ¼ of the pit perimeter, I assigned this cluster as sea star source. Cluster c had one pit, which was large (surface area 1236 cm²), had a major axis 22% larger than the minor axis, was 10 cm deep, and had sediment mounded on 50–75% of the pit perimeter, which was more than any other pit at PB. I were unable to assign a source to this pit because the characteristics of sediment mound and pit shape give conflicting indications of pit source based on literature descriptions of pits (Table 1). The sediment mound value indicates a sea star source; however, the pit shape indicates sea otter source, and size of the pit is very close to the lower limit of pit size observed by Kvitek et al. (1992).

Pit flag loss rate occurred and varied across sites. Flag loss was highest at the MS 0 m site, where 6 of the 7 flags deployed were lost in mid-July. Flag loss also occurred at PG from June to July when 4 of the 7 flags deployed at the time were lost. Flag loss was lower at PB (3 out of 20) and MS 10 m (8 out of 56). There was no flag loss at KB 10 m.

3.4.2 Persistence of characteristics distinguishing sea otter and sea star foraging pits

After 2 wk, the 2 experimental pit types (otter vs. star) did not have significantly different dimensions from each other (Table 2, Fig. 3). There were significant differences in the degree of change in pit dimensions among sites (Table 3) with most of these differences being between

intertidal and subtidal sites. At 0 m, all of the experimental pits at KB were filled in after 2 wk. At MS 0 m, 67% of experimental sea star pits were filled in, while all 6 of the experimental sea otter pits were still present. Across all sites, 90% of the experimental pits dug at 10 m were still visible after 2 wk. The pit characteristics that changed the most were pit depth (average -44% change) and sediment pile. After 2 wk, no sediment pile remained at 72% of sea otter pits and 62% of sea star pits.

There were no significant differences in clod card weight loss among sites, indicating there may be no differences in relative water motion (ANOVA, $p = 0.199$, $F = 1.699$), although my sample size was low. Sediment grain size composition was significantly different among sites (Table 4). Mean percent cover of sand, cobble, and boulders ranged from 4–92, 4–52, and 0–4%, respectively. Bedrock was not observed at any site. The KB 0 m site had the lowest percentages of sand and gravel (4% for both) and the highest cover of cobble at 52%. The MS 0 m site and PG had the next highest covers of cobble at 32 and 27%, respectively.

3.4.3 Predator importance based on shell litter

A total of 125 shells were collected over the study period. Fifty-six percent of the shells were otter-cracked, 42% were star-preyed, and 2% contained bore-holes. Across all sites, there was a significantly lower density of bore-holed shells than otter-cracked or star-preyed shells (ANOVA, $p < 0.001$ and $p = 0.011$, respectively) (Fig. 4). Density of otter-cracked and star-preyed shells was only different at PG (ANOVA, $p = 0.002$) (Fig. 4), with 70% of the shells being otter-cracked at this site. This indicates that sea otters and sea stars are of equal importance as predators of clams at most of my sites, while at PG, sea otters are more important. Clam

species preyed on by both sea stars and sea otters included *Clinocardium* sp., *Humilaria kennerleyi*, *Mya truncata*, *Saxidomus gigantea*, and *Serripes groenlandicus*. Sea stars included a wider range of clams in their diet and additionally preyed on *Diplodonta* sp., *Hiatella arctica*, *Leukoma staminea*, *Lyonsia* sp., *Macoma* sp., and *Mactromeris polynyma*. *S. gigantea* was the most common species in both otter-cracked and star-preyed shell litter (Table 5). The shell width of otter-cracked shells ranged from 27.07 to 94.72 mm with a mean of 57.26 ± 13.63 mm SD, while star-preyed shells ranged from 11.45 to 102.00 mm with a mean of 42.47 ± 22.75 mm SD; Fig. 5). There was a significant difference in the frequency distribution of shell widths of otter-cracked and star-preyed shells (KS test, $D = 0.5237$, $p < 0.001$).

There was no correlation between star-preyed shells and density of *P. helianthoides* (Spearman, $p = 0.686$). *P. helianthoides* density was higher at MS 10 m than PG (ANOVA, $p = 0.003$), but star-preyed shells were not more abundant than otter-cracked shells at MS 10 m. Density of *P. helianthoides* does not appear to be an indicator of the magnitude of sea star clam predation.

3.5 DISCUSSION

The results of this study showed conclusively that shell litter, but not pit dimensions, could be used to estimate clam predation by sea otters and sea stars in Kachemak Bay, Alaska. Distinguishing characteristics between experimental sea otter and sea star pits disappeared and many pits filled in within 2 wk. I conclude that shell litter is a more useful and less ambiguous method for determining sea otter and sea star clam predation in the intertidal and subtidal without direct observation. My study indicates that sea stars contribute to clam mortality as much as sea otters; however, further research is needed to examine possible biases due to difference in

shell litter deposition. This finding contrasts to the common perception that sea otters are the only significant clam predators in Alaska.

My hypothesis that recent (2 wk old or less) foraging pits can be distinguished based on measurable characteristics was not supported. I did not observe any patterns in the multivariate data cloud of pit dimensions that indicated that different types of predators were making them. I also found that the multivariate data did not align with any of the existing literature descriptions (Table 1). For example, the amount of piled sediment increased toward the lower right end of the non-metric multidimensional scaling (nMDS), which could indicate that pits in this portion of the graph are sea star pits (Kvitek et al. 1992); however, pit shape (% major axis > minor axis) and surface area do not show clear decreasing values in that direction (compare vector directions on Fig. 2). As such, I do not recommend using foraging pits to determine levels of clam predation by sea otters and sea stars separately. There is not enough quantitative information in the literature to clearly distinguish the types of pits made by each predator, and the lack of clustering in the pit dimensions indicates that either both predators make pits of very similar size and shape, or that one predator is responsible for all the pits observed. Foraging pits are more useful for determining the role of individual predators in study systems where only one pit digging predator occurs (Hines et al. 1997, Eldridge & Mensinga 2007, Dor et al. 2014), or there are large differences in the sizes of pits produced by different predators (Nelson et al. 1994).

My hypothesis that after 2 wk, sea otter and sea star pits can still be distinguished was not supported. After 2 wk, experimental sea otter and sea star pits were no longer significantly different from each other, largely because the differences in roundness and amount of piled sediment that distinguished pits at the beginning of the experiment were not present after 2 wk. These results suggest that the metrics typically found in the literature to differentiate foraging

pits are likely not accurate for pits older than 2 wk. Since sediment piles are quickly eroded, previous studies using sediment piles to distinguish pits may be underestimating the contribution of sea stars to foraging pits. As a result, the role of sea stars in shaping soft-sediment communities could be underappreciated in areas with sea otters. More than half of the recent shells that were collected were a result of sea star predation, indicating that they are currently important predators of clams at these sites in Kachemak Bay. The high degree of change in pits I observed over 2 wk is likely an important reason why I could not distinguish foraging pits. Very frequent resurveys would be necessary to accurately distinguish the source of foraging pits and to accurately quantify foraging pit dimensions, regardless of their source. In other study systems, surveys of foraging pits have involved frequent resampling (4 d, Hines et al. 1997; 24 h, O'Shea et al. 2012). In contrast, surveys of foraging pits attributed to sea otters have been repeated every 2 wk (Kvitek et al. 1988) or have not been repeated, using a snapshot approach (Kvitek et al. 1992, Boehm et al. 2007, Bodkin et al. 2012). A snapshot approach, combined with an inaccurate estimate of pit persistence, could result in underestimation of foraging. Appropriate sampling frequency will depend on infill rates, which may be influenced by sediment grain size, water motion, and potential for continued use of the pit.

The changes I observed in pit dimensions overtime may have been influenced by a lack of sea star activity in the pits (given that sea star activity can prevent infill), water motion, and sediment grain size. Sea stars were never observed using pits that had been previously marked with a landscaping flag or in my experimental pits, which were marked slightly differently, with a nail with flagging at the edge of the pit. While it is possible that the landscaping flag placed at the center of the pits deterred further use of the pits by sea stars or sea otters, I believe that the rate of pit reuse is low in my system, due to the lack of activity in my experimental pits. I also do

not believe that *Pycnopodia helianthoides* would be deterred by landscaping flags because I have observed them overturning bricks and large rocks in order to dig for clams underneath. I do not know of any evidence of sea otters reusing pits. The high rate of pit in-fill in this study differs from previous studies that found sea otter foraging pits persisting for 4 mo to 1 yr (Kvitek et al. 1992, Boehm et al. 2007, Bodkin et al. 2011). Pit persistence has also been studied in Australia, where most stingray foraging pits filled in within 7 d, but some pits became larger from continued use by the stingrays (O'Shea et al. 2012). Although *P. helianthoides* have been shown to be attracted to foraging pits (Kvitek et al. 1992), it seems that they were not attracted to my experimental pits since most experimental pits became smaller or filled in over time.

Wave exposure was relatively similar among my sites in Kachemak Bay, but this may explain the longer pit persistence in Kodiak Island and Prince William Sound, where tidal driven currents are weaker due to smaller tidal ranges. Stingray pits in Australia also filled in more quickly at exposed than at protected sites (O'Shea et al. 2012). I also observed differences in experimental pit persistence between the intertidal and subtidal sites with a higher rate of experimental pit disappearance at 0 m depth than at 10 m, but there was no difference in relative water motion. However, there were differences in sediment grain size with a higher proportion of cobble at KB 0 m. The larger sized rocks in the intertidal may cause pits to fill in more quickly than subtidal pits at the same site, which had a higher proportion of sand and gravel. Sediment transport is affected in part by sediment grain size (Larson & Kraus 1995). Larger sediment grains enable more water percolation than saturated small grain size sediment, leading to greater transport rates of sediment (Larson & Kraus 1995).

The difference in pit persistence across depth contours has important implications for interpreting foraging pit data. It should not be assumed that foraging pits are indicators of

foraging over the same time span at intertidal and subtidal sites because of these differences in their persistence. In contrast to western Prince William Sound, where intertidal foraging pits persisted several months (Bodkin et al. 2011), foraging pits at my intertidal sites may only represent foraging activities within the last 2 wk or less. Similarly, foraging pits and furrows formed by walrus in Bristol Bay are not observed in areas with dynamic sediment movement, even though walrus are known to forage in those areas (Bornhold et al. 2005). While I observed fewer pits at my intertidal sites (zero at KB and 3 at MS, I may be missing some foraging activity due to high infill rates. Kachemak Bay has a 9 m tidal range, so at high tide, the intertidal is very accessible to sea otters. Indeed I expected to see higher numbers of foraging pits in the intertidal since other studies using foraging pits and radio tags recorded frequent foraging in the intertidal (Gilkinson et al. 2011, Bodkin et al. 2012). The number of foraging pits may also have been low at my intertidal sites if clam abundance was low due to previous sea otter or sea star predation, recreational clam fishing, or other factors. I also found low numbers of shells at my intertidal sites (zero at KB and 4 at MS, which may also be indicative of low prey abundance.

My hypothesis that shell litter can be used to assign relative clam predation by sea otters and sea stars was supported. I observed very few shells with indications of other predators and were able to classify predation source for all shells collected. I did not observe any shells with contradicting predation signs (i.e. a shell with both bore-holes and otter-cracks). Like any method of determining predation rates, using shell litter has potential biases. Sea otters eat clams on the surface, so otter-preyed shells may be distributed farther from their origin than star-preyed shells, resulting in underestimation of sea otter predation. In California, sea otters were observed to move away from shore to eat on the surface after collecting clams in shallower water (Kvitek et al. 1988). Small clam prey of sea otters may also be underestimated because sea otters have

been observed to consume whole clams 3 to 5 cm long (Calkins 1978). However, these potential biases are outweighed by the higher confidence in identifying the source of clam mortality and benefits of additional information gained compared to using foraging pits. Surveys of shell litter provide the added benefit of being able to identify small individuals, which can be difficult in observational studies (Dean et al. 2002, Wolt et al. 2012). Unlike counts of foraging pits, shell litter can also be directly linked to the number of predated clams. Shell litter can be used to determine recent foraging activity of sea otters on clams, as in this study, as well as historical predation of clams at a site (Kvitek et al. 1992, Stewart et al. 2014). While shell litter is useful for distinguishing between sea otter and sea star clam predation, it does not account for all predation on clams. Clams are important diet items for wintering sea ducks, which consume small clams (≤ 4 cm) whole, so their fecal pellets need to be sampled to assess their predation on clams (Lewis et al. 2007). Crabs prey on clams by chipping away the edge of the clam valves (Boulding 1984, R. G. Kvitek pers com); however, at the sites I sampled, only 1 *Saxidomus gigantea* was found chipped in this way. Larger crab species, such as Tanner crab *Chionoecetes bairdi* generally would be found in deeper water than my sampling sites.

Multiple methods of determining sea otter foraging should be used to account for method biases. For example, Smith et al. (2015) found that estimates of diet specialization differed between stable isotope and observation methods, with stable isotopes providing less biased estimates of specialization. Shell litter, when combined with other methods, could help provide a more complete view of sea otter foraging on clams. In contrast to shell litter, direct foraging observations are time consuming, and clam species may be impossible to identify from great distances, although statistical methods can be used to account for these biases (Tinker et al. 2012). Observations also allow for a more complete prey dataset, which include soft-bodied

organisms (Dean et al. 2002). Scat collections are often done to determine sea otter prey, but these data are limited to sea otter haul out sites, and only prey with hard parts are observed (Faurot et al. 1986, Green & Brueggeman 1991, Doroff et al. 2012). Pairing shell litter with direct observations and scat collections will ensure that soft-bodied and small size class organisms are incorporated (Green & Brueggeman 1991).

To better predict changes in clam populations, I need to understand the relative contributions of sea otters and sea stars to their mortality. In Kachemak Bay, according to the shell litter, sea stars are as important as sea otters for clam predation, and as such, clam mortality due to sea stars should be considered in clam management strategies. In addition to preying on equal number of clams, sea stars also prey on a wider range of species and sizes of clams, including *Diplodonta* sp., *Hiatella arctica*, *L. staminea*, and *Mactromeris polynyma*. Size-specific predation pressure evident from the shell litter could be built into population models for clams. While the Kachemak Bay sea otter population has been rising since recolonization (Gill et al. 2009), its impact on clam populations is unknown. As the sea otter population recovers in Kachemak Bay, public perception is mixed, and there is concern that the population recovery is a threat to local clam fisheries. Sea otters also prey on Tanner crabs *C. bairdi*, fat innkeepers *Urechis unicinctus*, sea stars such as mottled stars *Evasterias troschelii*, green urchins *Strongylocentrotus droebachiensis*, octopus (*Octopus* sp.), mussels (*Mytilus* spp.), and fish (Calkins 1978, Garshelis et al. 1986, Green & Brueggeman 1991, Dean et al. 2002, Gill et al. 2009, Doroff et al. 2012), which are also present in Kachemak Bay. Although clams are a high-energy food source (Oftedal et al. 2007), sea otters may target prey that do not require excavation while they are still abundant.

Ecosystem-based management approaches require an understanding of natural sources of mortality for clams and reasonably accurate estimates of mortality from different predators. For example, in the North Sea, lesser sandeels are preyed on by predatory fish, sea birds, seals, and are fished by humans (Furness 2002). Predatory fish consume more sandeels than sea birds, seals, and the fishery, so management decisions made for predatory fish could have more effect on sandeel stocks than changing fishing practices on sandeels themselves (Furness 2002). Clams and shellfish in general have been a major component of the subsistence, recreational and commercial fisheries (valued at approximately \$4 billion USD) across Alaska (Salomon et al. 2007, Donkersloot 2012), and these fisheries are managed by Alaska Department of Fish and Game. Shell litter data could be used to determine predation rates by both sea otters and sea stars, and this information could then be factored into clam harvest limits. All field methods for studying sea otter foraging, including direct observation and scat samples, are time consuming and carry biases. If sea stars are not accounted for, the use of foraging pits to assess sea otter foraging in soft bottom habitats will probably result in overestimates of sea otter foraging that may be detrimental to local management efforts. If the goal is to determine clam mortality in the intertidal and shallow subtidal due to non-human predation, I recommend conducting surveys of shell litter in conjunction with scat and direct observations. Using shell litter surveys, I have shown that sea stars are equally important predators as sea otters in Kachemak Bay and should be included in clam management strategies; however, further research is needed to investigate potential biases in shell litter due to difference in shell deposition.

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3.7 TABLES AND FIGURES

Table 1. Literature descriptions of sea otter and sea star foraging pits by pit dimension along the Pacific coast and in Alaska, USA

Dimension/characteristic	Area/size	Pit depth (cm)	Shape
Sea otter source			
Sediment piled on one side of pit rim ^a	1300-2000 cm ^{2a} 15 to 45 cm across ^a 14,000 cm ² on average ^c	Up to 50 ^b 10-15 ^d	Elongate ^a
Sea star source			
Sediment evenly around perimeter	Smaller than otter pits ^a	6-14 ^e 5-23 ^f	Circular ^a
Literature basis: ^a Kvitek et al. (1992), ^b Calkins (1978), ^c Kvitek et al. (1988), ^d Boehm et al. (2007), ^e Sloan & Robinson (1983), ^f Mauzey et al. (1968)			

Table 2. A) A comparison of pit dimensions between experimental sea otter and sea star pits (Type) across and within sampling events (Set-up, After two weeks) and sites using a three-way PERMANOVA (bold values are significant assuming $\alpha = 0.05$). B) A pairwise comparison of the interaction between experimental pit type and sampling event using PERMANOVA (bold values are significant assuming $\alpha = 0.05$).

(A) Source	d.f.	Sum of square	Pseudo-F	p value
Type	1	48.57	1.68	0.216
Sampling Event	1	88.96	3.31	0.073
Site	5	54.17	0.40	0.930
Type x Sampling Event	1	22.74	4.84	0.022
Type x Site	5	45.39	1.92	0.134
Sampling Event x Site	5	136.95	8.23	<0.001
Type x Sampling Event x Site	5	23.64	1.42	0.141
Residual	112	372.55		
Total	135			
(B) Type x Sampling Event			t	p values
Otter, Star at Set-up			4.09	<0.001
Otter, Star After two weeks			0.77	0.532

Table 3. A comparison of percent change in dimensions of experimental pits among two intertidal and four shallow subtidal sites in Kachemak Bay, Alaska. The analysis was a one-way PERMANOVA with a random factor (site), performed with 9999 permutations (bold values are significant assuming $\alpha = 0.05$).

Source	d.f.	Sum of square	Mean Square	Pseudo-F	p value
Site	5	3.87×10^5	77492	5.97	<0.001
Residual	59	7.66×10^5	12979		
Total	64	1.15×10^6			

Table 4. A comparison of sediment grain size composition among two intertidal and four shallow subtidal sites in Kachemak Bay, Alaska. The analysis was a one-way PERMANOVA with a random factor (site) performed with 9999 permutations (bold values are significant assuming $\alpha = 0.05$).

Source	d.f.	Sum of square	Mean Square	Pseudo-F	p value
Site	5	46740	9347.9	9.96	<0.001
Residual	24	22522	938.42		
Total	29	69262			

Table 5. Proportions of clam species preyed on by sea otters, sea stars, and moon snails or octopus as shown by shell litter. n: number of shells. For star-preyed shells, ‘other’ includes *Hiatella arctica*, *Leukoma staminea*, *Lyonsia* sp., *Mactromeris polynyma*, and *Serripes groenlandicus*, which each made up 1.9% of star-preyed shell litter

Species	Otter-cracked (n = 70)	Star-preyed (n = 52)	Bore-holed (n = 3)
<i>Clinocardium</i> sp.	2.9	17.3	
<i>Diplodonta</i> sp.		3.8	
<i>Humilaria kennerleyi</i>	4.3	3.8	
<i>Macoma</i> sp.		7.7	33.3
<i>Mya truncate</i>	2.9	5.8	
<i>Saxidomus gigantea</i>	88.6	48.1	33.3
<i>Serripes groenlandicus</i>	1.4	1.9	
Unknown		3.8	33.3
Other		5.8	

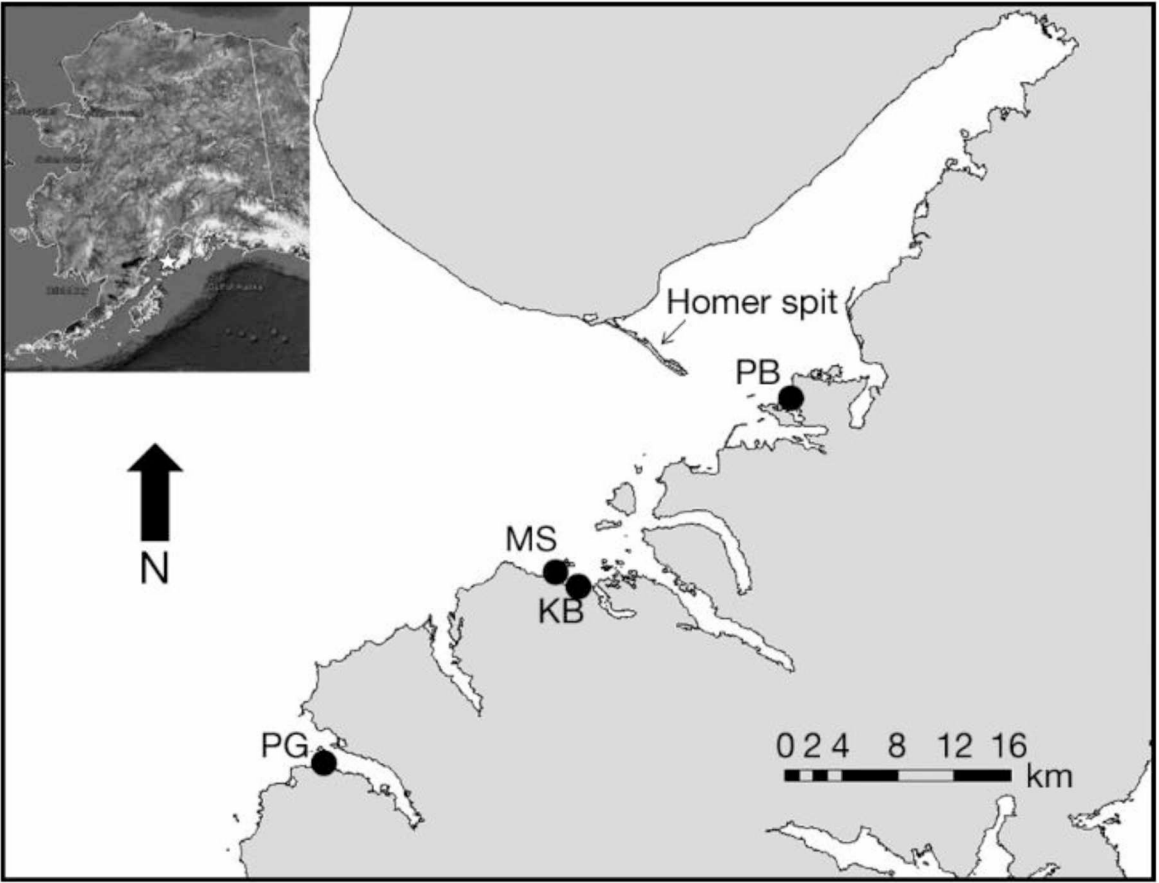


Figure 1. Map showing the locations of the four study sites within Kachemak Bay. The white star on the inset map shows the location of Kachemak Bay within Alaska. Site abbreviations are as follows: Port Graham (PG), Peterson Bay (PB), MS (McDonald Spit), and Kasitsna Bay (KB).

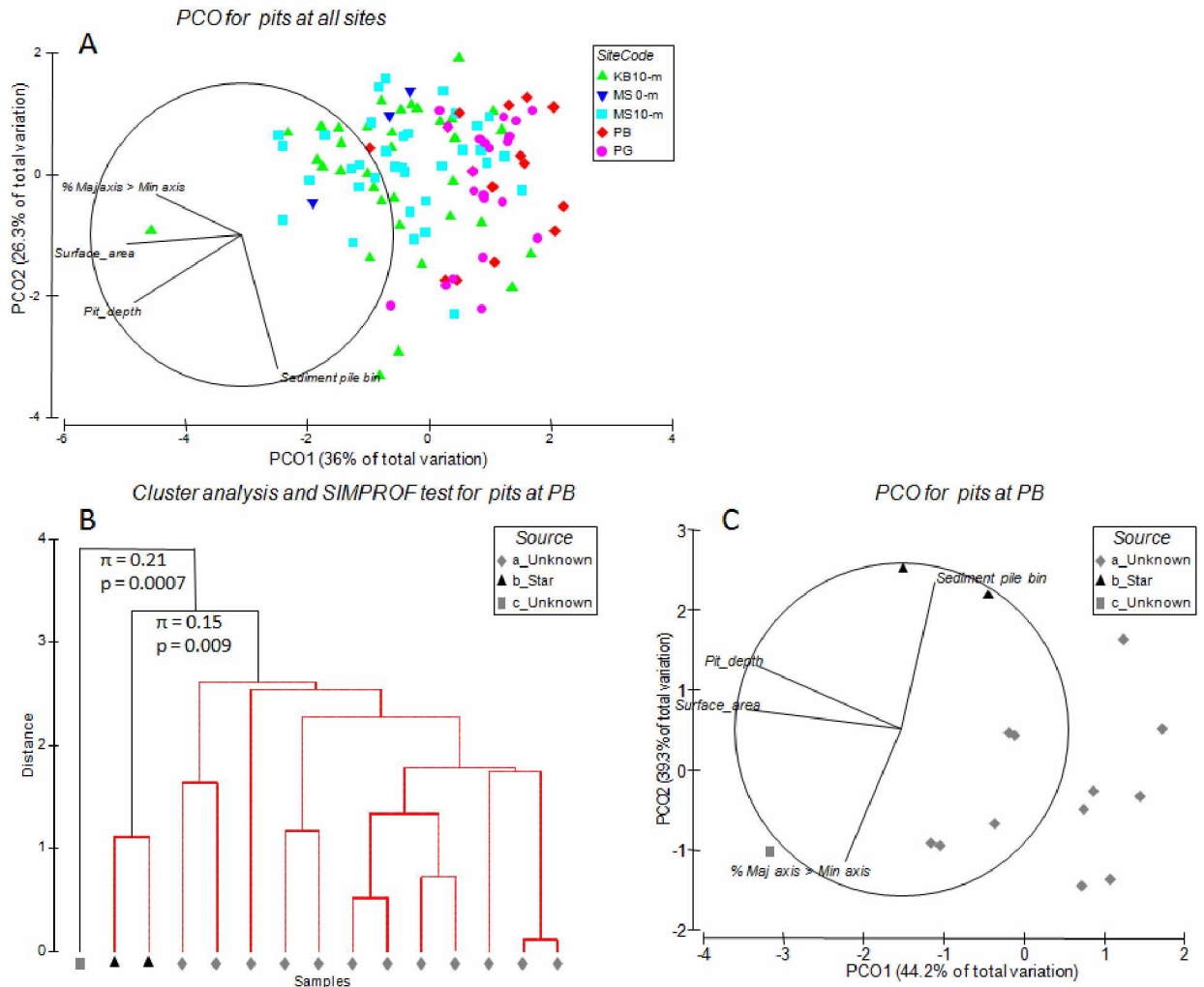


Figure 2. A) Principal coordinate analysis (PCO) plot based on Euclidian distance of dimensions of surveyed foraging pits color coded by site. Each point represents one pit. Solid lines represent vectors of pit dimension variables. Vectors show directions of correlations with the PCO axes. B) Dendrogram of foraging pits at site PB. Black nodes represent divisions of statistically significant subdivisions determined by SIMPROF tests, resulting in three clusters. Sample symbol corresponds to the cluster in which it was placed by the CLUSTER analysis. Test statistic (π) and p values are listed below statistically significant nodes. C) PCO plot of foraging pits at site PB, with symbols corresponding to clusters generated by CLUSTER analysis.

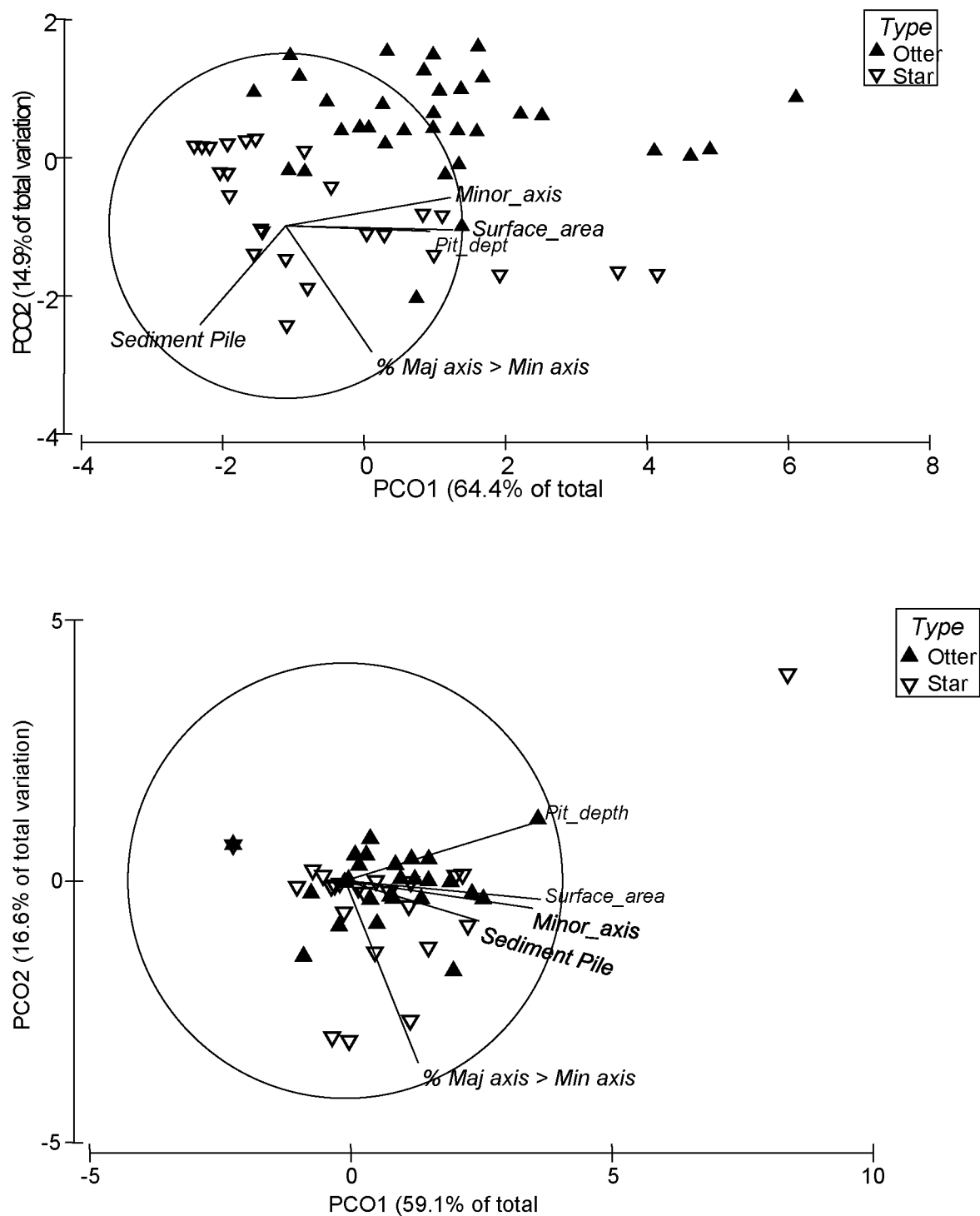


Figure 3. A) PCO plot showing clear separation in starting dimensions between experimental otter and sea star pits just after they were dug (Initial Set-up). B) PCO plot showing that after two weeks, the experimental otter and sea star pits are indistinguishable. In both plots, each point represents one pit.

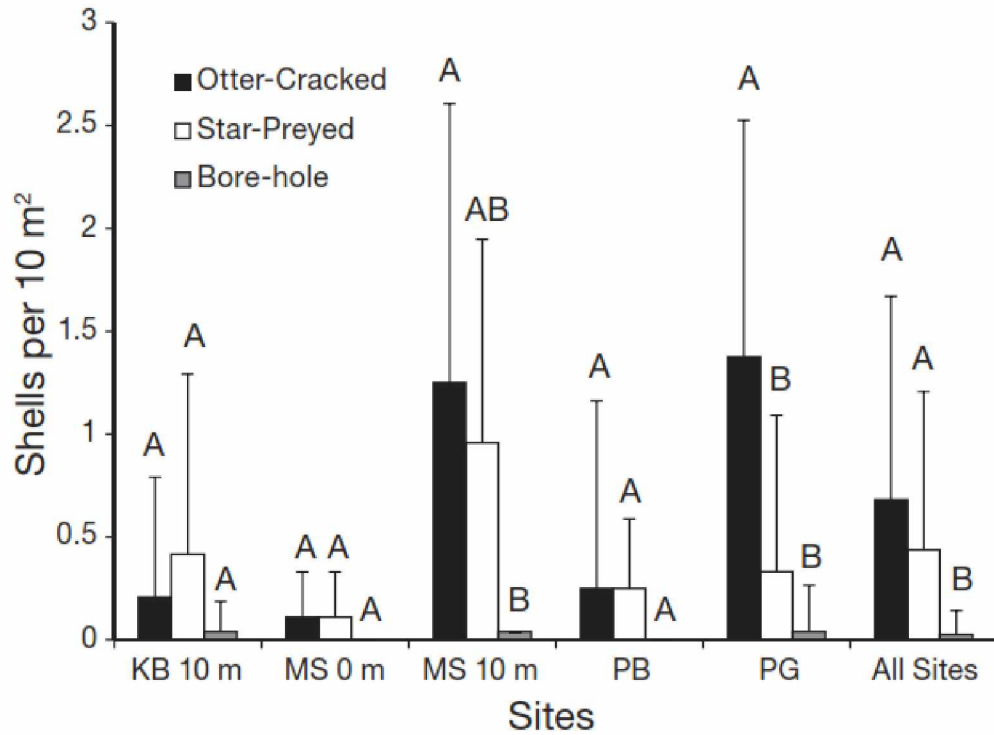


Figure 4. Densities of star-preyed and otter-cracked shells collected along same 2 x 10 m transects where foraging pits were surveyed. Separate ANOVAs were performed to compare density of otter-cracked, star-preyed, and bore-holed shells across all sites, and within each site. Letters above bars indicate significant differences for each separate test.

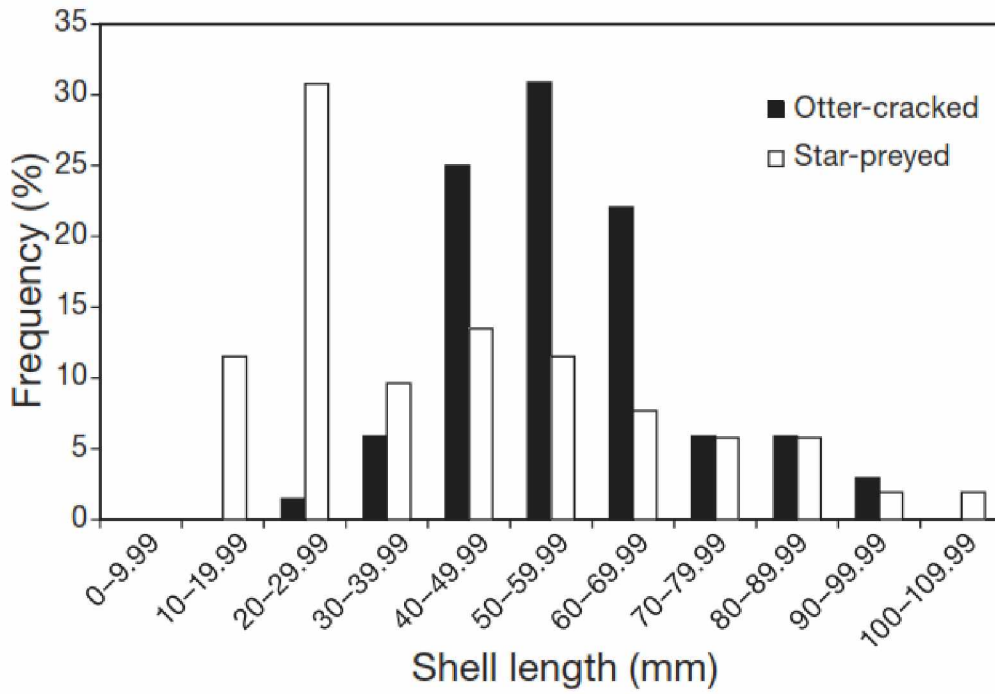


Figure 5. Range of sizes of clams preyed on by sea otters and sea stars as shown by shell litter. All shells collected with bore-holes (n = 3) were in the 20-20.99 mm size category (data not shown)

GENERAL CONCLUSION

This dissertation advanced our knowledge of the distribution and composition of kelp bed communities in a high latitude system by showing that community development patterns differ with proximity to glacial melt point sources. These differences were due primarily to glacial sediment loads that affected survival and interspecific competition at the kelp gametophyte stage. The research results also showed that both sea otters and sea stars can affect community structure by supplying shell litter, which serves as vital substrate for kelp. Recruitment is critical for population persistence and information on recruitment and succession for high latitude kelp beds is limited. My observation that kelp recruitment reflects adult distributions indicates that propagule dispersal may be limited and/or that settlement and early post-settlement processes limit recruitment. My lab experiment supported the possibility that early post-settlement processes limit kelp distribution to glacial melt areas by demonstrating that gametophyte survival is lower with high sedimentation. My field survey of kelp fecundity showed that spore supply is less likely to be responsible for restricting kelp abundance, as fecundity did not differ with relation to glacial influence. I also found shell litter caused by sea stars and sea otters was common in areas where mixed grain sediments are common, such as in glacial estuaries, suggesting that these may be critical for kelp attachment.

The first chapter of my dissertation examined correlations between development of the sessile kelp bed community on cleared rocks and potential drivers, including environmental and biological factors. There were major differences in the identity and abundance of initial recruits between the oceanic-influenced outer bay and glacially-influenced inner bay sites, and differences in the developing communities became more pronounced over time. These differences in early community development may indicate that the propagule pools differ

between the regions or that settlement or early-post settlement processes prevent the establishment of certain species (i.e., *Nereocystis luetkeana* in the inner bay). Environmental factors, especially inorganic sedimentation, differed between the regions. Contrary to my expectations, environmental factors associated with glacial melt were not important drivers explaining community development. Bottom water temperature and members of the established community surrounding the cleared rocks best explained the patterns of community development. Abundance of grazers, predators, and adult kelp in the surrounding community were very different between regions, similar to recruitment and community development on the cleared rocks. It is unclear whether the developing community is responding to the environment in similar ways as the surrounding community or whether the surrounding community is truly driving subsequent community development. As glacial discharge dynamics shift with climate change, monitoring changes in established communities may give us the information needed to predict changes in community development.

In chapter two, I investigated the potential influence of glacial melt on the distribution of two dominant kelps in Alaska, the canopy-forming *Nereocystis luetkeana* (hereafter *Nereocystis*) and the prostrate understory kelp *Saccharina latissima* (hereafter *Saccharina*). There was not a significant difference in sporophyte fecundity of either species between the oceanic-influenced outer bay and glacially-influenced inner bay sites. As kelp spores are small and energetically inexpensive to produce, the process of sporogenesis may not be slowed by low nutrient conditions in these species, so spore supply may not be the life history factor limiting kelp distribution in glacially influenced areas. However, my lab experiment with the early gametophyte stage found that sedimentation significantly affected the survival of both species. I also found that *Nereocystis* gained a competitive advantage under control/oceanic conditions,

while *Saccharina* gained a competitive advantage under higher sediment load conditions. These results agree with previous work where the gametophyte stage was shown to be sensitive to environmental stress (Ladah and Zertuche-González 2007; Cie and Edwards 2008). Mortality at the gametophyte stage could be a bottleneck for kelp distribution in glacially influenced areas. *Nereocystis* spore production in the summer may allow spores to settle during a window of opportunity before the highest mean rates of sediment deposition. The mismatch in timing of spore release between *Nereocystis* and *Saccharina* may allow gametophytes of *Nereocystis* to establish before *Saccharina* and gain a competitive advantage, as was observed in my experiment. If the amount or seasonality of sedimentation changes, high gametophyte mortality may be a bottleneck for the persistence of kelp beds and shifts in competitive interactions could affect species composition.

In chapter three, I found that sea otters and sea stars contributed roughly equally to predation on clams, based on shell litter. This is important because sea otters are generally assumed to be the main predators of clams and are attributed with causing clam declines. Although sea otters can consume large numbers of clams and impact infauna communities (Kvitek et al. 1992), they can also have other prey species, so they may not have large effects on clam populations at all times and locations. This research showed that sea star predation should also be considered when assessing clam populations. I also concluded that shell litter was more useful metric than foraging pits for determining relative predation by sea otters and sea stars. However, further research is needed to explore possible biases in shell litter data due to differences in shell litter deposition between sea otters and sea stars. Shell litter can be important habitat for sessile organisms (Kvitek et al. 1992; Zeeman et al. 2013) and may be especially critical for kelp establishment in parts of Alaska where hard substrate is limited such as in

glacially-fed estuaries. As sea otter and sea star populations change in response to the environment or human impacts, there may be indirect effects on kelp communities.

Understanding constraints on species abundance and distribution is a central question in ecology and is especially relevant now as human activity is affecting the environment at global and local scales in unprecedented ways. Changes in kelp distribution and abundance in response to increasing temperature have already occurred (Wernberg et al. 2010) and further shifts are predicted with future climate change (Assis et al. 2016). As kelp communities respond to increases in global mean sea temperature, interactions with local stressors must also be considered. Here I showed that glacial melt affects kelp recruitment and gametophyte survival, which indicates that changes in glacial melt dynamics could impact the persistence of kelp beds. Further research is needed to better understand the mechanics of how environmental conditions and biological factors affect kelp recruitment. Predators such as sea otters and sea stars are important to maintaining kelp bed resilience, and changes in their roles with climate change will affect the overall nearshore system.

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