SEA URCHIN ECOLOGY: EFFECTS OF FOOD-WEB MODIFICATION, CLIMATE CHANGE, AND COMMUNITY STRUCTURE

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ABSTRACT

Ecosystem structure and function of temperate rocky reef habitats are subject to change as a result of food-web modification, climate change, and changes in biological community interactions. Sea urchins are a global driver of change in nearshore marine habitats though their ability to heavily graze marine vegetation and force rocky reef ecosystems from kelp forest to sea urchin barren ground states. The Aleutian Archipelago in southwest Alaska provided an ideal natural laboratory to study sea urchin (*Strongylocentrotus* spp.) ecology following the functional loss of the keystone predator, the sea otter (*Enhydra lutris*) during the 1990s. The objectives of this dissertation were to 1) determine the important drivers of sea urchin demographics following the functional loss of their keystone predator; 2) determine how projected ocean warming and acidification may affect sea urchin physical condition; and 3) identify biological drivers of sea urchin recruitment in both kelp forest and barren ground habitats. To determine demographic drivers, I used a time series of benthic habitat, sea urchin demographic, and environmental data, dating back almost forty years. In the absence of sea otters, environmental conditions, specifically ocean temperatures, became more important to sea urchin demographics, but recruitment was the primary process affecting the resultant abundance and size class structure over time. To understand how predicted ocean warming and acidification could impact *S. polyacanthus* survival, growth, calcification, gonad development, and energy content, a 108-day laboratory experiment was conducted. This experiment determined that temperature caused a greater reduction in survival than acidification, and that projected changes in temperature and acidification will result in investment trade-offs between reproduction and maintenance or growth of somatic and calcified tissues. To determine how recruitment varied between kelp forest and sea urchin habitats, fine-scale surveys of benthic community structure found that specific taxa, and not overall community structure, correlated with sea urchin recruitment. Results from this dissertation will allow managers to make predictions about how sea urchin demography will change as a result of keystone predator loss and climate change and how that will affect nearshore community structure and function. Overall, my dissertation establishes likely pathways by which coastal habitats may change over time, in a system no longer under strong top-down control.

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DEDICATION

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To Kaia for sticking around to see me through the process.

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CHAPTER 1: INTRODUCTION

Sea urchins as a global driver of nearshore community change

Sea urchins are a dominant invertebrate in nearshore benthic habitats throughout the world, capable of overgrazing rich beds of marine vegetation, such as seagrass (Valentine & Heck 1991) or macroalgae (Estes & Palmisano 1974). Temperate rocky reef habitats can generally be characterized by two ecotypes: kelp forests, characterized by foliose macroalgae and a diverse faunal community, and sea urchin barrens, dominated by herbivorous sea urchins and crustose coralline algae (Filbee-Dexter & Scheibling 2014). These two habitat configurations can occur as alternate stable states, where the ecosystem can persist as either an urchin barren or kelp forest until some perturbation causes a large decline in the dominant taxa and a shift to the alternative state. The shift from kelp forests to sea urchin barrens and back often occurs in a non-linear fashion, due to hysteresis (Scheffer *et al.* 2001), whereby the abundance of sea urchins required to effect a shift from kelp forest to sea urchin barren versus sea urchin barren to kelp forest will not be equal. The hysteresis effect is reinforced by positive density-dependent effects on sea urchin demography that can act to stabilize sea urchin barrens (Ling *et al.* 2019). Shifts between alternate stable states on temperate rocky reef habitats are determined by factors that regulate sea urchin demographics – specifically abundance, size structure, and biomass – including predation and infectious disease (Lafferty 2004, Stevenson *et al.* 2016, Burt *et al.* 2018). Generally, in the absence of consistent predatory control, sea urchin demographics will tend toward a high density state, causing overgrazing of macroalgae, until some other disturbance or change reduces sea urchin abundance and allows macroalgae to reestablish (Ling *et al.* 2015). This pattern is apparent on a global scale, occurring on rocky reef habitats at temperate latitudes in both the northern and southern hemisphere (Krumhansl *et al.* 2016, Ling *et al.* 2015). Many factors contribute to the spatial and temporal changes in sea urchin demographics; however, several key drivers are common globally: variation in abundance of sea urchin predators (Estes *et al.* 2010, Burt *et al.* 2018), multifactorial effects of climate change (Johnson *et al.* 2011, Ling *et al.* 2009a), and local biological community organization (*i.e.*, species composition; Gagnon *et al.* 2004, Steneck *et al.* 2013). Each subsequent chapter of my dissertation focuses on one of the three aforementioned topics.

The loss of keystone control

Food-web modification has occurred at global scales under the direct and indirect influences from the overharvest and overfishing of predators (Estes *et al.* 2016, Ling *et al.* 2009b). The Aleutian Archipelago has long been a classic example of trophic cascades in a marine system; where a relatively simple three-tiered trophic interaction among sea otters (*Enhydra lutris*), sea urchins, and kelp was examined during times of sea otter presence and absence to document rocky reef habitat shifts between kelp forests and sea urchin barrens (Estes & Palmisano 1974). The first large scale removal of sea otters was due to the international commercial fur trade of the 18th and 19th century, when sea otters were nearly extirpated across their entire range in southwestern Alaska (Kenyon 1969). Sea otters received protected status under the Northern Fur Seal Treaty in 1911 (Kenyon 1969), after which a period of recovery occurred over the next eight decades. Around 1990, when sea otters had fully recovered at many islands across the Aleutian Archipelago and were still recovering at others (Estes & Palmisano

1974), a precipitous decline in abundance of over 90% reduced populations across the region by the end of the 1990's (Doroff *et al.* 2003, U.S. Fish & Wildlife Service 2013). While multiple factors may have played some role in driving this large-scale decline, most available evidence supports predation by killer whales (*Orcinus orca*) as the primary causal factor (Estes *et al.* 1998, Tinker *et al.* in prep). The addition of a fourth trophic level, an apex-predator that preyed on sea otters, released sea urchins from predatory control and allowed them to increase in size and abundance, greatly reducing macroalgal abundance and biomass (Estes *et al.* 1998). Following loss of keystone control by sea otters, it remains unclear what factors have become most important in shaping patterns of sea urchin demography. In other systems, where non-sea otter predators of sea urchins (*e.g.*, groundfish in Maine or decapod crabs in Norway; Filbee-Dexter & Scheibling 2014) have been overfished, other environmental factors can contribute to observed changes in sea urchin population dynamics. This chapter establishes some of the important drivers acting on sea urchins in the absence of their keystone predator. My findings from this chapter also provided a foundation for further investigations into environmental and biological forces that could regulate sea urchin demography, such as ocean temperature, a focus in Chapter 3, or the surrounding benthic community in my fourth dissertation chapter.

Climate change and sea urchins

Climate change is already influencing sea urchin population dynamics at temperate latitudes of both the northern and southern hemisphere (Ling *et al.* 2009a). In Norway, ocean warming has resulted in instability and collapse at some long-standing sea urchin barrens (Christie *et al.* 2019) and in Tasmania, changes in ocean currents and sea surface temperature have led to expansion of sea urchin barrens (Johnson *et al.* 2011). The North Pacific and, particularly, the southern Bering Sea are expected to be a "bellweather" region for climate change (Fabry *et al.* 2009), experiencing effects of ocean warming and acidification that are detrimental to calcifying benthic invertebrates, including sea urchins and their coralline algal prey (Rasher *et al.* in review). Determining how multiple stressors interact and act independently is necessary to assess if and how climate change will manifest in nearshore rocky habitats. Furthermore, species-specific responses must be considered, as the functional response of organisms can vary among species (Ries *et al.* 2009). In the Aleutian Archipelago, a single species of green sea urchin, *Strongylocentrotus polyacanthus,* dominates in sea urchin barrens. While little work has been done on this species, it is a close relative of *S. droebachiensis*, which has been examined for responses to ocean warming and acidification at multiple life stages. In *S. droebachiensis,* the effects of ocean warming and acidification are strongest for juveniles, whereas adults are better able to acclimate to changing conditions (Dupont *et al.* 2013). This chapter, along with associated research by (Rasher *et al.*, in review), filled data gaps by assessing the response of *S. polyacanthus* to predicted warming and acidification scenarios and established pathways through which predicted environmental changes could influence sea urchin demography.

Biological controls in a dynamic system

Irrespective of presence of a keystone predator in a system, other factors can influence sea urchin behavior, growth, and survival (Konar 2000, Filbee-Dexter Scheibling 2014). Following the loss of a keystone predator, the surrounding biological community may become even more important in shaping local patterns of sea urchin demography (Ebert 1977 and see Chapter 2). In Pacific marine systems, the importance of co-predation by sea stars and other sea urchin predators was made apparent when sea star wasting syndrome released sea urchins from predatory control at recruiting size classes and resulted in increased sea urchin abundances at small and medium size classes (Burt *et al.* 2018). In Maine and Norway, crabs can regulate the abundance of small sea urchins (Steneck *et al.* 2013; Christie *et al.* 2019), and in California, spiny lobster (*Panulirus interruptus*) and California sheep head (*Semicossyphus pulcher*) also influence patterns of sea urchin behavior and demography (Tegner and Dayton 1981). While top-down effects of predators are likely to influence apparent patterns of recruitment, bottom-up relationships between sea urchin recruits and other species in the community could also influence apparent recruitment via larval settlement processes (Himmelman 1986). When choosing where to settle, sea urchin larvae may use structural and even chemical cues to select settlement substrate that are often produced by the surrounding biological community (Rowley 1989). Across the Aleutian Archipelago, nearshore biological community structure has been described across known biogeographic boundaries (Konar *et al.* 2017) and between kelp forest and sea urchin barren states (Metzger *et al.* 2019). Exploring relationships between the biological community and sea urchin recruitment may elucidate pathways that regulate sea urchin demographics, irrespective of a keystone predator, and shed light on species interactions among sea urchins and other members of the benthic community. My fourth chapter filled data-gaps on the biological drivers of sea urchin recruitment and together with the preceding manuscript chapters, presents a novel perspective on the factors that can influence sea urchin demography.

Research objectives

The objectives of this dissertation were to 1) determine the important drivers of sea urchin demographics following the marked reductions in abundance of their keystone predator; 2) determine how modern and future ocean warming and acidification may impact sea urchin performance; and 3) identify biological controls on sea urchin recruitment in both kelp forest and sea urchin barren habitats. Each of these objectives forms a chapter within my dissertation. Results will inform managers and policy makers at local, state, and federal levels about how patterns of sea urchin demographics can change across space and time, with implications for coastal ecosystem structure and function on temperate rocky reef habitats in a changing ocean.

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CHAPTER 2: HERBIVORE POPULATION DEMOGRAPHICS BECOME MORE SENSITIVE TO ENVIRONMENTAL FORCING FOLLOWING LOSS OF A KEYSTONE PREDATOR[1]

ABSTRACT

Sea otter populations rapidly declined throughout the Aleutian Archipelago during the 1990's, leaving most islands devoid of these keystone predators by the 2000s. This functional extinction of sea otters resulted in a broad-scale transition from dense kelp forests to sea urchin-dominated ecosystems. The top-down control and subsequent release of herbivorous sea urchins from sea otter predation has created an ideal scenario to assess the importance of environmental drivers to sea urchin demographics. In this study, sea urchin populations were surveyed across 15 Aleutian islands over a 35 year period to understand how patterns of sea urchin demography (density, biomass, and size structure) varied through different ecological regimes including periods of 1) sea otter presence when kelp forests were dominant (1987-1994), 2) sea otter decline when the ecosystem was in transition (1997-2000), and 3) sea otter absence when urchin barrens were dominant (2008-2010 and 2014-2017). When sea otters were present in the system, sea urchin demographics were generally similar across the Archipelago, and bottom-up controls were relatively unimportant compared to top-down forces. However, during periods of sea otter decline and absence, patterns of sea urchin density, biomass and size structure varied across environmental gradients. In particular, differences among island groups were driven largely by

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[1] Weitzman BP, Konar BH, Edwards MS, Kenner MC, Rasher DB, Tinker MT, and Estes JA (in prep) Herbivore population demographics become more sensitive to environmental forcing following loss of a keystone predator. Marine Ecology Progress Series

variation in local ocean temperature, bathymetric complexity, and spatial extent of habitat. Sea urchin recruitment also varied among different island groups, corresponding to ecoregions delineated by oceanic passes across the Archipelago. The functional extinction of sea otters has revealed the importance of environmental forcing in the absence of top-down control, and further highlighted the importance of top-down control of herbivore demographics by a keystone predator.

INTRODUCTION

Keystone species strongly influence structure and function of diverse ecosystems by regulating the demography of their prey (Paine 1969, Power *et al.* 1996, Pace *et al.* 1999). In many regions of the world, top predators have been removed from ecosystems by anthropogenic causes, resulting in profound changes in abundance and organization of lower trophic levels (Estes *et al.* 2011). With loss of keystone predators, herbivorous prey can increase in size and abundance to the point where increased grazing rates can cause communities to switch from a state dominated by primary producers to one dominated by herbivores (Hairston *et al.* 1960, Terborgh & Estes 2010). These changes are exemplified on temperate rocky reefs, where the removal of keystone predators, such as sea otters (*Enhydra lutris*) or sea stars (*e.g.*, *Pycnopodia helianthoides*) often causes a marked increase in herbivorous sea urchins, resulting in a shift from kelp forests to their alternate state of sea urchin barrens (Estes & Palmisano 1974, Estes *et al.* 2010, Burt *et al.* 2018). Sea urchin barrens have also become more common across temperate kelp forest ecosystems worldwide due to food web modification and climate change (Ling *et al.* 2014, Estes *et al.* 2016, Sheppard-Brennand *et al.* 2017). Sea urchin barrens will generally persist until some episodic or acute perturbation, such as disease (Feehan & Scheibling 2014, Lafferty 2004), storm events (Hereu *et al.* 2012), or predator recovery (Steneck *et al.* 2002), reduces sea urchin density and biomass (Filbee-Dexter & Scheibling 2014).

In addition to the top-down effects of keystone predators, environmental forces can play an important role in structuring sea urchin demographics by influencing recruitment patterns. Examples from Norway (Fagerli *et al.* 2013, 2015, Rinde *et al.* 2014, Nyhagen *et al.* 2018), Australia (Ling *et al.* 2019), the northeast Atlantic coast (Ling *et al.* 2009), the Gulf of Maine (Steneck *et al.* 2002), and recently parts of the Aleutian Islands (Konar *et al.* 2017, Metzger *et al.* 2019) have shown variable influences of environmental drivers on patterns of sea urchin demography (Table 2.1). For example, changes in sea surface temperature have facilitated range expansion of some high-latitude sea urchin populations (Johnson *et al.* 2011). Salinity, temperature, and current velocity influence early life phases of the sea urchin life cycle, such as dispersal patterns and planktonic larval duration (Starr *et al.* 1993, Ling *et al.* 2009, Ebert 2010). Bathymetric features of shallow subtidal sea urchin habitats (such as exposure to incoming storms, slope of the seafloor, slope variability, mean water depth, depth variability, and spatial extent of deep or shallow water habitat) can also influence sea urchin larval movement, survival, and their ability to recruit from deep water or complex refugia (Feehan *et al.* 2014, Parnell 2015, Ling *et al.* 2016). In oceanic island systems like the Aleutian Archipelago, geophysical properties of island size, elevation, and steepness serve as a proxy-index for potential inputs from the terrestrial system (*e.g.*, freshwater runoff, nutrients) to the marine system (Croll *et al.* 2005, Renner *et al.* 2012) and could also influence current patterns around islands. The aforementioned environmental factors are likely to influence the supply of recruits, ultimately maintaining sea urchin barrens, as well as adult sea urchin density and body-size structure (Raymond & Scheibling 1987, Rowley 1989, Fagerli *et al.* 2013, 2014, 2015).

The Aleutian Archipelago is a volcanic island chain spanning approximately 1900 km between the Alaska Peninsula, United States in the east and the Kamchatka Peninsula, Russia in the west, and separating the Bering Sea from the North Pacific Ocean. Environmental gradients across the Aleutian Archipelago are mirrored by clines in marine ecosystem dynamics (Hunt & Stabeno 2005, Konar *et al.* 2017). Variation in oceanographic properties, such as temperature, salinity, current velocity, and bathymetry drive broad-scale patterns in pelagic marine community structure, while the oceanic passes that separate island groups create boundaries between ecoregions (Piatt *et al.* 2018). The oceanic passes vary in depth, width, and total volume transport (Figure 2.1; Reed & Stabeno 1993, Ladd *et al.* 2005, Hunt & Stabeno 2005, Stabeno & Hristova 2014). Variation in nearshore benthic community structure is consequently largely defined by these biogeographic regions (Estes & Duggins 1995, Konar *et al.* 2017).

Sea urchin demographics may be similarly influenced by environmental complexity; however, little is known about how environmental forces influence sea urchin demographics in a system that has lost its keystone predator. The Aleutian Archipelago serves as an ideal model system in which to evaluate how sea urchin demographics are influenced by environmental forcing across a changing landscape of predator abundance. Sea otters were nearly extirpated across the North Pacific for their fur in the 19th century, not receiving a reprieve from harvest until their protected status by the Northern Fur Seal Treaty in 1911 (Kenyon 1969). By that time, less than a dozen remnant colonies of sea otters remained; these subsequently increased in abundance and distribution to repatriate much of the Aleutian Archipelago by the 1970's (Estes & Palmisano 1974). However, in the early 1990s a precipitous decline in sea otter populations occurred across the entire Aleutian Archipelago, likely due to killer whale (*Orcinus orca*) predation (Estes *et al.* 1998). By the early 2000s, sea otter abundance had been reduced by 90% at most islands (Doroff *et al.* 2003). This dramatic reduction in sea otter abundance propelled a rapid shift in ecosystem state within the nearshore zone, from kelp forests to sea urchin barrens, with associated changes in ecosystem structure, diversity, and function (Estes & Duggins 1995, Steneck *et al.* 2002, Stewart & Konar 2012, Edwards *et al.* 2020). By the late 2000s, sea otters were still not recovered (Estes *et al.* 2010), and the nearshore benthic habitat around most Aleutian Islands remained in the urchin barren state. The potential for a large scale shift back to the kelp forest state may be contingent on the recovery of sea otters; however, sea urchin demographics will continue to vary due to other influences, such as differences in local habitats (Konar 2001).

The goal of this study was to compare the density, biomass, and size structure of the sea urchins following the functional extinction of their keystone predator, sea otters, and related variability in urchin demography to a suite of environmental parameters. To do this, we used data obtained from 13 Aleutian Islands that spanned 30 years to explore how sea urchin demography changed among periods when otters were functionally present at pre-decline abundances and the benthic habitat was in a kelp dominated state, during a period when otters were in decline, and during two periods post-decline when the benthic habitat was in a sea urchin dominated state. We tested the hypotheses that sea urchin density and biomass would increase in the absence of sea otter predation, and that size distributions would shift toward larger individuals. We then explored which environmental factors were most important to patterns of variability in sea urchin demography among sea otter time periods of pre-decline, end of the decline, roughly a decade post-decline, and 15-20 years post-decline.

METHODS

Sea Urchin Data

Density, biomass, and body-size structure of Aleutian green sea urchins (*Strongylocentrotus polyacanthus*) were compiled from a 30-year data set (1987-2017) collected from 235 distinct, randomly selected, permanent sites that were distributed among 15 islands of the Aleutian Archipelago (Figure 2.1 and Table 2.1; Estes *et al.* 2010, Ebert *et al.* 2018). While *S. droebachiensis* could have occurred across this range, it was presumed that *S. polyacanthus* predominates and occurs exclusively across the Aleutian Archipelago, while *S. droebachiensis* is the only green sea urchin to the east, along the Alaska Peninsula and the Gulf of Alaska. Distinctions between the two *Strongylocentrotus* species require genetic determination, and while the exact range of overlap between species remains poorly resolved, preliminary surveys supported *S. polyacanthus* predominating across the Aleutian Archipelago, west of Samalga Pass and *S.droebachiensis* to the east (Dasher *et al.* 2012). During each sampling time, at least six rocky reef sites were selected per island using a randomized grid placed around each island, or based the largest logistically workable area at large islands. Generally, most islands contained 15-30 permanent sites that were sampled more than twice during the study. Sites were initially marked and resurveyed using line ups, NOAA nautical charts, and institutional knowledge, until handheld GPS became available for navigation to specific coordinates using small boats. While data were available across depths from 3 m to 33 m, we only used data from sites in 6-8 m depth, because those data had the most continuous spatial and temporal record, and because 6-8 m was the target depth in sampling years 2014-2017. At each site, up to twenty 0.25-m^2 quadrats were placed on the seafloor, and divers removed all the sea urchins contained within each quadrat, or until at least 200 total individuals were collected. A minimum of four quadrats were sampled even if 200 urchins were collected in the first quadrat to estimate spatial variability in density. In some instances, however, fewer than 200 individuals were collected within 20 quadrats when densities were low. Test diameters of individual urchins were measured to the nearest mm using calipers. Size-frequency data were truncated at a lower limit of 5 mm due to the mesh size of collection bags used over the course of study. Sea urchin biomass density was calculated using a published size (test diameter; TD) to wet mass (grams) relationship (-7.857+(2.992*Log[TD])) for *S. polyacanthus* (Estes & Duggins 1995).

Environmental Data Acquisition

Rationale for collection of environmental metrics is provided in Table 2.1. Environmental variables were quantified at site or island scales, depending on the resolution of the available data. Site-level data were derived using the latitude and longitude of each site, while island-level data were derived from a calculated centroid among sites for each island. Centroids were calculated in a GIS (ArcMap10.3, ESRI) as the mean distance among site coordinates by each island. Oceanographic data were obtained from publicly available datasets hosted by the Alaska Ocean Observing System (AOOS data portal, https://www.aoos.org/aoos-data-resources). We used their virtual sensor tool with modeled climate data for the south Bering Sea to extract values of surface ocean temperature, salinity, and current velocity for each island. The oceanographic data resolution was at 5-km cells, so a value for each metric was extracted from the cell containing the island’s centroid position. The oceanographic data were modelled for the entire water column, from 2002-2040, by the Pacific Marine Environmental Laboratory and the Canadian Centre for Climate Modelling and Analysis (Ortiz *et al.* 2014) and to support predictive modelling of oceanographic changes throughout the Bering Sea (Pilcher *et al.* 2019). We averaged annual means from three different models for the upper 20 m of the water column for ocean temperature, salinity, and current velocity from 2002-2017 to characterize the mean and variation in temperature, salinity, and current velocity for each island.

Bathymetric variables were quantified for each sampling site by creating a 1-km buffer ring (0.5-km radius) around each site's geoposition and clipping segments of coastline and bathymetry raster to the boundaries of the site buffer. Bathymetry data were obtained from the National Oceanographic and Atmospheric Administration (Zimmermann *et al.* 2013) and processed in ArcMap10.6, from a raster grid file at 20-m resolution. Within each site buffer ring, a mean and variance of depth and bathymetric slope were calculated among all raster cells below the 0 m isobath. The total area of cells contained within each buffer ring was calculated to represent the area of seafloor around a site, serving as a coarse proxy for potential exposure; where land features would reduce the total area from the maximum of 0.79 km^2 (area of 1 km buffer with no land). The size of the coastal shelf around each site was calculated as the area within each buffer ring between the 0 and 200 m isobaths. Total area of shallow-habitat (< 60 m depth) and deep-habitat (> 60 m depth) were also calculated within each buffer ring.

Geophysical attributes of each island were calculated using vector data from U.S. Geological Survey topographic and coastline segments for the Aleutian Archipelago in ArcMap10.6 and applying the spatial analyst geometry toolkit. Island size and shape were determined by measuring the perimeter (km) and area (ha) of each island and then calculating a ratio of perimeter:area. Island elevation was determined by calculating the maximum and mean elevation (m) for each island. Island thickness was calculated as another measure of island shape, where thickness represents the greatest distance from the edge to center of an island's land mass. Island steepness was calculated as the mean slope of land for each island.

Spatiotemporal analysis of sea urchin demography

For spatial analyses we examined Islands and island regions at their grouped scale (Table 2.2), where sampling areas and islands in close proximity were combined *i.e.*, the Semichi islands were comprised of Shemya, Allaid, and Nizki islands, Attu included Massacre Bay and Pisa Point, Tanaga included Warm Springs Bay and Tanga Bay, Ogliuga included Skagul Island, and Umnak included Anangula Island. Analyses of sea urchin data were performed in Primer-e v7 (Clarke & Gorley 2015). To examine change in urchin demographics over the sea otter decline, four periods of time, representing different ecosystem states, were identified between 1987 and 2017: 1) in the midst of the sea otter decline, predominantly kelp forest state (Pre-decline, 1987-1994); 2) sea otters and kelp in latter stages of decline, system in transition (End of decline, 1999-2004); and approximately 10 years following the sea otter decline, sea urchin barren state (Post-decline 1, 2008-2010); and 4) approximately 15-20 years after sea otter decline (Post-decline 2, 2014-2017) . We limited consideration to island-year combinations with at least four sites sampled during the year in question (Table 2.2). Changes in sea-urchin abundance and biomass among the four time periods and 15 islands were analyzed using separate univariate two-way, fixed-factor permutational analyses of variance (PERMANOVA, Anderson *et al.* 2008), with each resemblance matrix based on Euclidean Distances.

Urchin size frequency distributions were determined by first summing the number of individuals collected from each site within discrete 5-mm size class bins. The counts in each bin were then averaged across the different sites at each island to provide an estimate for each island-year sample combination. Each of the 5-mm size class bins were treated as an ordered variable within a multivariate analysis of the complete size structure. Relative abundances in the different size class bins were standardized to a proportional scale, and a Manhattan Distance based resemblance matrix was constructed, with no transformation applied to preserve the frequency distributions (Clarke *et al.* 2014). To test differences in size frequencies among the four time periods and 15 islands, a two-way fixed factor PERMANOVA was performed on the resemblance matrix, with permutations done under a reduced model. Binned size data were also used to construct line plots and metric multidimensional scaling (mMDS) ordinations for visualizing patterns in sea urchin size distributions among island-period samples.

Size-frequency data were next collapsed into broader size categories to determine the general size of sea urchins driving differences in frequency distributions within each time period. Here, size categories were defined as: recruit (≤ 20 mm), small (21-35 mm), medium (36-55 mm), large (56-65 mm), and extra-large (66-100 mm). These categories were determined based on the size-selective preferences by sea otters for predating medium and larger sea urchins (Estes & Duggins 1995) and the likelihood that sea urchins < 20 mm in test diameter were less than 2 years old and unlikely to have reached sexual maturity (Brady & Scheibling 2006, Scheibling & Hatcher 2013). To determine which size categories were contributing most to differences in size frequency distributions among time periods, a similarity percentage analysis (SIMPER) was performed on the binned data, grouped by time period and island, with a cut-off of size classes that explain > 70 % of variation among periods. A recruitment index was calculated based on the proportion of sea urchin recruits that were ≤ 20 mm in each sample. To test how sea urchin recruitment varied among the four time periods and 15 islands, a Euclidean Distance based resemblance matrix was constructed using the raw data, and a two-way fixed-factor univariate PERMANOVA was performed on the resemblance matrix using unrestricted permutations. Bubble plots were overlain on the nMDS of sea urchin size distributions to show differences in the recruitment index among island-period combinations. Statistically significant patterns were determined by alpha ≤ 0.05.

Correlations of Environmental Data with Sea Urchin Size Distributions

Correlations of environmental variables with sea urchin size distributions were determined using the Bio-Env (BEST) procedure in Primer v7 (McArdle & Anderson 2001). Environmental variables were compared using draftsman plots to identify correlations among predictor variables and determine necessary transformations. Island area, perimeter length, bathymetric slope, variability of slope, and island mean and max elevation were excluded due to autocorrelation > 0.8 with other variables, leading to the selection of 11 environmental variables: temperature, salinity, current velocity, exposure, deep habitat area, shallow habitat area, bathymetric slope, depth variability, island size (perimeter:area), steepness, and thickness. Prior to the BEST analysis, variables were transformed to achieve the greatest spread of points and achieve ‘normality’. Variables of island size, steepness, depth variability, and deep habitat were log transformed; salinity was exponentially transformed, and all other variables were left untransformed. All variables were normalized. The BEST routine was performed on the standardized and cumulated Manhattan distance matrix of sea urchin size structure, generated as described above. Each sea otter period was analyzed independently: Pre-decline, Decline, Post-decline 1, and Post-decline 2, with permutation test to produce a significance value and ρ (Rho) statistic for comparison of BEST fit among analyses. The BEST variable selection procedure was used to determine which variables were most correlated with patterns of sea urchin size structure, when only a limited number of variables were to be used, beginning with a single variable and increasing to six variables. Correlation values for the ten best-fit multiple environmental variable models were compared by the Spearman-rank correlation value. Principal component analysis was used to describe the differences in environmental variables among islands.

RESULTS

Sea urchin densities varied significantly among time periods (PERMANOVA: pseudo-F = 3.389, p(perm)=0.018) and islands (pseudo-F = 32.647, p(perm)=0.001), but the trends among time periods were not consistent across the different islands (time period x island interaction: pseudo-F = 8.721, p(perm)=0.001) (Table 2.3). In particular, while sea urchin densities varied among periods of Pre-decline to Decline, Post-decline 1, and Post-decline 2 at Attu, Semichi, Kiska, Amchitka, and Seguam (pairwise tests: $p(perm) < 0.05$), densities at Agattu, Hawadax, Ogliuga, Tanaga, Yunaska, Umnak, and Unalaska were not significantly different among time periods. Further, sea urchin densities at Adak and Chuginadak were significantly different between Pre-decline and Post-decline 1 (p(perm)=0.001), but no significant differences were observed between Pre-decline and Post-decline 2 at these islands. No significant differences were observed between Post-decline 1 and Post-decline 2 periods for any of the islands, indicting densities were stable (Figure 2.2). Together, sea urchin densities were likely to experience their greatest degree of change immediately following loss of predatory control by sea otters and then remain at high densities.

Similar to sea urchin density, sea urchin biomass also varied significantly among time periods (PERMANOVA: pseudo-F = 10.697, p(perm)=0.001) and islands (pseudo-F = 7.943, p(perm)=0.001), but the trends among time periods were not consistent across the different islands (time period x island interaction: pseudo-F = 4.350, p(perm)=0.001) (Table 2.3). In particular, while sea urchin biomass varied among periods of Pre-decline to Decline, Post-decline 1, and Post-decline 2 at Attu, Agattu, Kiska, Amchitka, Ogliuga, Seguam, and Adak (pairwise tests: p(perm) < 0.05), biomass at Hawadax, Yunaska, Chuginadak, Umnak, and Unalaska were not significantly different among periods. Sea urchin biomass at Tanaga and the Semichi islands (Shemya, Allaid, Nizki combined due to proximity) were significantly different between Pre-decline and Post-decline 2, but they were not different between Pre-decline and Post-decline 1. No significant differences were observed between Post-decline 1 and Post-decline 2 periods for any island, indicating biomasses did not change significantly after the initial shift following the loss of sea otters (pairwise tests: p(perm) > 0.05)(Figure 2.2). Together these results were similar to density; however, biomass was likely to exhibit greater variability in the years following the sea otter decline.

As with both density and biomass, sea urchin size distributions varied significantly among time periods (PERMANOVA: pseudo-F = 55.700, p(perm)=0.001) and islands (pseudo-F = 61.519, p(perm)=0.001), but the trends among time periods were again not consistent across the different islands (time period x island interaction: p(perm)=0.001) (Table 2.3). Specifically, size frequencies varied among periods of Pre-decline to Decline, Post-decline 1, and Post-decline 2 at Attu, Agattu, Semichi, Kiska, Ogliuga, Tanaga, Adak, and Seguam (pairwise tests: p(perm)

< 0.05), but size frequencies did not differ between these periods at Hawadax or Chuginadak. Further, size frequencies at Amchitka, Yunaska, Umnak, and Unalaska were significantly different between Pre-decline and Post-decline 1 ($p(perm) < 0.05$), but not between Pre-decline and Post-decline 2 ($p(perm) > 0.05$). No differences were observed between Post-decline 1 and Post-decline 2 at any of the islands ($p(perm) > 0.05$), except for the Semichis, where they did differ ($p(perm) = 0.047$). Together, this revealed differing spatial patterns among islands during each time period, with islands in the same island group often having significantly different size distributions (Table 2.3).

Examination of the size classes that shaped patterns of variation in urchin size frequencies revealed that recruits (< 20 mm) and small sea urchins (21-35 mm) dominated the size distributions during the Pre-decline period on all islands (SIMPER). This pattern, however, shifted in the Decline period, where small and medium (36-55 mm) urchins increased at Attu and Semichi, while recruits and small urchins remaned predominant at Kiska, Amchitka, and Adak (note: Agattu, Hawadax, Ogliuga, Tanaga, Atka, Seguam, Yunaska, Chuginadak, Umnak, and Unalaska were not sampled in the Decline period). Differences among islands continued into the Post-decline 1 period, where recruits and small sea urchins continued to drive size structure patterns at Kiska, Hawadax, Amchitka, Ogliuga, Tanaga, Adak, Atka, Seguam, Chuginadak, and Yunaska; while Attu, Agattu, and Semichi were shaped by medium and large (56-65 mm) urchins. East of Samalga Pass, the Fox Islands (Unmak and Unalaska) showed a change in the Post-decline 1 period, where size structure at Umnak was most influenced by medium and extra-large (66-100 mm) sea urchins, and size structure at Unalaska was shaped by small and medium urchins. By the Post-decline 2 period, recruits and small urchins still remained dominant in the size distributions at Kiska, Hawadax, Amchitka, Ogliuga, Tanaga, Adak, Chuginadak, Yunaska, and Unalaska; while Umnak and Atka shifted to small and medium urchins, and Attu, Agattu, and Semichi were increased in the driving size classes to large and extra-large urchins (Figure 2.3). Together this revealed that the Near Islands, where sea otters were still recovering at the time of their recent decline, were dominated by large sea urchins; whereas at other islands, where sea otters had reached high densities prior to the recent decline, there were increases in the preponderance of large sea urchins, but they did not dominate the size structure.

Urchin recruitment varied significantly among time periods (PERMANOVA: p(perm)=0.000) and islands (p(perm)=0.005), with the trends among time periods being consistent across the different islands (time period x island interaction: p(perm)=0.104) (Table 2.3). Specifically, Attu, Semichi, Atka, and Umnak had significantly lower recruitment indices than Kiska, Hawadax, Amchitka, Ogliuga, Tanaga, Adak, Seguam, Yunaska, and Chuginadak (pairwise tests: p(perm)<0.05). Agattu and Unalaska had also low recruitment, but they were not significantly different from the other islands due to high variability. Amchitka consistently had a significantly higher recruitment than all other islands. Generally, the Near Island group (Attu, Agattu, and Semichi islands) had lower recruitment than other islands in the western and central Aleutian Archipelago, while the eastern islands had a dearth of sea urchins. The recruitment was higher when sea otters were present in the system and decreased at most islands during Post-decline periods (Figure 2.4). Islands that had a more variable and lower recruitment exhibited greater variability in size distributions among time periods (Figure 2.5).

The environmental variables were generally weakly correlated with sea urchin size structures, but correlations grew stronger as over time since the sea otter decline (Table 2.4). In the Pre-decline period, a combination of three environmental variables, namely island size (perimeter:area), exposure and temperature, best explained the relationship with sea urchin size distributions, but these showed only a weakly significant correlation with the size distributions (ρ=0.329, p=0.001). The single variable most correlated with sea urchin size distributions during this period was island size (ρ=0.260). In the decline period, a combination of four variables, namely island size, steepness, exposure, and deep habitat area best explained the relationship with sea urchin size distributions, but these again showed even a weaker, but still significant, correlation with the size distributions (ρ=0.155, p=0.001). The single variable most correlated with urchin size structure was again island size (ρ=0.152), but this correlation value was the same value observed for the best two variables: island size and salinity, and for the best three variables: island size, exposure, and current velocity. These correlations again increased in strength during the Post-decline 1 period when two variables, namely island size and temperature, were most correlated with sea urchin size distributions (ρ=0.375, p=0.001). During this period, the single most correlated variable was temperature (ρ=0.354). These correlations again increased in strength in the Post-decline 2 period, when temperature alone exhibited the best correlation with size distributions (ρ=0.403, p=0.001). Together, this revealed that during the two Post-decline periods, the strongest correlations involved some combination of temperature, island size, and/or exposure (Table 2.4). The environmental gradients across the Aleutian Archipelago were strongest for temperature and salinity (Figure 2.6), yet, when all physical variables were considered together, patterns of environmental conditions did not follow the same gradients shaped by temperature and salinity. Rather, these appeared more strongly influenced by differences in static physical parameters, such as island size or bathymetry among the islands and island groups (Figure 2.7).

DISCUSSION

Our study explored variation in sea urchin density, biomass, and size structure across the Aleutian Archipelago, a strongly top-down driven system. In particular, we determined factors that can shape patterns of sea urchin demography with and without the influence of sea otter predation. Our results confirmed that the loss of keystone predation by sea otters led to greater variability in sea urchin size structures, and that other environmental drivers became more important in controlling sea urchin demography. While correlates with the most important environmental variables were generally weak, they nonetheless showed a pattern of influence that increased following the loss of sea otters. Therefore, it is likely that environmental variables play only a small, albeit significant, role in shaping patterns of sea urchin demographics at the scales measured in this study.

Keystone species can cause profound changes in ecosystem structure and function via top-down control by predators of their prey (Paine 1969); however, susceptibility of an ecosystem to top-down control may be influenced by several environmental factors (Power *et al.* 1996, Menge 2000). Because environmental forces are always present, they have the ability to feed back through the food web and affect the strength and influence of species interactions (Schmidt *et al.* 2018). In systems characterized by strong top-down interactions, responses to the addition or removal of a top-predator can elicit variable ecosystem responses (Estes *et al.* 2016), depending in part on the strength of bottom-up forcing. In the Aleutian Archipelago, sea urchin demographics were similar among islands when they were under top-down control (*i.e.*, sea otters present), and were generally characterized by small-bodied sea urchins in moderate abundances. However, following the functional extinction of sea otters from the Archipelago, variability in sea urchin demographics increased across space and time as sea urchin recruitment and environmental variables became more important. Our interpretation of this switch is that, when present in the system, sea otters effectively mask the roles of locally variable environmental forces and sea urchin recruitment. This masking of environmental control by predator effects has been observed in other ecosystems, where environmental forcing became more obvious and more important when top-down control was relaxed (Pasanen-Mortensen *et al.* 2017). While environmental forcing did become more influential on sea urchin demographics following the loss of sea otters, the correlations were still quite weak, suggesting that we may not have identified the full array of important environmental drivers, and/or measured them at appropriate scales, and that there are likely many other local factors shaping sea urchin demographics.

Spatial variability in the historical recovery of sea otters across the Aleutian Archipelago prior to the onset of their decline in the 1990's likely contributed to the variable responses of sea urchin demographics among periods in this study (Estes 1990, Doroff *et al.* 2003, Rasher *et al.* in review). While sea urchin densities did not significantly change across time periods, biomass did increase at most islands. This discrepancy suggests that biomass – which is a function of survival, growth, and size of the recruiting sea urchins – may better reflect the degree of top-down control by otters, while densities are more a reflection of local recruitment dynamics. The Islands of Four Mountains island group were somewhat anomalous in that they displayed no significant change in sea urchin demographics across time periods; however, these steep volcanic islands experienced limited or no sea otter recovery (prior to the decline) due to a dearth of shallow water habitat (Doroff *et al.* 2003). In contrast, urchin body size distributions in the Near, Rat, Adreanof and Delarof island groups were similar when sea otters were present, but diverged in periods of otter decline and absence.

Differences in urchin demographics between the Near Islands and other island groups in later years of sea otter absence (Post-decline 2) appeared to reflect differences in the rate of sea urchin recruitment (Figure 2.5). The Near Islands exhibited the largest change in sea urchin size structure with a decline in sea otter abundance, primarily due to an increase in large sea urchins and very little to no recruitment of smaller urchins after the decline. Sea otter densities in the Near Islands and Islands of Four Mountains had just began to recover by the 1970s from the fur harvest by the time the population collapsed again in the 1990s. This pattern was in contrast to other island groups (the Adreanof and Delarof and Rat Islands), where sea otters were thought to have recovered to near carrying capacity by the 1950's (Doroff *et al.* 2003, Estes *et al.* 2009). Sea otters preferentially feed on large sea urchins, > 45 mm (Estes and Duggins 1995), which may explain why large sea urchins were more abundant in the Near Islands, where sea otters had not recovered to near carrying capacity. At islands like the Islands of Four Mountains, where there was very little shallow habitat, it is probable that large sea urchins may find refuge at depth and migrated into the shallows rapidly following the loss of sea otter predation. Differences in sea otter population status at the start of this study may therefore help to explain the preponderance of large sea urchins in the Near Islands relative to other island groups, but do not explain why there are so few large urchins elsewhere, nor why there are so few small individuals in the Near Islands.

Regardless of time period, sea urchin demographics differed markedly across Samalga Pass, which separates the Fox Islands in the east from islands in the central and western Aleutian ecoregions (Piatt *et al.* 2018), and corresponds to a major biogeographic boundary in kelp forest communities (Konar *et al.* 2017). Top-down control by sea otters was evident to the west of Samalga Pass, but their influence at the adjacent island groups, the Fox Islands and Islands of Four Mountains, was limited. Differing oceanographic characteristics between the Alaska Coastal Current, which floods the eastern islands in warmer, fresher, more coastally influenced water, and the Alaska Stream, which flows through the western side of Samalga Pass with colder, saltier, more oceanic water (Hunt & Stabeno 2005), may impact sea urchin life histories, with spillover effects on islands adjacent to and downstream of Samalga Pass. The temperature and salinity gradients across the Aleutian Archipelago appear to reflect these regional oceanographic patterns (Figure 2.6). Most of the sampling for this study took place to the west of Samalga Pass, where the Alaska Stream supplies cooler, saltier water, and variability in salinity was relatively low across islands except for the break to the east of Samalga Pass, where the Alaska Coastal Current is much warmer and fresher (Hunt & Stabeno 2005). Sea urchins exhibit variable morphology, growth, and/or reproduction depending on environmental conditions (Konar 2000, Vadas *et al.* 2002). Consequently, temperature and salinity can influence sea-urchin barren formation by altering the timing of their spawning, grazing, growth, and/or recruitment rates (Johnson *et al.* 2011, Ling *et al.* 2014).

In contrast to the differences in sea urchin recruitment among Island groups, recruitment within island groups was generally consistent (Figures 2.3 and 2.4). Variability around the mean recruitment index among islands suggests that islands may fall into different categories of recruitment: consistent and low, variable and moderately low, consistent and high, and variable and moderately high (Figure 2.5). Regional differences in small sea urchin recruitment could therefore be due to differences in local habitat quality or environmental conditions that influence the growth and survival of settling larvae. The specific factors that determine which of the four recruitment patterns occurred at a given island were not well resolved in this study; however, much of the variation was explained by the biogeographic breaks formed by large ocean passes (Hunt & Stabeno 2005, Konar *et al.* 2017). Samalga Pass (Figure 2.1) was a particularly important biogeographic break point; sea urchin barrens were virtually non-existent to the east of Samalga Pass, while barrens were predominant to the west of Samalga Pass (Konar *et al.* 2017). The differences between east and west of the pass are likely due to the differences in climate between the Aleutian/Bering Sea and the Gulf of Alaska (Hunt & Stabeno 2005) as water temperature can also influence green sea urchin reproductive phenology (Byrne *et al.* 2009, Rinde *et al.* 2014), and episodic patterns of recruitment as exhibited by green sea urchins in the northern Gulf of Alaska (Estes & Duggins 1995, this study).

Interactions among sea urchins of different size classes could be shaping some of the observed variability in demographic patterns to the west of Samalga Pass. For example, large sea urchins could potentially displace smaller ones, impeding growth and altering behavior (Nishizaki & Ackerman 2007). Small urchins could be more cryptic and difficult to detect in the presence of larger conspecifics as they can cannibalize smaller individuals (Legault & Hunt 2016). Cannibalism may also be supporting the large individuals dominating sea urchin populations at the Near Islands, thus limiting recruitment through density dependent responses (Legault & Hunt 2016). Alternative life history strategies could also explain the observed discrepancies in demography between the west and east of Samalga Pass: green sea urchins may exhibit a fast or slow growth morph, dependent on available resources in the barren grounds (Vadas *et al.* 2002). In the urchin barren state, there is little food available to support the high densities of sea urchin; yet, sea urchins can persist by reabsorbing their internal organ stores and eventually their calcified test to survive in a semi-dormant state until resource conditions improve, for an indeterminate length of time (Russell 1998). Diseases are also a potential density dependent response; however, unlike sea urchin barrens in other systems (Feehan & Scheibling 2014, Filbee-Dexter & Scheibling 2017), disease outbreaks have not been documented across the Aleutian Archipelago, although occasional diseased individuals were noted over the years of sampling (authors, pers. obs.).

Environmental variables were weakly correlated with patterns of sea urchin demography, but most of the variation in demography was unexplained by the variables considered. Biological interactions with the surrounding community could potentially explain some of the observed variation. Differences in benthic community structure across biogeographic regions may play a large role in limiting or enhancing recruitment and survival of juvenile sea urchins (Hereu *et al.* 2005, Feehan *et al.* 2014, Metzger *et al.* 2019). For example, differences in the assemblage of fleshy red algae or crustose coralline algae can structure patterns of sea urchin settlement via differing chemical cues (Nielsen *et al.* 2015). Similarly, biogenic habitats can act as refugia for newly settled sea urchins from non-sea otter predators (Fagerli *et al.* 2014, Jennings & Hunt 2016); such as the sea star, *Pycnopodia helianthoides,* which can exert strong top-down control of small and recruiting sea urchins (Burt *et al.* 2018). Differences in sea star assemblages have been documented across regions of the Aleutian Archipelago with *P. helianthoides* occurring predominantly east of Samalga Pass (Jewett *et al.* 2015, Konar *et al.* 2017). However, observations of *P. helianthoides* west of Samalga Pass, from Chuginadak to Adak (Authors pers. obs.) suggest that there may be occasional dispersal across Samalga Pass (Hunt & Stabeno 2005), or that perhaps larval *P. helianthoides* were transported by transiting vessel traffic or fishing boats. Other invertebrates, such as crabs, could also limit sea urchin survival and control local sea urchin abundances (Fagerli *et al.* 2014). Differences in kelp forest communities across

Samalga Pass (Konar *et al.* 2017) may influence predator-prey interactions and allow for top-down control of sea urchins, in the absence of sea otters, while also influencing refuge habitat for occasionally settling sea urchin recruits (Feehan *et al.* 2014).

Our study has shown that sea otters, when sufficiently abundant, can buffer and overwhelm effects of environmental control on sea urchin demographics. Now that sea otters are functionally extinct from the Aleutian Archipelago, sea urchin demographics have become more sensitive to changes from environmental forces, a pattern that will likely persist into the future. Spatial variability of sea urchin demography is expected to increase as environmental forces exert more bottom-up control in the absence of sea otters through time. Environmentally controlled systems may be at a greater risk from climate change impacts: with ocean warming predicted to increase into the future, sea urchin populations will likely respond, with consequences for the surrounding ecosystem.

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FIGURES

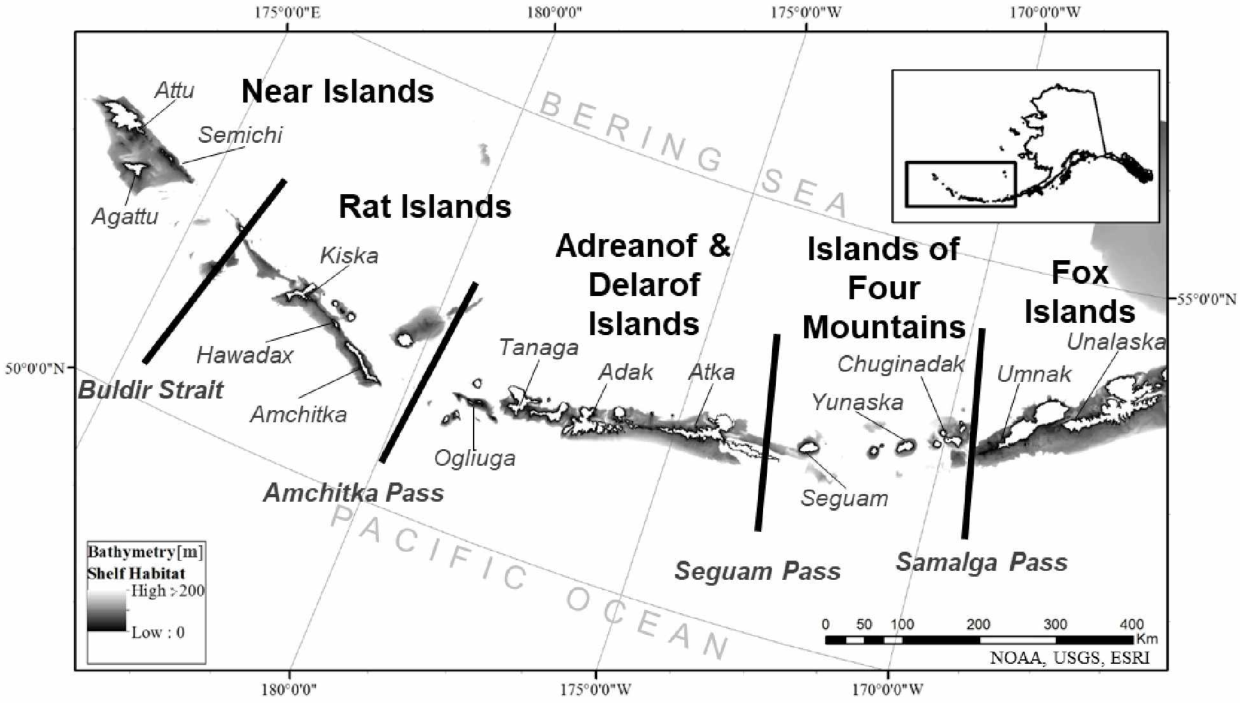

Figure 2.1. Map of the Aleutian Archipelago with labels for study islands and major oceanic passes that separate island groups from west to east: Near Islands (Attu, Agattu, Semichi), Rat Islands (Kiska, Hawadax, Amchitka), Adreanof and Delarof Islands (Ogliuga, Tanaga, Adak, Atka), Islands of Four Mountains (Seguam, Yunaska, Chuginadak), and Fox Islands (Umnak, Unalaska). Nearshore bathymetry (gray shading) shows continental shelf area (depth < 200 m).

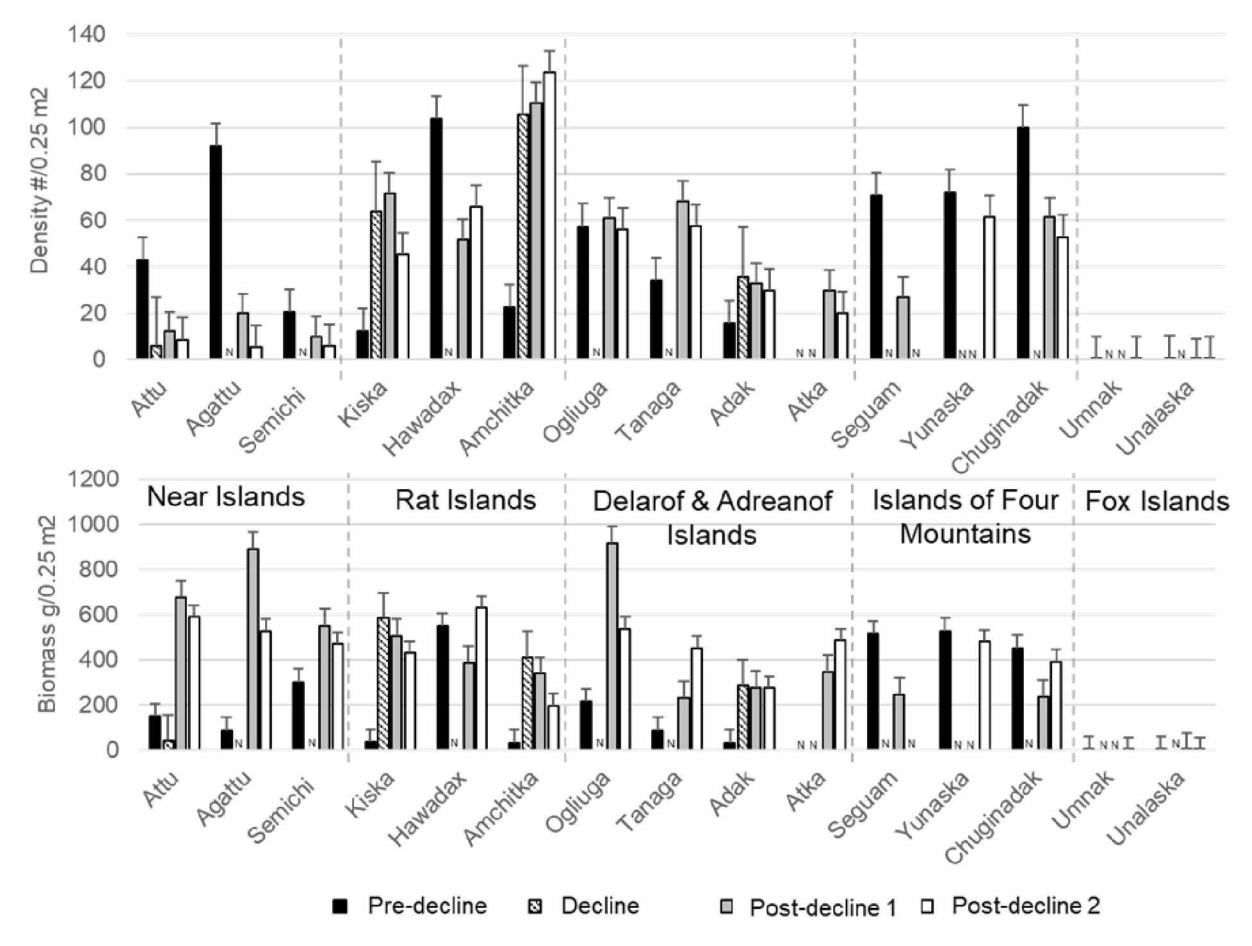

Figure 2.2. Mean sea urchin density and biomass per 0.25 m^2, averaged by island (from west to east) and sea otter periods: Pre-decline (black), Decline (dark gray), Post-decline 1 (light gray), and Post-decline 2 (white). Error bars denote standard error. “N” indicates no data. Dashed vertical lines denote major passes that separate the island groups shown in Figure 2.1.

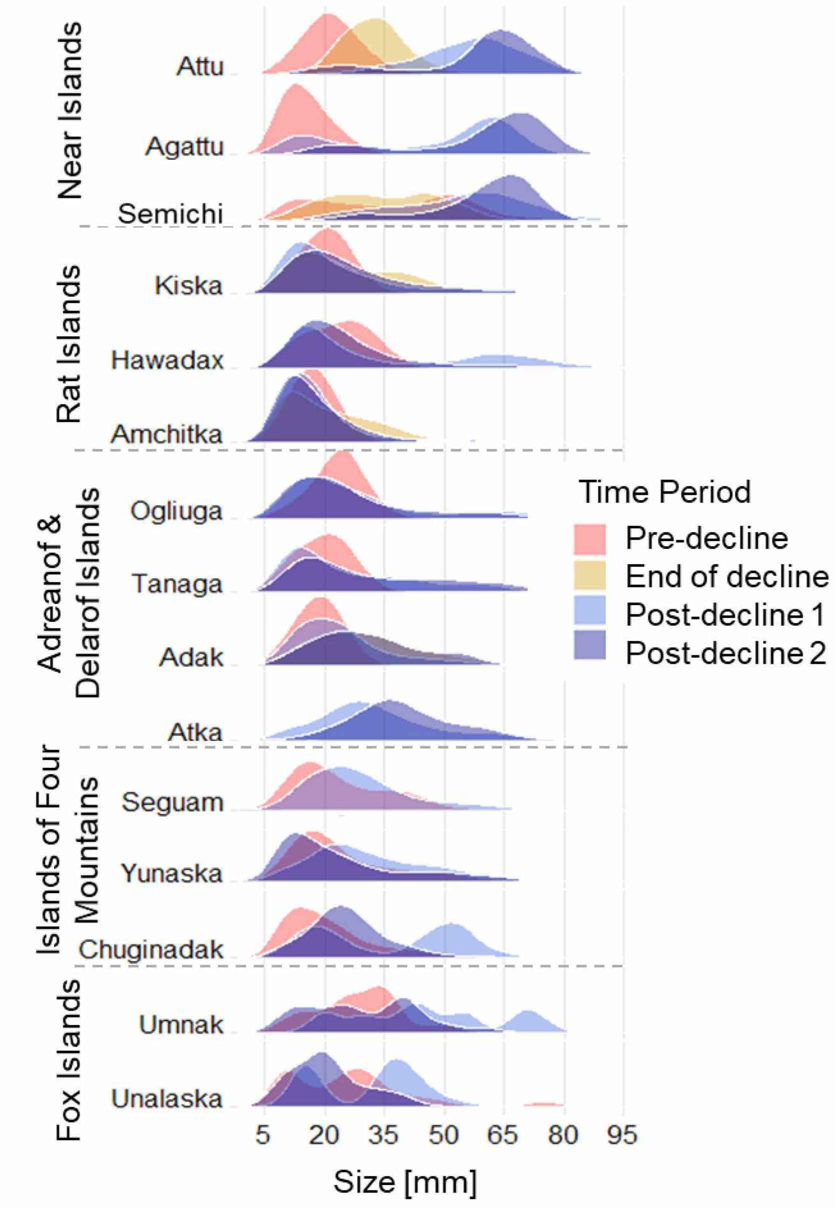

Figure 2.3. Proportional sea urchin size frequency distributions with sizes averaged by island (from west to east) and sea otter period. Y-axis for each plot is from 0-100 %. No data shown for Pre-Decline: Atka; End of Decline: Hawadax, Ogliuga, Tanaga, Atka, Seguam, Yunaska, Chuginadak, Umnak, and Unalaska; and Post-Decline 2: Seguam. Horizontal dashed lines denote major passes that separate island groups shown in Figure 2.1.

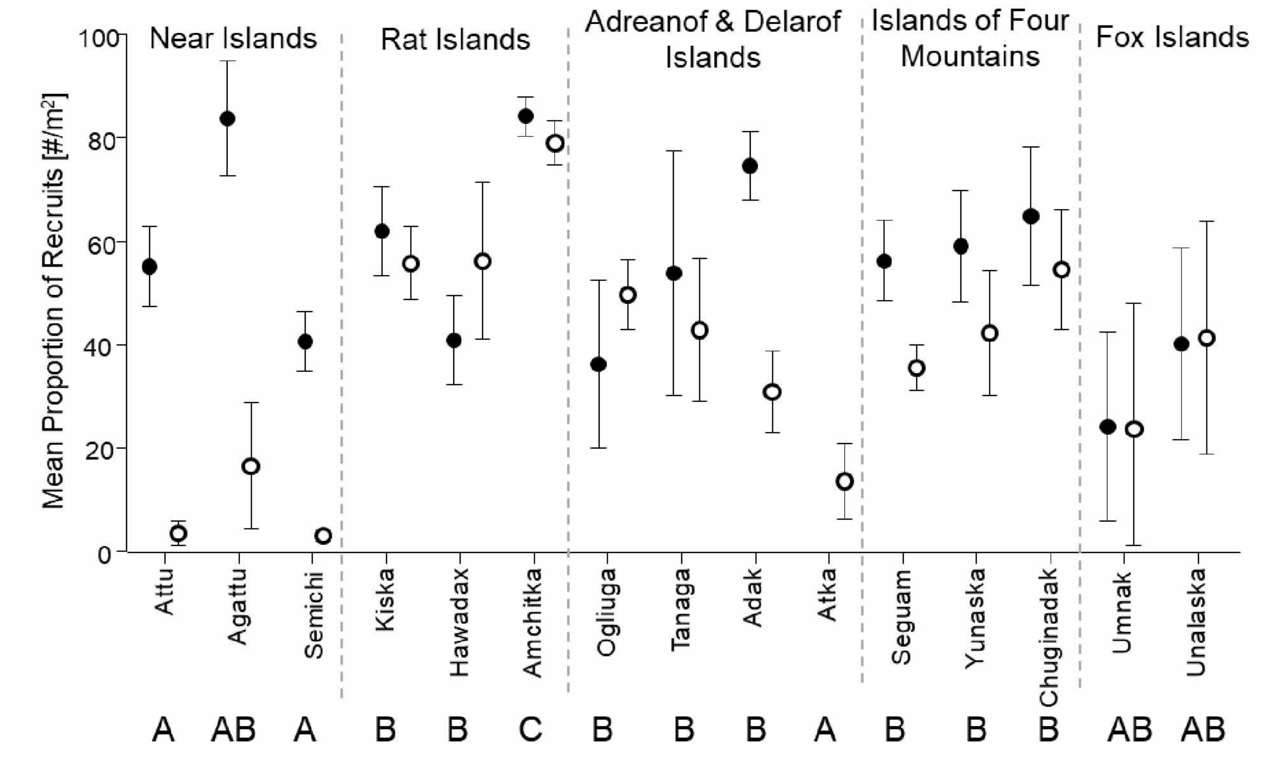

Figure 2.4. Sea urchin recruitment index means by island from west to east for pre-decline (closed circles) and mean post-decline (open circles) periods. Error bars show +/-1 standard deviation. Letters A, AB, B, and C denote pairwise significant among islands by PERMANOVA (p(perm)<0.05) during post-decline periods. Dashed vertical lines denote island groups. No data for Atka pre-decline period.

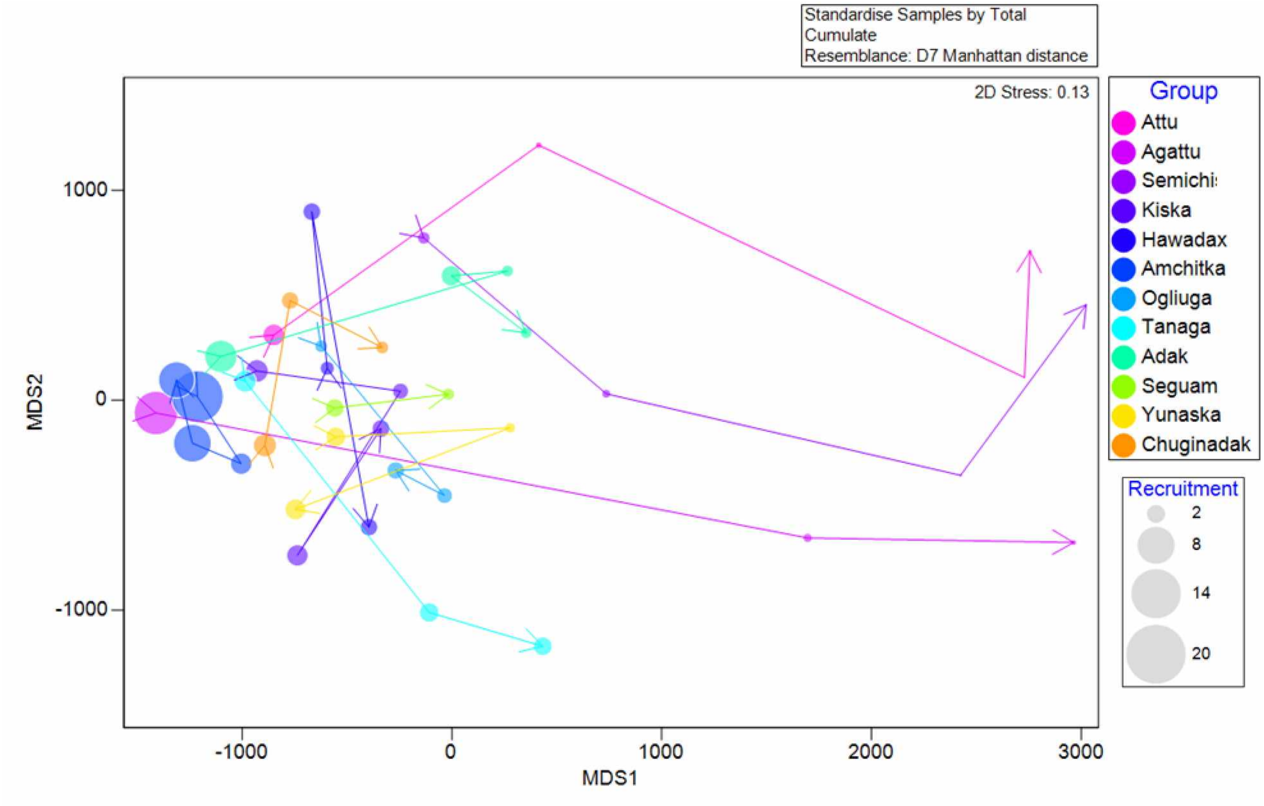

Figure 2.5. Metric MDS plot of sea urchin size distribution by island and sea otter period. Bubble size depicts the average recruitment index (proportion of sea urchins ≤ 20 mm per 0.25 m^{-2}) for each island-period. Arrows sequentially connect the periods from pre-decline to decline, to post-decline 1 to post-decline 2, except where only 3 points are connected and decline data were not available. Atka and Umnak/Unalaska were excluded due to no pre-decline data and limited sample size, respectively.

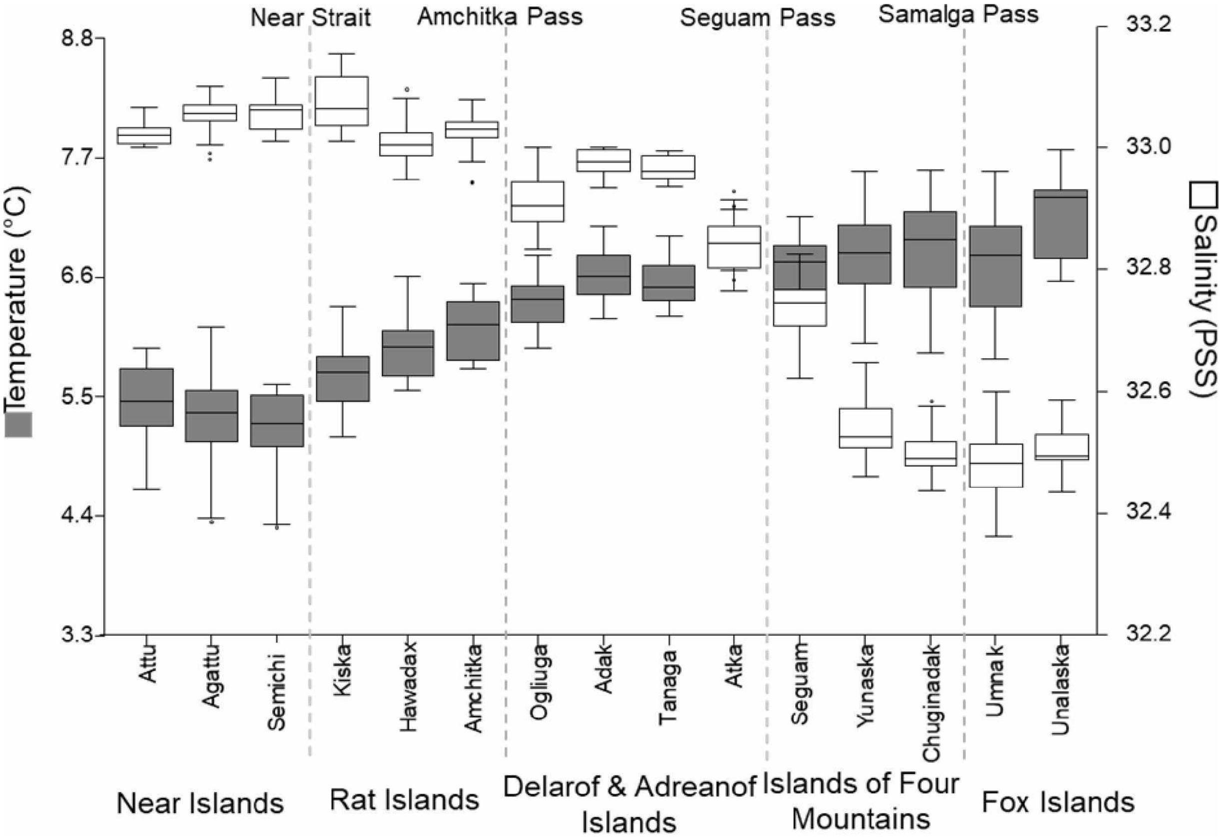

Figure 2.6. Box plot of mean sea surface temperature (gray) and salinity (white) across the upper 20 m of the water column, averaged from PMEL CCMA models across years 2002-2017 by island from west to east. Dashed vertical lines denote major passes that separate island groups.

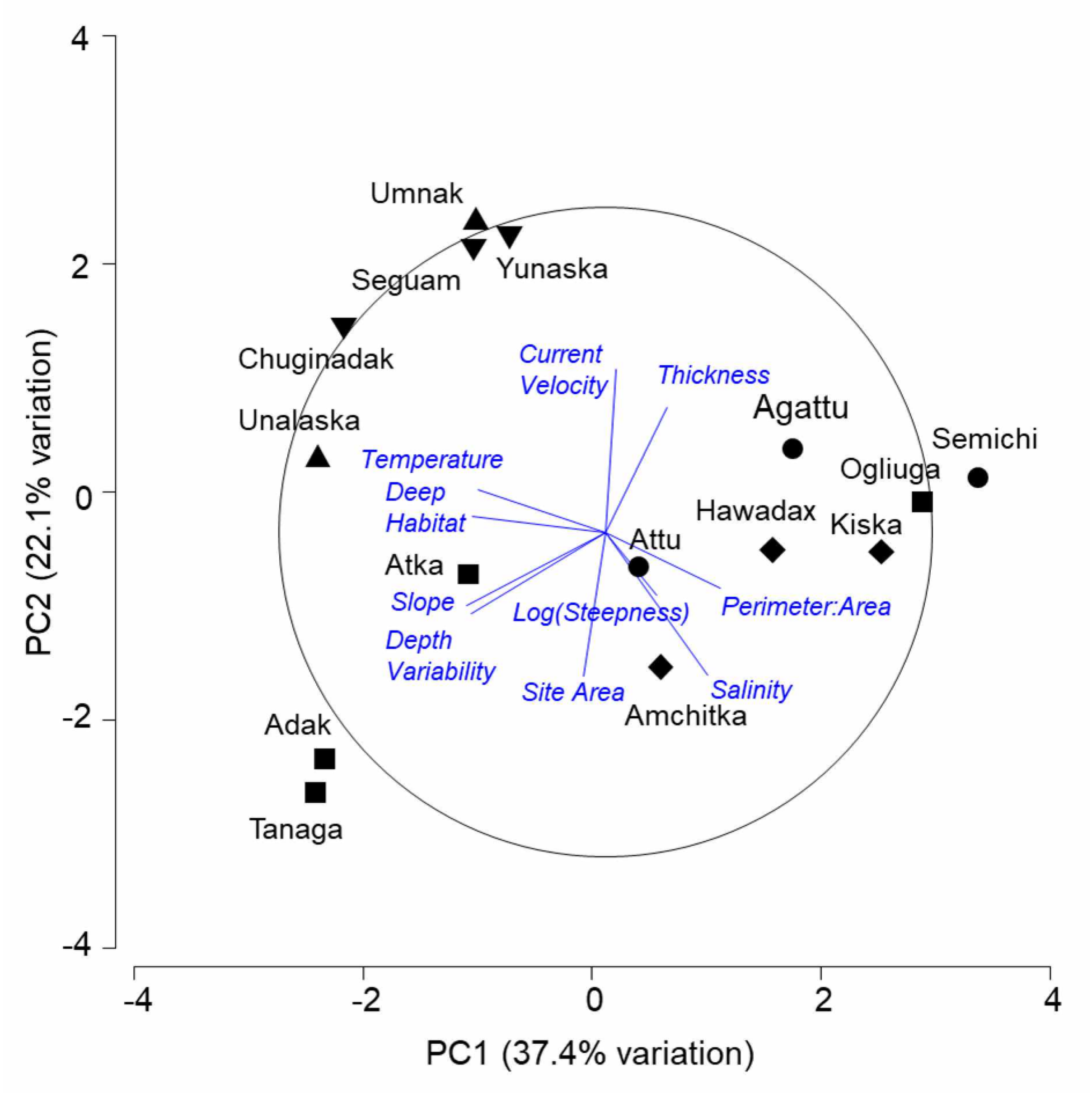

Figure 2.7. Principal component analysis (PCA) of environmental variables, coded by island group: Near Islands (circles), Rat Islands (diamonds), Delerof and Adreanof Islands (squares), Islands of Four Mountains (down-triangles) and Fox Islands (up-triangles). The blue vectors depict the direction and strength of correlation of variables where the circle represents the correlation fit (if perfectly correlated, the vector line would extend to the circle).

Table 2.1. Examples of environmental variables that can potentially influence sea urchin demographics in temperate sea urchin barrens. The specific environmental variables examined in this study are listed by the type of influence. Rationale for inclusion was based on referenced sources and expected influence on demography (via survival reproduction, recruitment, or growth) from a given type of environmental driver: positive (+), negative (-), mixed, or unknown (?) is given. This table is not an exhaustive review of the literature and presents examples from temperate sea urchin barrens where sea otters are not a functional component of the ecosystem.

Examples of environmental influences on sea urchin demography

Type of Influence	Variable in this study	Scale in this study	Rationale	Expected Influence + / - / ?	Sources
Oceanographic	Sea Surface Salinity	Island	*Strongylocentrotus* spp. have a generally low tolerance to low and highly variable salinities.	-	Starr *et al.* 1993, Estes & Duggins 1995, Ling *et al*. 2009, Johnson *et al*. 2011, Rinde *et al*. 2014, Frey & Gagnon 2015, Rasher *et al*. in review
	Sea Surface Temperature	Island	Temperature can influene the behaviour, reproduction, grazing, and growth of green sea urchins. Particularly important in large scale climate studies	mixed	
	Sea Surface Current Velocity	Island	Can influence patterns of sea urchin demographics by driving recruitment and local community structure	mixed	
Bathymetric	Exposure	Site	Important local driver of sea urchin behaviour, size structure, and ecological function.	mixed	Estes & Duggins 1995, Konar 2000, Bahzin 2002, Steneck *et al*. 2002, Feehan *et al*. 2014, Parnell 2015, Ling *et al.* 2016, Fagerli *et al.* 2013, 2015, Rinde *et al*. 2014, Frey & Gagnon 2015, Nyhagen *et al*. 2018
	Slope	Site	Slope will shape patterns of sea urchin behaviour in response to perturbation across depth ranges	+	
	Slope Variability	Site	Variability in slope can serve as a measure of complexity of local habitat; influencing sea urchin behavioural responses to perturbations across depth ranges	+	
	Depth	Site	Depth will shape patterns of sea urchin behaviour and ecological function	mixed	
	Depth Variability	Site	Variability in depth can serve as a measure of the complexitity of the local habitat; influencing sea urchin behaviour and ecological function	+	
	Shallow Habitat	Site	The amount of shallow habitat within the foraging depths of sea otters and also in the ideal depth range for macroalgal production	+	
	Deep Habitat	Site	The amount of deep water inaccessible to sea otters that could serve as a deep water refugia.	+	
	Amount of Shelf habitat	Site	The amount of habitat on the continental shelf (0-200 m water depth)	+	
Geophysical	Shape	Island	Can influence local currents, weather patterns, and degree of coastal vs oceanic influence. Geophysical structure of the shoreline can influence other environmental forces	?	Bahzin 2002, Ebert *et al*. 2010
	Mean Elevation	Island		?	

Table 2.2. Number of sites sampled by island and year. Italicized numbers (< 4) denote samples excluded from analysis due to inadequate sample size.

Island Group	Island	*Time period*											
		Pre-decline				End of decline		Post-decline 1		Post-decline 2			
		1987	1990	1993	1994	1999	2000	2008	2010	2014	2015	2016	2017
Near Islands	Attu	10	14	18	*2*	-	21	22	-	6	4	-	6
	Agattu	-	-	6	-	-	-	6	-	-	4	-	-
	Semichis	33	-	*1*	29	-	-	33	-	6	6	-	5
Rat Islands	Kiska	-	-	20	-	-	20	20	-	6	6	-	5
	Hawadax	-	-	-	13	-	-	15	*1*	-	6	-	-
	Amchitka	29	-	-	-	31	11	31	-	6	5	-	6
Adreanof & Delarof Islands	Ogliuga	-	-	-	4	-	-	10	-	6	6	-	6
	Tanaga	-	-	-	13	-	-	4	-	6	-	5	-
	Adak	28	-	-	-	30	29	30	-	6	4	6	6
	Atka	-	-	-	-	-	-	10	-	-	-	*3*	6
Islands of Four Mountains	Seguam	-	-	-	10	-	-	-	7	-	-	-	-
	Yunaska	-	-	-	12	-	-	-	-	-	-	-	6
	Chuginadak	-	-	-	12	-	-	12	-	-	-	6	-
Fox Islands	Umnak	-	-	-	8	-	-	-	-	-	-	6	-
	Unalaska	-	-	-	12	-	-	-	*2*	-	-	6	-

Table 2.3. PERMANOVA results for main-tests of sea urchin density, biomass, size distributions, and recruitment index.

PERMANOVA table of main-test results

Sea Urchin Metric	Density			Biomass			Size Distribution			Recruitment Index		
Source	df	*Pseudo-F*	p(perm)	df	*Pseudo-F*	p(perm)	df	*Pseudo-F*	p(perm)	df	*Pseudo-F*	p(perm)
Island	14	32.637	0.001	14	7.9425	0.001	14	61.519	0.001	14	9.7409	0.005
Period	3	3.3887	0.018	3	10.697	0.001	3	55.7	0.001	3	11.783	0.009
Island x Period	28	8.7211	0.001	28	4.3497	0.001	30	13.837	0.001	31	2.4654	0.104

Table 2.4. Correlation values from BEST analysis of environmental variable with sea urchin size distributions. Among all islands in each period, the number of variables (No. Vars.), Spearman-rank correlation value (Corr.), and variables included (Variables codes) in the best correlation combinations are shown. Strength of correlation statistic (ρ-value) and significance of test by permutations (perms=999) separate the results for best correlations with a limited variable set and best correlations by combination variable set.

Correlations with Sea Urchin Size Distributions by TimePeriod

Code	Variable Name
1	Island Size
2	Island Thickness
3	Island Steepness
4	Exposure (site area)
5	Bathymetric Slope
6	Depth Variability
7	Shallow Habitat Area
8	Deep Habitat Area
9	Salinity
10	Temperature
11	Current Velocity

Sea Otter Period	Pre-decline			End of decline			Post-decline 1			Post-decline 2		
	No. Vars.	Corr.	Variables	No. Vars.	Corr.	Variables	No. Vars.	Corr.	Variables	No. Vars.	Corr.	Variables
Number of Variables, Correlations, Variables included	1	0.260	1	1	0.152	1	1	0.354	10	1	0.403	10
	2	0.318	1,4	2	0.152	1,9	2	0.375	1,10	2	0.371	4,10
	3	0.329	1,4,10	3	0.152	1,4,11	3	0.352	1,4,10	3	0.328	1,4,10
	4	0.327	1,2,4,10	4	0.155	1,3,4,8	4	0.312	1,4,10,11	4	0.287	1,4,8,10
	5	0.321	1,2,4,9,10	5	0.150	1,3,4,8,11	5	0.267	1,4,8,10,11	5	0.236	1,4,8,10,11
	6	0.298	1,2,4,7,9,10	6	0.151	1,3,4,8,10,11	6	0.220	1,4,8-11	6	0.192	1,2,4,8-10
ρ-value	0.329			0.155			0.375			0.403		
Sig. of Sample Stat.	0.1%			0.1%			0.1%			0.1%		
10 Best variable combinations: Number of variables, correlations, variables included	3	0.329	1,4,10	4	0.155	1,3,4,8	2	0.375	1,10	1	0.403	10
	4	0.327	1,2,4,10	1	0.152	1	1	0.354	10	2	0.371	4,10
	3	0.326	1,4,9	2	0.152	1,9	3	0.352	1,4,10	3	0.328	1,4,10
	4	0.323	1,2,4,9	3	0.152	1,4,11	2	0.321	4,10	2	0.321	1,10
	4	0.322	1,4,9,10	4	0.152	1,4,9,11	4	0.312	1,4,10,11	3	0.310	4,8,10
	5	0.321	1,2,4,9,10	6	0.151	1,3,4,8,10,11	1	0.309	1	3	0.296	4,10,11
	2	0.318	1,4	3	0.151	1,4,8	3	0.305	1,10,11	2	0.294	8,10
	3	0.317	1,2,4	4	0.151	1,4,8,9	2	0.296	10,11	2	0.289	10,11
	4	0.313	1,3,4,10	2	0.151	4,11	2	0.291	1,4	4	0.287	1,4,8,10
	5	0.308	1-4,10	2	0.150	1,4	3	0.288	1,8,10	3	0.281	4,9,10

CHAPTER 3: RESPONSE OF ALEUTIAN GREEN SEA URCHINS (*STRONGYLOCENTROTUS POLYACANTHUS*) TO THE COMBINED EFFECTS OF OCEAN ACIDIFICATION AND WARMING[2]

ABSTRACT

Climate change may substantially alter nearshore ecosystems of the northwestern Pacific, especially where calcifying organisms dominate the benthos. Increased ocean acidification is predicted to have negative physiological effects on most calcifying taxa, but manifestation of these impacts will also depend on the individual and interactive effects of seawater warming. In the western Aleutian Archipelago, sea urchins currently dominate the benthos and have denuded kelp forests throughout the region, creating vast barrens. To understand how climate change will influence the performance and demography of this dominant herbivore (*Strongylocentrotus polyacanthus*), we conducted a 4-month experiment, in which adult sea urchins were subjected to combinations of $p\mathrm{CO}_2$ and temperature treatments that spanned pre-industrial (335-371 µatm), present day (480-499 µatm), predicted near-future (829-929 µatm), and predicted far-future (2962-3475 µatm) levels of $p\mathrm{CO}_2$ under three temperature scenarios (6.2-6.6, 8.6-8.9, and 12.3-12.6 °C). Specifically, we tested how survival, growth, calcification, reproductive investment, and caloric content of *S. polyacanthus* adults responded to each $p\mathrm{CO}_2$ and temperature combination. Overall, temperature had a much stronger effect on urchin condition than did $p\mathrm{CO}_2$. At warmer temperatures, sea urchin tests did not exhibit any growth and reductions in size were observed under increasing $p\mathrm{CO}_2$. Survival was reduced at high temperatures, whereas

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[2] Weitzman, B.P., Rasher, D.B., Lawton, K.L., Westfield, I.T., Ries, J.B., and Konar, B.H. (in prep) Response of Aleutian green sea urchins (*Strongylocentrotus polyacanthus*) to the combined effects of ocean acidification and warming. Journal of Experimental Marine Biology and Ecology

calcification was reduced by both increasing temperature and $p\mathrm{CO}_2$. The gonad index increased with $p\mathrm{CO}_2$, irrespective of temperature, by 5-20% across treatments and while caloric content did not show a significant relationship with temperature and $p\mathrm{CO}_2$, it was found to positively correlate with gonad content, nearly threefold across the range of gonad indices measured in this study. These patterns indicate that *S. polyacanthus* survival, growth, and resistance to predation are likely to be reduced as this region continues to warm, but that reproductive effort may increase with increasing $p\mathrm{CO}_2$. As such, our results suggest that sea urchin demographics could be affected by near-future climate change, with implications for ecosystem function across temperate rocky reefs.

INTRODUCTION

Rising atmospheric carbon dioxide (CO_2) concentration (from ~350 ppm to ~490 ppm) since the Industrial Revolution has resulted in a warming of the atmosphere and acidification of the global ocean (Orr *et al.* 2005, Fabry *et al.* 2009). Ecosystem responses to ocean acidification are expected to be varied, with both winners and losers in a warmer, more acidified ocean (Ries *et al.* 2009). Calcifying marine organisms face physiological challenges in a hypercapnic environment that stresses metabolic pathways. However, responses can vary from negative to neutral to positive among genera and across life stages (Hofmann *et al.* 2010, Kroeker *et al.* 2010, Espinel-Velasco *et al.* 2018). Benthic invertebrates with a pelagic larval dispersal phase are expected to incur deleterious effects from ocean acidification at multiple points of ontogeny and development (Yu *et al.* 2011, Dupont *et al.* 2013, Gaylord *et al.* 2015).

Moreover, these effects of ocean acidification are likely to interact with seawater warming in complex ways, creating the need to study both stressors simultaneously (Kroeker *et al.* 2013).

The impacts of ocean warming and acidification on organismal performance and demography may scale up to affect ecosystem structure and function by influencing primary and secondary productivity and by modifying species interaction strengths (Hofmann *et al.* 2010, Kelly *et al.* 2013, Queirós *et al.* 2015). Sea urchins are both a prey resource and dominant benthic herbivore within temperate nearshore ecosystems, and they can shape community structure and function through their grazing of macroalgae, the dominant source of benthic primary production (Filbee-Dexter and Scheibling 2014). For example, where demographic controls have been removed (*e.g.*, predators) or occur sporadically (*e.g.*, disease), sea urchins can overgraze kelp forests resulting in a barren ecosystem with lower biodiversity and productivity. Sea urchin barrens often persist as an alternate stable state to kelp forests, until some perturbation reduces sea urchin density and enables kelps to reestablish (Filbee-Dexter & Scheibling 2014). Any stressors that influence patterns of sea urchin demography could alter the role sea urchins play in shaping coastal habitats, and the amount of energy available to consumers. If sea urchin energy density changes as a result of climate change, they become more or less desirable to calorie-focused predators like sea otters (*Enhydra lutris*), which have been shown to forage optimally (Ostfeld 1982) and track the reproductive cycles of their invertebrate prey (Tinker *et al.* 2008, Oftedal *et al.* 2007).

Global oceanic change – specifically, ocean warming and/or acidification – can influence the development of barrens through changes in sea urchin larval development, grazing intensity, and distribution (Johnson *et al.* 2011, Ling *et al.* 2014). Temperature can directly influence growth (Siikavuopio 2008) and grazing rates (Traiger 2019) and increasing ocean temperature has been directly tied to the expansion of sea urchin populations in temperate oceans (Ling *et al.* 2014). Direct impacts of ocean acidification on sea urchins vary across life stages. Adults have shown some resilience to the effects of acidification (*e.g.* Ries *et al.* 2009); however, negative carry-over effects may influence the fitness of their offspring (Dupont & Thorndyke 2013). Some adult sea urchins have slower somatic and gonadal growth associated with the metabolic costs of a high $p\mathrm{CO}_2$ environment (Dupont *et al.* 2013). Environmental stressors affect the trade-offs between investment in growth and reproduction, leading to demographic effects, such as lower reproductive output or increased mortality (Ling *et al.* 2009). The ultimate outcome of these tradeoffs may be lower sea urchin biomass due to either fewer or smaller sea urchins, reducing food availability for their predators. Stressors experienced by individual adults could scale up to affect population dynamics, altering the role that sea urchins can play in benthic ecosystems as both a grazer of primary production and a prey resource for consumers (*e.g.*, sea otters, sea ducks, or fishes).

No study has yet examined the effects of environmental change on the Aleutian green sea urchin (*Strongylocentrotus polyacanthus*), a close relative of *S. droebachiensis*. Where multiple sea urchin species occur, they generally partition habitat use based on size (Burt *et al.* 2018) and tolerance of wave exposure and salinity (Bazhin 2002). Although multiple species of green sea urchins occur throughout the northern hemisphere and are relatively well studied, distinct populations and species may respond to environmental stressors quite differently (Norderhaug *et al.* 2016). *S. polyacanthus* has—following the functional extinction of sea otters—broadly denuded the western Aleutian Archipelago of kelp forests in recent decades (Estes *et al.* 2010). Patterns of demography that lead to overgrazing are sensitive to environmental forcing and are expected to be influenced by future changes in ocean temperatures (Chapter 2; Weitzman *et al.*

in prep). Recent synthesis of oceanographic and geochemical data suggest that the south Bering Sea is indeed warming, and that increasing atmospheric $p\text{CO}_2$ can lead to acidified ocean conditions in coastal areas (Pilcher *et al.* 2019). Determining the response of *S. polyacanthus* to ocean warming and acidification will help to inform whether the ecological impact of this grazer could change in the near future, and whether *S. polyacanthus* will remain a viable and energy-rich food source for sea otters, should they begin to recover in the ecosystem (Estes & Palmisano 1974, Estes *et al.* 2010).

In this study, we measured the individual and interactive effects of seawater temperature and $p\text{CO}_2$ on adult *S. polyacanthus* survival, growth, calcification, reproductive investment (gonad-somatic indices), and caloric (energy) content by way of a 4-month laboratory experiment. We used a factorial series of temperature and $p\text{CO}_2$ corresponding to pre-industrial (1850-1900), modern (present-day), near-future (2050), and far-future (2100) conditions for the Aleutian Archipelago under an IPCC "business-as-usual" scenario (Pachauri *et al.* 2014), to test for independent and interacting effects of both variables. We chose to focus on a suite of sea urchin response metrics that (a) describe the direct energetic costs or benefits that sea urchins could incur with environmental change, and (b) are relevant to the organism's role as both an herbivore and prey resource in the ecosystem.

METHODS

Specimen collection

Divers collected large *S. polyacanthus* (~ 45-60 mm test diameter) from the shallow subtidal zone (~ 8 m water depth) at Adak Island, Alaska, in fall 2015 and transported them to the Marine Science Center at Northeastern University in Nahant, Massachusetts. There, 180 sea urchins were acclimated to laboratory conditions at 8.6 °C for two weeks before being moved into 42-L experimental aquaria for an additional two weeks. After the four-week acclimation period, sea urchins were stained with calcein, a fluorescent dye that would be incorporated as a growth band in the test to track growth. Following staining, conditions were incrementally changed to target temperature and $p\mathrm{CO}_2$ levels over the course of one week for each treatment level. Sea urchins were housed individually in cages, with chips of *Clathromorphum nereostratum*, a dominant crustose coralline alga across the Aleutian Archipelago, for the duration of the experiment to mimic food source conditions at barren grounds. Five sea urchins in separate cages were kept in each of three tanks per treatment, subjecting 15 individuals to each temperature and $p\mathrm{CO}_2$ combination (tank was later included in statistical models as a random factor). Sea urchins evaluated in this study also were used to examine the interaction between *S. polyacanthus* and *C. nereostratum* (Rasher *et al.* in review) to determine the effects of increasing warming and $p\mathrm{CO}_2$ on grazing rate; details of the facility and experimental design can be found in that paper. A brief synopsis of the relevant experimental design is provided below.

Laboratory experiment

A 108-day controlled laboratory experiment was used to test the influence of seawater temperature and $p\mathrm{CO}_2$ on sea urchin physical condition (metrics described below). Temperature and $p\mathrm{CO}_2$ treatments were fully replicated across all possible treatment combinations to allow for robust interpretation of individual and interactive effects. Experimental treatments spanned pre-industrial (335-371 µatm, nominal 350), present-day (480-499 µatm, nominal 490), predicted near-future (829-929 μatm, nominal 900), and predicted far-future (2962-3475 μatm, nominal 3250) pCO_2 levels, across three temperature scenarios to mimic present-day (6.2-6.6 °C), near-future (8.6-8.9 °C), and far-future (12.3-12.6 °C) ocean temperatures. Water quality was monitored daily, and every 11 days a full water chemistry panel of temperature, salinity, pH, total alkalinity (TA), and dissolved inorganic carbon (DIC) was completed following best practices (Dickson *et al.* 2007). From these measurements, water chemistry metrics of pCO_2 of gas in equilibrium with sea water, pH on seawater scale, carbonate ion concentration, bicarbonate ion concentration, dissolved CO_2 in sea water, and aragonite saturation state were calculated over the course of the experiment.

Sea urchin physical condition responses

Survival was quantified as the number of days that each sea urchin survived within its given treatment during the experiment (108 days maximum). Every 28 days, aquaria were inspected for sea urchin mortality, and to measure calcified tissue mass of the live sea urchins (see below). Sea urchins that perished during the experiment were frozen whole. At the end of the 108-day experiment, all remaining (living) sea urchins were measured for test diameter and calcified tissue mass and then sacrificed to determine gonad-somatic indices and caloric content of soft-tissue.

Growth was determined by measuring the width of the sea urchin test, excluding spines. At the start and end of the 108-day experiment, the maximum test diameter (TD) of each sea urchin was measured. TDs were obtained first by standardized overhead photographs, set up at the start of the experiment and left un-manipulated until the final photograph, and analyzed with software (ImageJ), and secondarily using dial calipers, rounded to the nearest tenth in millimeter. At the end of the experiment, all sacrificed sea urchins were dissected to remove soft tissues.

Calcified tissue mass was measured initially and then every 28 days during the experiment (n = 4 measurements) to provide an estimate of net calcification. During each sampling period, buoyant weights of each individual were obtained in triplicate by hanging subjects from a digital scale while fully submerged in a sea water bath similar to the treatment conditions (Courtney *et al.* 2013). This process allowed for all non-calcified tissues to be neutrally buoyant such that the mass quantified represented only the calcified skeleton minus the mass of the seawater displaced by the skeleton, following Archimedes' principle (Ries *et al.* 2009). This method provides a relative measure of calcification rate among experimental treatments and not an absolute calcification rate. Because the relationship between the buoyant weight and dry weight of an urchin skeleton is highly linearly correlated (Ries *et al.* 2009), the change in buoyant weight of an urchin skeleton is proportionate to its change in dry weight.

After dissections for soft tissues, gonad and somatic (all soft tissue within the test and surrounding the aboral surface) tissue were separated, and the wet weight of each was recorded. Tissues were then frozen separately for transport to the U.S. Geological Survey, Alaska Science Center (Anchorage, AK) for calorimetry. Frozen tissues samples were kept separate and again weighed wet before being placed into a freeze-drier (Labconco FreeZone) at -40 °C for 48 hours, and then finally weighed dry. Gonad:somatic tissue ratios, known as the gonad-somatic index (GSI), were calculated from the freeze-dried tissues (to control for water content) for each specimen to determine the proportion of gonad tissue in each sea urchin specimen. GSI was calculated by dividing the gonad mass by somatic mass and multiplying by 100. Only individuals that survived until the end of the experiment (n=112) were analyzed for comparison among treatments, and those with some reproductive tissue present (n=105) were assessed in the GSI and calorimetry comparisons.

Freeze-dried tissues were combusted using bomb calorimetry to obtain the caloric content of soft-tissue within the sea urchins, which represents the amount of edible energy that could be available to a predator, such as the sea otter. Gonad and somatic tissue samples were homogenized, after final weighing, using a mortar and pestle. The homogenized powder was placed in a pellet press to produce pellets with a mass between 0.02 and 0.20 g. Pellets were combusted in a pre-calibrated semi-micro bomb calorimeter (6725 Semi-micro Oxygen bomb calorimeter with 1109A Oxygen combustion vessel) to determine the caloric content (calories per gram; [cal/g]) for each sample (Oftedal *et al.* 2007). The calorimeter was calibrated daily by conducting five separate runs of a standard, 0.2 g benzoic acid pellet, all falling within the range of 6318 +/- 75.8 cal/g for each standard.

Statistical analyses

Survivorship was analyzed using a cox-proportional hazards model to determine the probability of survival under differing treatments of temperature and pCO_2, while assigning the degree of risk posed by each treatment. Hazards models were performed in R (v10.6.1) using the survival package (Therneau 2018).

Primer-e v7 was used to assess the overall multivariate response of physical condition metrics and the independent univariate responses of calcification rate, test diameter, and GSI (Anderson *et al.* 2008, Clarke & Gorley 2015) to temperature and pCO_2. Permutational analysis of variance (PERMANOVA) was used for both the multivariate and univariate tests, where the treatment variables, temperature and pCO$_2$, were treated as fixed factors with an interaction term, and tank was included as a random factor. Pairwise post-hoc testing was done for significant fixed factors, beginning with the interaction term, if it was found to be significant. For the multivariate test, all data were normalized, and a Euclidean Distance matrix was constructed to compare similarity responses among metrics across all treatments. Data were left untransformed for univariate tests of each metric (Clarke & Gorley 2015) and Euclidean Distance matrices constructed for each metric independently. All PERMANOVAs were performed with unrestricted permutations of the full model for 9999 permutations, and significance was determined by the p-value ($p(perm) \leq 0.05$). The linear response of sea urchin physical condition metrics to experimental treatment was tested using a mixed model with temperature and pCO$_2$ treated as fixed factors with tank as a random factor in the nlme package (Pinheiro *et al.* 2019) in R (v10.6.1). To quantify the relationship between test diameter and calcified tissue mass with aragonite saturation state, response curves were fit using linear regression in nlme. The relationship between the gonad-somatic index (GSI) and energy content was also established by linear regression using nlme.

RESULTS

Experimental treatment conditions

While the actual conditions varied somewhat from the nominal target values, we were successful in maintaining aquaria at consistent temperature and pCO$_2$ levels over the course of the experiment. However, the distant-future treatment at 3250 µatm fluctuated more than the other $p\mathrm{CO_2}$ treatments on an absolute basis (Table S3.1) and was included to obtain a response to severe conditions, such as those arising from seasonal upwelling of deeper, more acidified waters (Feely *et al.* 2008). Mean, +/-1 standard deviation, and range for all measured and calculated water chemistry parameters were used for all analyses and no single aquarium experienced a die-off of organisms due to anomalies in temperature or water chemistry.

Survivorship

Of the 180 sea urchins in the study, 25 perished, leaving 155 survivors at the end of the 108-day experiment, for an overall survival rate of 86%. Sea urchin survival significantly declined with increasing temperature ($p < 0.001$); however, increasing $p\mathrm{CO_2}$ had no detectable impact on survival ($p = 0.273$). The hazard coefficient for temperature was 1.63 (range: 1.28 – 2.07), whereas for $p\mathrm{CO_2}$ it was 1.00 (range: 0.99 – 1.01), indicating that temperature increased mortality, while $p\mathrm{CO_2}$ had a variable or neutral influence on the probability of mortality. After 108 days, the probability of survival at 6°, 9°, and 12° C was 1.0, 0.88, and 0.73, respectively (Figure 3.1a); while the probability of survival at 350 µatm, 490 µatm, 900 µatm, and 3250 µatm was 0.89, 0.85, 0.80, and 0.94, respectively (Figure 3.1b).

Physical condition response

Overall, temperature had a stronger effect on the sea urchin response metrics than did $p\mathrm{CO_2}$, and increased temperature exacerbated the effects of a hypercapnic environment (Figure 3.2). The multivariate response of growth, calcification, and reproductive investment was sensitive to both temperature (*p(perm)* < 0.001, *pseudo-f* = 6.408) and $p\text{CO}_2$ (*p(perm)* <0.001, *pseudo-f* = 3.513). However, the interaction was not significant (*p(perm)* = 0.320, *pseudo-f* = 1.106). Pairwise tests of temperature revealed that all three treatments were significantly different (6° vs. 9° C (*p(perm)* = 0.017, t = 1.915; 9° vs. 12° C (*p(perm)* = 0.016, t =1.880); 6° vs. 12° C (*p(perm)* < 0.001, t = 3.464). Pairwise tests for $p\text{CO}_2$ treatments 350 vs. 490 µatm (*p(perm)* = 0.134, t = 1.392) and 350 vs. 900 µatm (*p(perm)* = 0.467, t = 0.916) were not significant. By contrast, 490 vs. 900 µatm (*p(perm)* = 0.006, t = 2.189), 350 vs. 3250 µatm (*p(perm)* = 0.01, t = 2.130), 490 vs. 3250 µatm (*p(perm)* = 0.015, t = 1.943), and 900 vs. 3250 µatm (*p(perm)* = 0.003, t = 2.333) were significant.

Growth

Sea urchin growth was determined by change in TD in each individual sea urchin. Growth showed a significant negative response to temperature (*p(perm)* = 0.006, *pseudo-f* = 6.374)(Figure 3.3a). Shrinkage of the test is possible and has been documented as a reason why sclerochronology of sea urchin tests may be futile (Narvaez *et al.* 2016). The growth response to $p\text{CO}_2$, however, was not significant (*p(perm)* = 0.8245, *pseudo-f* = 0.300) and was highly variable across $p\text{CO}_2$ levels (Figure 3.2). The interaction was not significant (*p(perm)* = 0.784, *pseudo-f* = 0.527). Pairwise tests showed that sea urchin growth rates differed for 6.5° vs 9.5° C (*p(perm)* = 0.0473, t = 2.026) and 6.5° vs. 12.5° C (*p(perm)* = 0.003, t = 3.092), but not for 9.5° vs. 12.5° C (*p(perm)* = 0.184, t = 1.336).

Calcification

Net calcification rate during the 108-day experiment showed a significant negative response to increasing temperature (*p(perm)* < 0.001, *pseudo-f* $= 27.448$) and $p\mathrm{CO_2}$ (*p(perm)* < 0.001, *pseudo-f* $= 12.624$). The interaction term was weakly significant (*p(perm)* $= 0.042$, *pseudo-f* $= 2.252$), whereby the negative effect of increasing $p\mathrm{CO_2}$ on net calcification was exacerbated by increased temperature (Figure 3.3b). Generally, the highest $p\mathrm{CO_2}$ treatment caused the greatest reduction in skeletal mass across all temperature treatments, and the change in mass was significantly different (*p(perm)* < 0.05) from the lower $p\mathrm{CO_2}$ treatments. Further exploration of calcification against aragonite saturation state fit with a quadratic function revealed a parabolic response across aragonite saturation states, which increased in fit with temperature (Figure 3.4).

Gonad-somatic Index

The dried gonad-somatic index (GSI) was used to eliminate error in weights from water content. The proportion of reproductive tissue varied considerably among individuals in the experiment, from 0.00% up to 92.6%. Unlike the other response metrics, the effect of temperature on GSI was not significant (*p(perm)* $= 0.546$, *pseudo-f* $= 0.598$), nor was the interaction term (*p(perm)* $= 0.353$, *pseudo-f* $= 1.118$). However, an effect of $p\mathrm{CO_2}$ was statistically significant (*p(perm)* $= 0.043$, *pseudo-f* $= 2.820$), whereby GSI appeared to be positively correlated with increasing $p\mathrm{CO_2}$ at intermediate levels (Figure 3.3c). Pairwise tests of $p\mathrm{CO_2}$ showed that differences between 350 and 490 μatm (*p(perm)* $= 0.181$, $t = 1.341$), 350 and

900 μatm (*p(perm)* = 0.287, t = 1.085), 350 and 3250 μatm (*p(perm)* = 0.350, t = 1.110), and 900 and 3250 μatm (*p(perm)* = 0.879, t = 0.159) were not significant, while differences between 490 and 900 μatm (*p(perm)* = 0.010, t = 2.673), 490 and 3250 μatm (*p(perm)* = 0.016, t = 2.492) were significant. Because the GSI and energy content were unknown at the initiation of the experiment, these results only document the response of sea urchins assuming that they were similarly gravid at the time of collection, rendering interpretation of this response as somewhat speculative.

Energy content

Energy content (calories per gram) of all soft tissues varied across treatments and showed no statistically significant relationship with temperature (*p(perm)* = 0.396, *pseudo-f*0.947), $p\mathrm{CO}_2$ (*p(perm)* = 0.096, *pseudo-f* = 2.132), or their interaction (*p(perm)* = 0.419, *pseudo-f* = 1.009). Further investigation of the relationship between GSI and energy content, however, revealed a positive relationship between GSI and calories per gram (slope = 21.1 cal/g/GSI, $R^2 = 0.52$; Figure 3.5a), likely due to the higher calorie content in lipid-rich gonad tissue relative to somatic tissue.

DISCUSSION

Overall, the response of adult *S. polyacanthus* to ocean warming and acidification was variable among sea urchin response metrics and influenced more strongly by temperature than by $p\mathrm{CO}_2$. At near and far future temperature scenarios, warming waters are likely to cause greater variability, and more deleterious effects, in sea urchin physical condition (Figure 3.2). Survival may be reduced due to physiological stress and could be further reduced *in situ* owing to weaker calcified tissues that cannot provide the same defenses to predators or protection from the physical stress of major storms and/or fishing activities. Although survival and calcification may be negatively impacted by warmer conditions, gonad and energy content appeared to show more variable responses to increasing temperature and $p\mathrm{CO}_2$ conditions. Increases in gonad tissues may signify an attempt to maximize reproductive output, but those increases may also make the sea urchin more appealing to consumers, like seas otters, who will preferentially feed on more energy rich, gravid prey. Under near-future ocean warming and acidification scenarios, sea urchin demographics could change across the Aleutian Archipelago. These results suggest that ocean warming could influence sea urchin demographics by increasing the risk of mortality while simultaneously reducing adult growth and calcification. The effects on sea urchin demography could also be exacerbated by ocean warming and acidification compromising early life history success via possible carry-over impacts (Dupont *et al.* 2013). Sea urchins that can withstand increased temperatures may need to invest more energy in growth and maintenance at a cost to their offspring. *S. polyacanthus* may be able to acclimatize to warmer and more acidic conditions over longer time scales (as observed with *S. droebachiensis*; Dupont & Thorndyke 2013), but this 108-day experiment on *S. polyacanthus* suggests that global oceanic change will alter the physiology and, potentially, ecology of this dominant species.

The functional response of *S. polyacanthus* was similar to that of other species of sea urchins (with respect to calcification rate) and was best described with a quadratic function (Ries *et al.* 2009). The parabolic response suggests that under intermediate $p\mathrm{CO}_2$ levels, the calcification rate is likely to modestly increase, but will decrease at higher levels (Figure 3.4).

Thus, at intermediate levels of $p\mathrm{CO}_2$, but cooler temperatures, there could be potential for sea urchins to respond with positive calcification and perhaps increased growth rate. Given that calcification was the only response metric with a significant interaction between temperature and $p\mathrm{CO}_2$, it must be interpreted that near-term ocean warming in the region will exacerbate the negative effects of $p\mathrm{CO}_2$ on calcification rate, pushing it beyond intermediate levels, where a positive effect was observed (Figure 3.3b).

The shrinkage of sea urchin test diameters observed in our experiment likely occurred due to stressful physiological conditions. Test shrinkage is not uncommon in *in situ* studies of sea urchin growth (Narvaez *et al.* 2016). We did not observe the calcein markers on test plates and while it was unfortunate to not have marked bands to evaluate growth at a finer resolution; the absence of the mark supports observations of test shrinkage. Nevertheless, our findings consistently showed that increasing temperature, but not $p\mathrm{CO}_2$, has a large negative effect on *S. polyacanthus* growth. It is possible that if conditions warm as predicted, *S. polyacanthus* will exhibit slower growth and shift toward smaller-bodied phenotypes, as observed in *S. droebachiensis* (Vadas *et al.* 2002). Grazing rates, while dependent on the type of macroalgae being consumed (Suskiewicz & Johnson 2017), are increased at higher temperature and higher $p\mathrm{CO}_2$, as evidenced by the associated grazing study of *S. polyacanthus* on the crustose coralline alga, *Clathromorphum nereostratum* (Rasher *et al.* in review). The increased grazing rate could have allowed for the sea urchins to gain more calories and afforded them an ability to maintain their skeletal tissues, moreso than if they were starved completely (Byrne & Hernández 2020)

Despite not being statistically significant, the pattern we documented of increasing GSI with increasing $p\mathrm{CO}_2$, but not temperature, suggests that *S. polyacanthus* could maintain reproductive output even if growth and maintenance are compromised by near-term ocean warming. Furthermore, as pCO$_2$ increases, it appears to amplify gonad production within the sea urchin, possibly representing a strategy to maximize reproduction prior to making a trade-off for growth and maintenance (Sokolova *et al.* 2012). This finding suggests that near-future ocean acidification may result in an increase in the reproductive output and total energy density of sea urchins.

The Aleutian Archipelago is predicted to experience rapid ocean warming and acidification over the next several decades (Fabry *et al.* 2009). Our laboratory study suggests that a shift toward warmer conditions could influence *S. polyacanthus* population demographics by increasing mortality, decreasing growth, and skewing size distributions towards smaller size classes. Conversely, calcification rate and gonad production could increase. Indeed, work evaluating the physical drivers of recent sea urchin population dynamics in the Aleutian Archipelago found temperature to be an important predictor of sea urchin size and abundance through space and time (Chapter 2; Weitzman *et al.* in prep). Such changes in sea urchin survival, growth, and size distribution will likely affect community-level grazing rates on macroalgae, thus influencing ecosystem structure (Estes *et al.* 2010). Our study also suggests that sea urchins of the near-future could have more variable GSI and thus influencing the energy density available to consumers like sea otters (the keystone predator in the ecosystem). However, the ways in which sea urchin physiology could scale up to impact sea otter demographics in the future will depend on the degree to which sea urchin quality vs. quantity is affected by global oceanic change at the population level, and how those changes factor into sea otter foraging behavior and energetics (Tinker *et al.* 2008). Future research should focus on understanding how lower trophic level responses to global change will translate through the food web to upper trophic level consumers.

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FIGURES

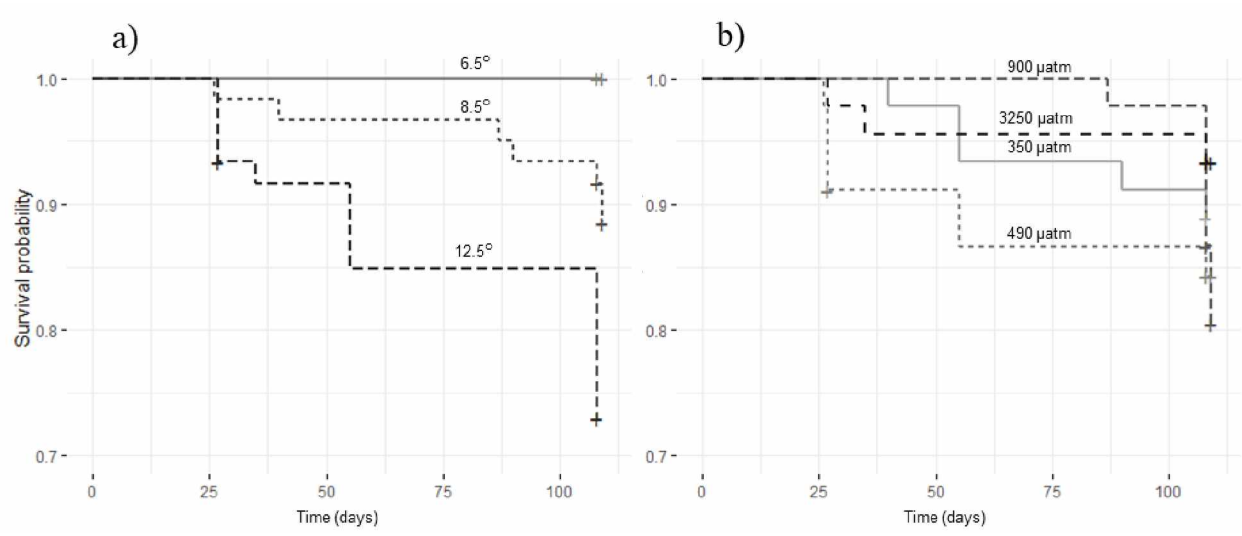


Figure 3.1. Probability of survival over time (days) by, a) temperature (6.5°, 8.5°, 12.5° C) and, b) $p\text{CO}_2$ (350, 490, 900, 3250 µatm) for the 108-day experiment on 180 sea urchins. Each step change represents the predicted change in survival based on documented mortality events over the course of study.

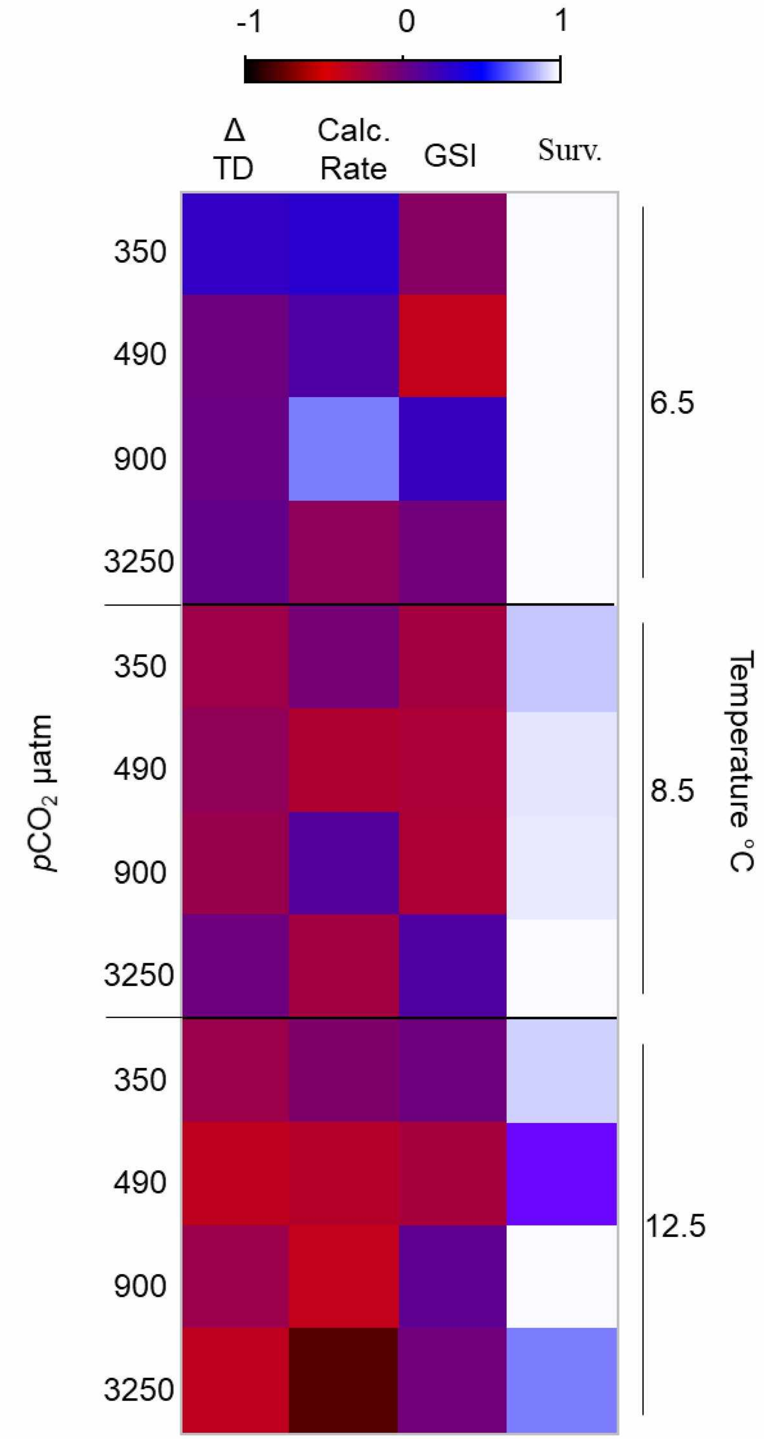


Figure 3.2. Heatmap of the proportional response for change in sea urchin test diameter (ΔT), net calcification rate (Calc. Rate), and dried gonad-somatic index (GSI) averaged by temperature and $p\mathrm{CO}_2$ treatment. Color scale denotes change from negative (dark red) to positive (light blue); neutral values are shaded purple. Survival (Surv.) shown as probability of survival from 0 (blue) to 1 (white).

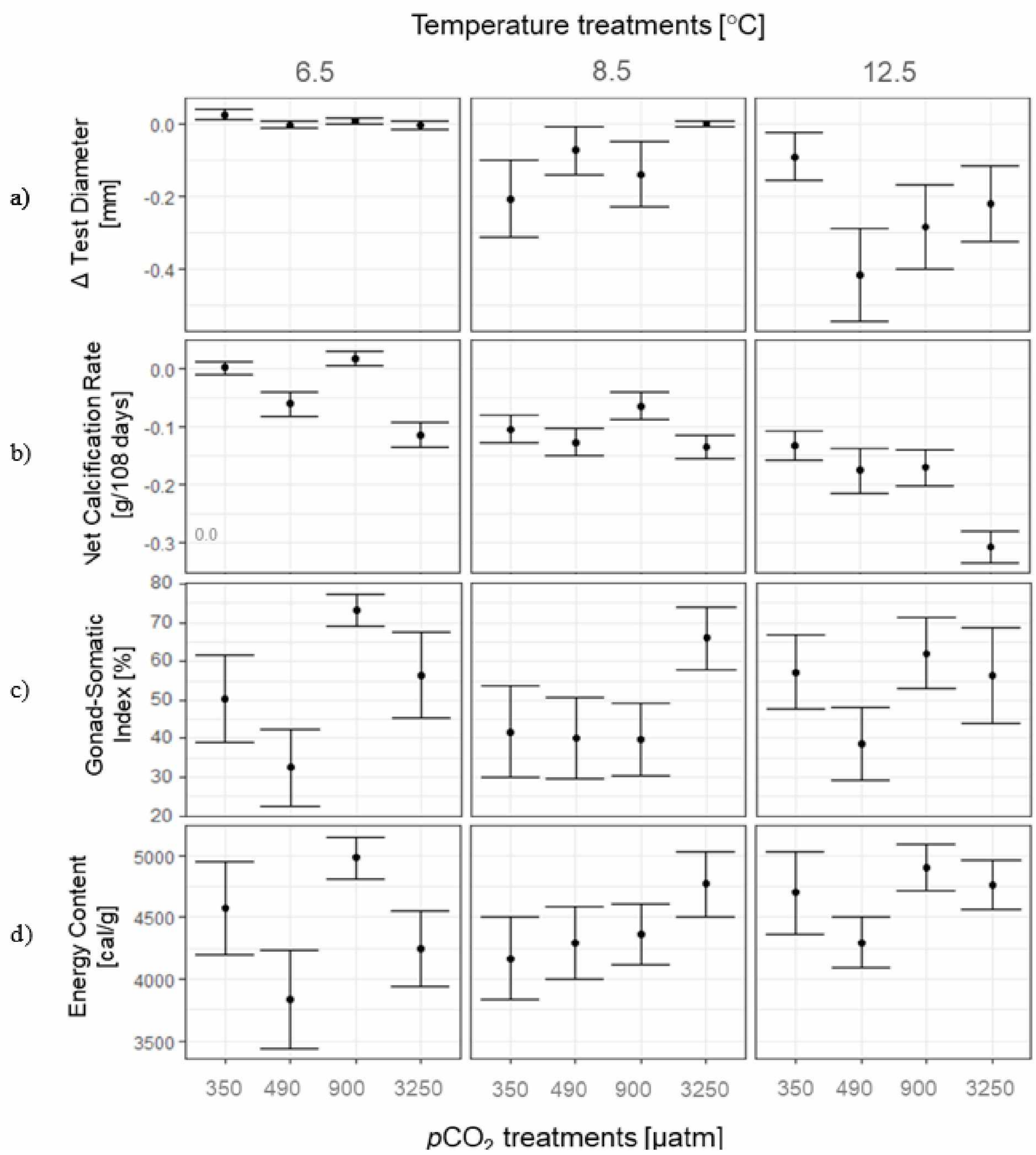


Figure 3.3. Sea urchin response metrics show by plots of mean±1SD for a) change in test diameter, b) net calcification rate, c) gonad-somatic index, and d) energy content per gram of tissue; for each experimental treatment of increasing seawater temperature and $p\mathrm{CO}_2$.

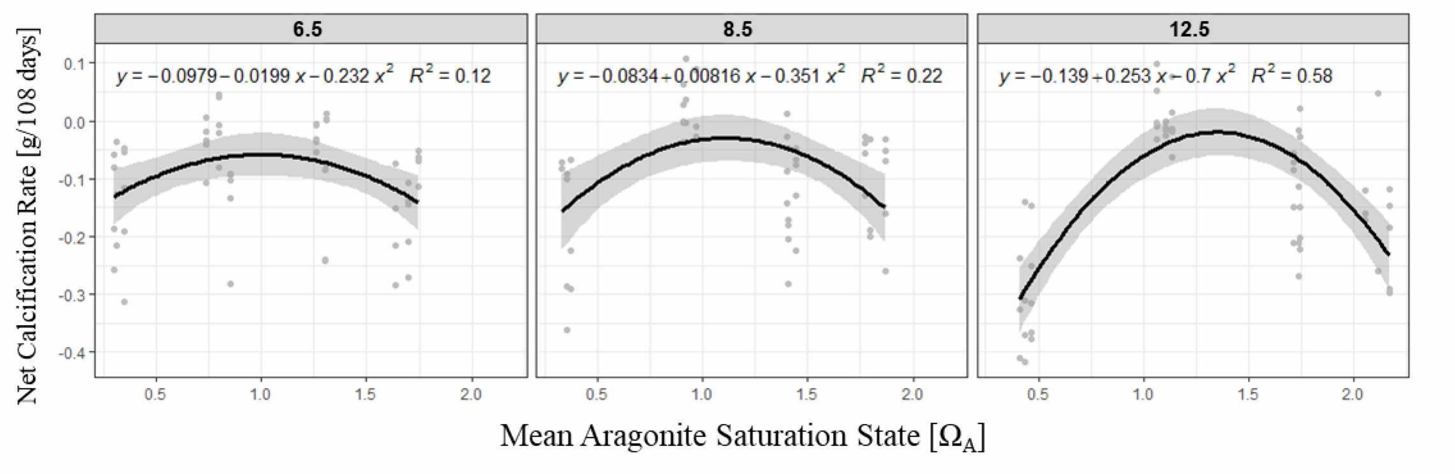


Figure 3.4. Functional response curves of net calcification rate by the mean aragonite saturation state over the course of the experiment with equations and R^2 for each temperature treatment. Black line is the fit for quadratic polynomial function and gray shaded region shows the 95% confidence interval.

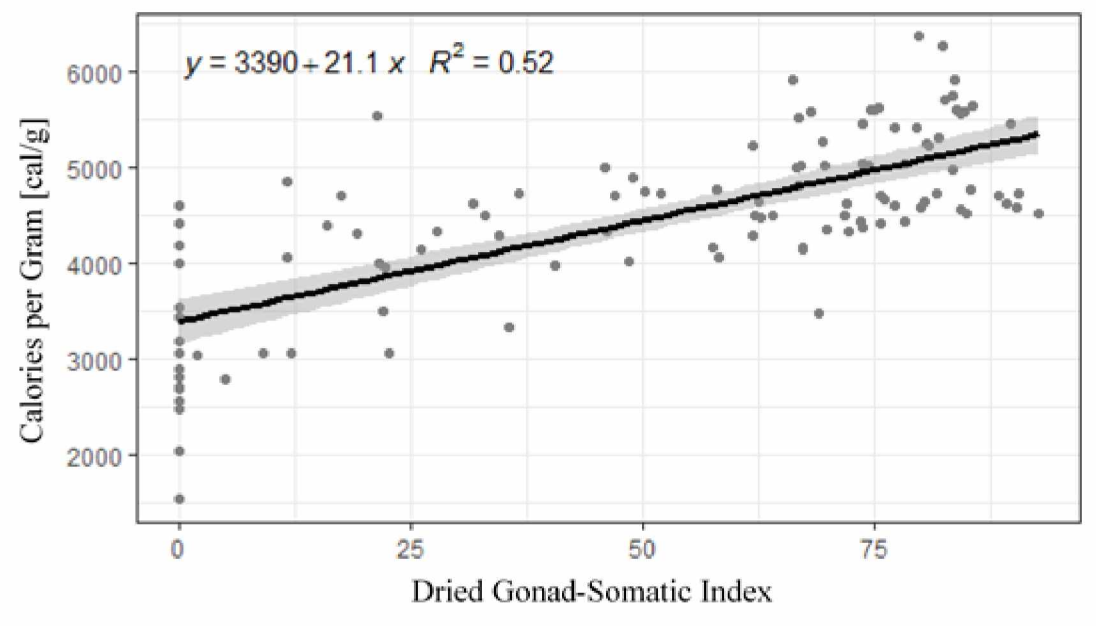
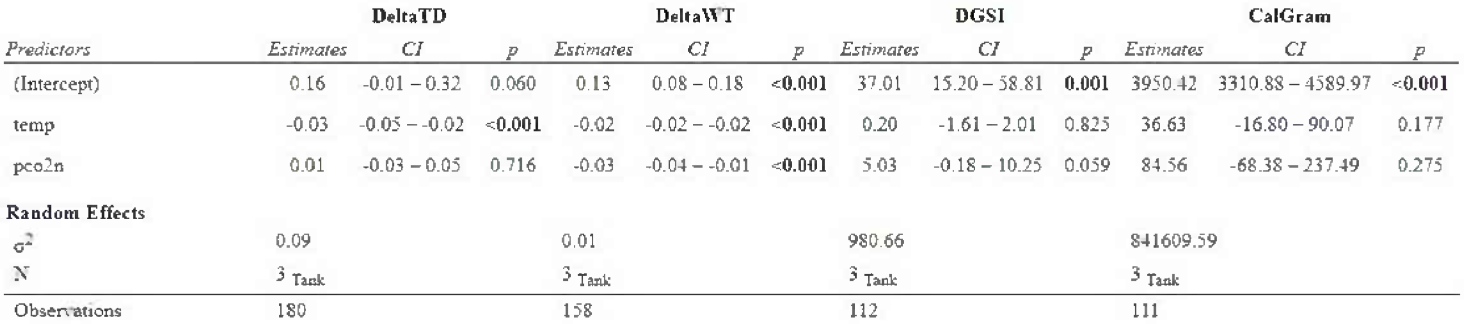


Figure 3.5. Fit of linear regression of energy content by the dried somatic index (GSI) for the calories per unit of mass of combined gonad and somatic tissue in *Strongylocentrotus polyacanthus*. Data points show the observed calories per gram for each individual sea urchin sample while black line and gray shading show linear slope and 95% confidence intervals.

Table 3.1. Estimates and confidence intervals (CI), with significance statistics (p, bold if significant) of fixed-effects: temperature and pCO_2, on each of the four response metrics: change in test diameter (DeltaTD), net calcification rate (DeltaWT), gonad-somatic index (DGSI), and energy content (CalGram). Tank was included as a random effect in the model (σ^2), in which there were 3 per treatment (N), with each tank containing 5 sea urchins, and the number of surviving urchins at the end of the experiment (Observations).



	DeltaTD			**DeltaWT**			**DGSI**			**CalGram**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	0.16	-0.01 – 0.32	0.060	0.13	0.08 – 0.18	**<0.001**	37.01	15.20 – 58.81	**0.001**	3950.42	3310.88 – 4589.97	**<0.001**
temp	-0.03	-0.05 – -0.02	**<0.001**	-0.02	-0.02 – -0.02	**<0.001**	0.20	-1.61 – 2.01	0.825	36.63	-16.80 – 90.07	0.177
pco2n	0.01	-0.03 – 0.05	0.716	-0.03	-0.04 – -0.01	**<0.001**	5.03	-0.18 – 10.25	0.059	84.56	-68.38 – 237.49	0.275
Random Effects												
σ^2	0.09			0.01			980.66			841609.59		
N	3_{Tank}			3_{Tank}			3_{Tank}			3_{Tank}		
Observations	180			158			112			111		

Table S3.1. From Rasher *et al.* in review. Average measured and calculated seawater parameters from the laboratory experiment. Measured: salinity (Sal), temperature (T), pH on NBS scale (pH$_{NBS}$), total alkalinity (TA), and dissolved inorganic carbon (DIC). Calculated: pCO$_2$ of gas in equilibrium with seawater (pCO$_{2\,(gas\text{-}e)}$), pH on seawater scale (pH$_{SW}$), carbonate ion concentration ([CO$_3^{2-}$]), bicarbonate ion concentration ([HCO$_3^-$]), dissolved CO$_2$ ([CO$_2$]$_{(SW)}$), and aragonite saturation state (Ω_A). SD = standard deviation; N = number of observations.

TREATMENT		335 µatm/ 6.37ºC	490 µatm/ 6.42ºC	929 µatm/ 6.52ºC	3250 µatm/ 6.21ºC	350 µatm/ 8.90ºC	480 µatm/ 8.57ºC	829 µatm/ 8.74ºC	2962 µatm/ 8.86ºC	371 µatm/ 12.48ºC	499 µatm/ 12.39ºC	901 µatm/ 12.39ºC	3475 µatm/ 12.30ºC
MEASURED PARAMETERS													
Sal	(psu)	31.942	31.963	31.943	31.941	31.892	31.878	31.883	31.878	31.924	31.929	31.918	31.940
	SD	0.17	0.18	0.18	0.17	0.14	0.13	0.13	0.12	0.14	0.13	0.12	0.14
	Range	31.53 - 32.29	31.56 - 32.29	31.46 - 32.26	31.56 - 32.29	31.59 - 32.19	31.56 - 32.16	31.56 - 32.16	31.56 - 32.16	31.66 - 32.26	31.69 - 32.26	31.69 - 32.23	31.53 - 32.26
	n	123	123	123	123	123	123	123	123	123	123	123	123
Temp	(ºC)	6.37	6.42	6.52	6.21	8.90	8.57	8.74	8.86	12.48	12.43	12.39	12.30
	SD	0.78	0.84	0.82	0.83	0.41	0.42	0.48	0.42	0.38	0.31	0.37	0.59
	Range	3.90 - 8.60	4.70 - 7.90	4.50 - 8.60	3.20 - 7.60	8.20 - 10.30	7.80 - 10.10	7.80 - 9.80	7.90 - 9.90	11.80 - 13.60	12.00 - 13.00	11.50 - 13.30	11.20 - 14.00
	n	123	123	123	123	123	123	123	123	123	123	123	123
pH$_{NBS}$		7.99	7.85	7.62	7.05	8.03	7.88	7.68	7.14	8.11	8.00	7.74	7.14
	SD	0.06	0.05	0.06	0.07	0.06	0.05	0.06	0.05	0.29	0.26	0.21	0.07
	Range	7.62 - 8.11	7.73 - 8.06	7.43 - 7.76	6.87 - 7.18	7.90 - 8.13	7.64 - 7.98	7.52 - 7.80	7.02 - 7.27	7.90 - 9.92	7.86 - 9.59	7.58 - 8.98	6.97 - 7.34
	n	123	123	123	123	123	123	123	123	123	123	123	123
Alk	(µM)	2066	2067	2099	2339	2052	2077	2108	2329	2098	2140	2177	2544
	SD	48	47	37	62	41	32	41	47	33	21	21	222
	Range	1985 - 2124	1935 - 2145	2006 - 2164	2250 - 2451	1942 - 2107	2013 - 2127	2036 - 2184	2255 - 2440	2031 - 2142	2095 - 2188	2142 - 2224	2243 - 3103
	n	32	32	32	33	32	33	31	29	33	33	33	31
DIC	(µM)	1913	1965	2066	2466	1884	1959	2053	2434	1911	1995	2109	2660
	SD	42	38	29	93	61	31	36	51	47	21	26	226
	Range	1832 - 1975	1866 - 2035	2021 - 2115	2254 - 2612	1735 - 1940	1880 - 2001	2004 - 2123	2349 - 2558	1805 - 1985	1963 - 2042	2072 - 2154	2328 - 3198
	n	32	33	33	31	32	33	32	30	33	33	31	28
CALCULATED PARAMETERS													
pCO$_{2\,(gas\text{-}e)}$	(ppm-v)	335	490	929	3250	350	480	829	2962	371	499	901	3475
	SD	66	110	303	807	65	82	109	392	66	66	126	671
	Range	230 - 532	359 - 941	570 - 2309	1062 - 4632	228 - 467	335 - 775	647 - 1051	2346 - 3744	272 - 584	431 - 806	722 - 1186	1635 - 4528
	n	32	32	32	30	31	33	31	28	33	33	31	28
pH$_{sw}$		8.08	7.94	7.71	7.19	8.08	7.95	7.73	7.25	8.06	7.95	7.72	7.23
	SD	0.08	0.06	0.09	0.09	0.08	0.06	0.06	0.06	0.06	0.05	0.06	0.09
	Range	7.88 - 8.22	7.76 - 8.06	7.46 - 7.94	7.05 - 7.45	7.95 - 8.21	7.75 - 8.09	7.62 - 7.83	7.14 - 7.36	7.86 - 8.15	7.75 - 8.00	7.61 - 7.81	7.09 - 7.42
	n	31	31	32	28	31	33	31	29	33	33	31	27
[CO$_3^{2-}$]	(µM)	110	85	53	19	119	93	61	23	137	111	72	29
	SD	21	12	9	5	14	12	8	3	14	10	9	9
	Range	55 - 148	54 - 110	27 - 69	14 - 35	91 - 145	61 - 125	40 - 75	18 - 29	108 - 159	72 - 127	56 - 86	19 - 57
	n	33	31	31	29	31	33	31	29	32	33	31	28
[HCO$_3^-$]	(µM)	1785	1855	1969	2285	1752	1843	1954	2273	1760	1863	2000	2478
	SD	46	36	27	68	69	33	35	46	58	25	27	214
	Range	1702 - 1850	1770 - 1942	1924 - 2017	2139 - 2407	1580 - 1825	1763 - 1904	1903 - 2020	2203 - 2383	1635 - 1848	1836 - 1917	1960 - 2049	2182 - 3010
	n	31	31	32	28	31	33	31	29	33	33	31	27
[CO$_2$]$_{(SW)}$	(µM)	17	24	44	167	16	22	39	139	15	20	37	147
	SD	4	4	9	36	3	4	6	18	2	2	5	24
	Range	12 - 28	18 - 39	30 - 79	80 - 229	11 - 22	16 - 36	30 - 55	109 - 175	11 - 19	17 - 24	30 - 48	99 - 186
	n	32	31	31	29	31	33	31	29	32	32	31	27
Ω_A		1.7	1.3	0.8	0.3	1.8	1.4	0.9	0.4	2.1	1.7	1.1	0.4
	SD	0.3	0.2	0.1	0.1	0.2	0.2	0.1	0.1	0.2	0.1	0.1	0.1
	Range	1.0 - 2.3	0.8 - 1.7	0.4 - 1.1	0.2 - 0.9	1.4 - 2.2	0.9 - 1.9	0.6 - 1.1	0.3 - 0.5	1.7 - 2.4	1.5 - 2.0	0.9 - 1.3	0.3 - 0.6
	n	32	31	31	31	31	32	31	30	32	32	31	28

CHAPTER 4: BIOLOGICAL CORRELATES OF SEA URCHIN RECRUITMENT IN KELP FOREST AND URCHIN BARREN HABITATS[3]

ABSTRACT

Shifts between the alternate stable states of sea urchin barren grounds and kelp forests are well described and correspond to sea urchin density. In the north Pacific, green sea urchins (*Strongylocentrotus polyacanthus*) are the dominant herbivores that graze kelp forests. Sea urchin recruitment is an important driver of sea urchin demography that influences density of sea urchins and their subsequent grazing pressure, particularly in the absence of top-down control from a keystone predator, such as the sea otter (*Enhydra lutris*). To understand how the biological community may influence patterns of sea urchin recruitment, we compared sea urchin recruit (size ≤ 20 mm) densities with biomass of other benthic organisms in both barren ground and kelp forest habitats at a small spatial scale (0.25 m^2), at nine islands across the Aleutian Archipelago. Densities of sea urchin recruits were inversely related with densities of large conspecifics. Patterns of biological community structure between the two habitats did not explain patterns of sea urchin recruits; however, the same ten specific taxa were correlated with sea urchin recruits in each habitat. The taxa that showed strong positive correlations included *Codium, Constantinea, Schizymenia,* and Hydrozoans, while strong negative correlations were observed with *Pachyarthron* and *Pugettia*. Weak positive correlations were also observed with *Alcyonidium* and Ascidaceans in both habitats; while, weak and variable relationships were detected with *Polysiphonia* and *Corallina* between habitats. The observed species-specific

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relationships may be due to small sea urchin displacement by larger conspecifics, larval responses to settlement cues, post-settlement survival via biogenic refugia, or potentially by predation. Our findings suggest that certain macroalgal and invertebrate taxa can have strong positive or negative effects on sea urchin recruitment, regardless of habitat. These potential species-specific interactions would likely be preserved in the presence or absence of the keystone predator, influencing patterns of recruitment and the propensity for a given site to flip from kelp forest to sea urchin barren.

INTRODUCTION

Sea urchins are often the key herbivore causing the transition between the alternate stable states of kelp forest (high fleshy macroalgal cover and low urchin density) to barren ground (low fleshy macroalgal cover and high urchin density) habitats on temperate rocky reefs (Estes & Duggins 1995, Gagnon *et al.* 2004, Filbee-Dexter & Scheibling 2014). Habitat shifts towards sea urchin barrens have been reported across temperate latitudes, globally (Johnson *et al.* 2011, Ling *et al.* 2015, Krumhansl *et al.* 2016). Sea urchins can have important effects on marine habitats, as they heavily graze fleshy macroalgae and cause bioerosion of biogenic reef habitats (Steneck *et al.* 2017, Rasher *et al.* in review). They also provide a key food source for upper trophic levels, such as the sea otter (*Enhydra lutris*) in the north Pacific (Watt *et al.* 2000, Larson *et al.* 2015). Urchin demographics influence the role that urchins play in an ecosystem as an herbivore or as prey. Demographic factors, such as size, fecundity, survival, and recruitment, can all affect population density, grazing rates, and movement (Himmelman *et al.* 1986, Dumont *et al.* 2006). The effects of urchins on habitat and ecosystem structure and their role in food webs are well known, yet, the drivers of sea urchin demography are complex. Sea urchin demographics may be influenced by top-down processes (*e.g.*, predation or disease) and by environmental gradients (Ebert 2010, Ling *et al.* 2015) and can vary greatly across regions due to environmental forcing on ontogenetic processes (Estes & Duggins 1995). Recruitment, which is a function of both larval settlement and post-settlement survival, is a key demographic process in sea urchin populations that is often under strong environmental control. Biological drivers can have a strong influence on sea urchin recruitment through multiple pathways that influence sea urchin post-settlement distribution, growth, and survival. For example, the whipping action of kelps, particularly *Desmarestia viridis* and *Eualaria fistulosa*, can physically prevent sea urchins from overgrazing by keeping the surrounding area free from large sea urchins (Konar *et al.* 2014).

Top-down control of sea urchin abundance in the Aleutian Archipelago of Alaska has been lost since the precipitous sea otter declines in the 1990s, which were apparently caused by killer whale (*Orcinus orca*) predation (Estes *et al.* 1998). The factors that influence sea urchin recruitment in the absence of top-down control by sea otters can help explain how benthic ecosystems function in the absence of keystone predators. The presence of both barren ground and kelp forest habitats across the Aleutian Archipelago offers an ideal opportunity to investigate how biological features influence sea urchin recruitment within these two habitats. Kelp forests are more biodiverse and productive than barren grounds, with a large amount of food available to sea urchins that can survive. The differences in community structure between kelp forest and barren ground habitats may be associated with differences in sea urchin recruitment (Himmelman 1986) due to differences in pre- and post-settlement processes that regulate growth and survival of newly recruited sea urchins (Rowley 1989).

Here, we ask how the surrounding biological community influences patterns of sea urchin recruitment, and whether taxa that are correlated with recruit density differ between kelp forest and barren ground habitats. We hypothesized that given the different community structures between barren grounds (low fleshy macroalgal cover and high urchin density) and kelp forests (high fleshy macroalgal cover and low urchin density), there are different biological correlates of sea urchin recruitment. However, if there were similar species associated with sea urchin recruitment in both habitats, this would suggest overarching species interactions that are key drivers to sea urchin recruitment, regardless of habitat state.

METHODS

At nine islands in the Aleutian Archipelago, from Chuginadak in the east to Attu in the west (Figure 4.1), a total of 360 benthic community quadrats were examined from kelp forest and barren ground habitats in August 2016 and 2017. At each island, two representative sites were identified within each habitat type; based on the presence or absence of consistently dense subcanopy kelps across the entire area to be sampled (see Metzger *et al.* 2019 for details). At each site, divers using scuba scraped all mobile and sessile epibiota from each of ten haphazardly placed 0.25-m^2 quadrats into a fine mesh pillow case. All invertebrates and macroalgae were returned to the shipboard laboratory for species identification and quantification of total wet biomass (grams). All organisms were visually identified to the finest taxonomic resolution possible with the aid of light microscopes and species keys. Test diameters of all sea urchins were measured to the nearest millimeter using calipers to determine size frequencies within each quadrat.

Samples were the quadrat level data (n = 180 per habitat) from each of ten 0.25-m^2 quadrats per site nested within habitat (2 levels: Barren or Kelp) and nested in Island (9 levels: Attu, Semichis: Nizki/Alaid, Kiska, Amchitka, Tanaga, Adak, Atka, Yunaska, and Chuginadak). All sea urchin and community structure data used for analyses were obtained from published datasets for epibenthic community abundance (Edwards & Konar 2018a) and biomass (Edwards & Konar 2018b) available via the Biological & Chemical Oceanography Data Management Office (web portal: www.bco-dmo.org). Data were analyzed using PRIMER v7 and PERMANOVA+ (PRIMER-e ltd, Quest Research Limited; Anderson *et al.* 2008, Clarke *et al.* 2014, Clarke & Gorley 2015).

Individual sea urchins were assigned a size class (Recruit: ≤ 20 mm, Small: 21-35 mm, Medium: 36-54, or Large: ≥ 55 mm; Estes & Duggins 1995, Brady & Scheibling 2006, Scheibling & Hatcher 2013) and standardized to a common proportional scale among all samples. Each size bin was treated as an ordered variable and a Bray-Curtis similarity matrix (with 0.01 dummy variable added) was constructed to compare size distributions between habitats and among islands. From the same quadrats, biomass of the surrounding biological community (fleshy and upright coralline macroalgae and invertebrates) was fourth-root transformed, to down-weight dominant taxa and allow for consideration of the full biological community. The biomass data were then constructed into a Bray-Curtis (with 0.01 dummy variable added) similarity matrix to test for differences in the biomass of the surrounding biological community. Community biomass data were visualized using non-metric multidimensional scaling (nMDS) to visualize similarity in sea urchin recruitment among all quadrats across all islands, by habitat. Bubble plots were imposed on points in nMDS space to depict relative differences in sea urchin recruit densities, and vectors were overlain showing the correlated community taxa driving separation among points by their Spearman-rank correlation.

Differences in sea urchin recruit densities and community biomass, between habitats, were separately tested by a 2-way crossed permutational ANOVA (PERMANOVA, Anderson *et al.* 2008) with habitat treated as a fixed factor and island treated as a random factor. A similarity percentage analysis (SIMPER) was used to identify the taxa most important in explaining the dissimilarity in community structure between habitats, pooled across islands. The biological community was visualized in composition and relative biomass, by habitat and across islands using a shade plot, with taxa arranged by their index of association to one another for the top 50 taxa that contribute to observed patterns between habitats. A distance-based linear regression (DistLM, McArdle & Anderson 2001) analysis was used to statistically determine the taxa that were significantly correlated with sea urchin recruit densities; using the fourth-root transformed biomass by quadrat as the predictor variable. To identify taxa that were significantly correlated (if p-value < 0.05) with sea urchin recruit density in both habitats, DistLM and nMDS were constructed for barren ground and remnant kelp forest habitats independently, to derive statistical scores and visualize correlations among all samples within each habitat.

RESULTS

Sea urchin size-frequency distributions were variable between habitats and among islands (Figure 4.2). Standardized sea urchin size frequencies did not significantly differ between habitats ($p(\text{perm}) = 0.06$, pseudo-$F = 2.4$); however, the interaction between habitat and island was significant ($p(\text{perm}) = 0.001$, pseudo-$F = 8.0$) suggesting that the random island effects, may have influenced the differences in size distributions among islands, but further interpretation of the random factor is not appropriate. Generally, and as expected, sea urchins occurred at higher densities in the barren ground habitat than in the kelp forest habitat. Sea urchins also varied in density among islands. The mode of the size distribution occurred at the recruit size class at high density islands (Kiska, Amchitka, and Tanaga), while the mode of the size distribution at moderate density islands (Adak, Atka, Yunaska, and Chuginadak) occurred at the small or medium size class highest densities. Attu and the Semichi islands had the lowest sea urchin densities, and the mode of the size distribution at these islands occurred at the largest size class. Densities of large and small sea urchins were significantly different among islands. In quadrats with higher densities of large urchins, recruit densities were significantly lower ($p(perm) < 0.05$; Figure 4.3). While some islands had significantly higher densities of recruits, recruits were observed in both habitats at all islands.

Community structure as measured by biomass significantly differed between barren ground and kelp forest habitats ($p(perm) = 0.003$, pseudo-$F = 11.5$) at all islands ($p(perm) < 0.001$), despite a significant interaction term between habitat and island ($p(perm) = 0.001$, pseudo-$F = 9.4$). In total, 170 taxa were identified in the benthic biomass scrapes; 116 were observed in barren ground and 148 were observed in kelp forest habitats. Among all taxa, 27 explained 70% of the observed dissimilarity between barren ground and kelp forest habitats (Table 4.1). Taxa that contributed at least 5%, individually, to dissimilarity between habitats were the kelps, *Thalassiophyllum* (7.15%), *Eualaria* (6.34%) and *Saccharina* (4.66%); and sea urchins, *Strongylocentrotus* (4.62%). Most taxa driving the dissimilarity between habitats, occurred in greater biomass in kelp forests, except for: *Strongylocentrotus*, the green alga

Codium, the upright coralline alga *Pachyarthron*, the rock jingle *Pododesmus*, and the limpet *Lottia*, which occurred in greater biomass in barren grounds (Figure 4.4; Table 4.1).

Recruit density across all quadrats was correlated with specific invertebrate and macroalgal taxa in both barren ground and kelp forest habitats (Figure 4.5). While overall benthic community structure differed between habitats and sea urchin recruits were correlated with slightly different taxa between habitats, ten taxa were significantly correlated with recruit density in both habitats ($p < 0.05$, Table 4.2). Of these ten taxa, the geniculate coralline alga, *Pachyarthron* and the crab, *Pugettia*, showed strong negative correlations with sea urchin recruits, while the green alga *Codium*, the fleshy red algae, *Constantinea* and *Schizymenia*, and hydroids exhibited strong positive correlations (Figure 4.5). While significantly correlated in both habitats, the bryozoans, *Alcyonidium*, the tunicate class, Ascidiacea, the filamentous red alga, *Polysiphonia* and geniculate coralline alga, *Corallina*, all showed weaker correlations with sea urchin recruits than the aforementioned taxa. *Alcyonidium* and Ascidiacea generally were positively correlated with sea urchin recruits. *Polysiphonia* and *Corallina* exhibited mixed correlations with sea urchin recruits, dependent on habitat: in barren grounds, there was a negative correlation with *Polysiphonia* and a neutral relationship with *Corallina*, while in kelp forests, there was a weak positive correlation with *Polysiphonia* and a negative correlation with *Corallina* (Figure 4.5).

DISCUSSION

Variability of sea urchin recruitment over space and time is an important determinant of demographic structure and population dynamics in sea urchins. Our results suggest that specific taxa can play an important role in shaping patterns of sea urchin recruitment, through potentially positive or negative interactions with sea urchin recruits that are likely more pronounced in the absence of the keystone predator in the system, sea otters. By examining correlations between other benthic taxa and density of sea urchin recruits at the quadrat level in two alternate stable state habitats, barren grounds and kelp forests, our findings pinpoint which taxa may be important biological drivers of sea urchin recruitment. We rejected our initial hypothesis that the taxa driving patterns of sea urchin recruits would differ between barren ground and kelp forest habitats; because although some of the correlated taxa differed, the most strongly correlated taxa with sea urchin recruits were similar in both habitats suggesting species-specific interactions that were not habitat-specific. Also, despite differences in sea urchin abundance between habitats, size distributions did not significantly differ between habitats; however this pattern varied among islands and suggested that local processes, such as physical differences or other species not accounted for in this study (*e.g.*, fishes or large motile invertebrates), likely shaped patterns of growth and survival among samples.

Densities of sea urchin recruits were different between habitats and among islands; however, where they occurred, sea urchin recruits were positively associated with the encrusting green alga, *Codium*, the red algae, *Constantinea* and *Schizymenia*, and Hydrozoa. In contrast, sea urchin recruits were negatively associated with the geniculate coralline alga, *Pachyarthron*, and the decorator crab, *Pugettia*. Sea urchin recruit densities also were inversely correlated with large sea urchins (Figure 4.3). An important caveat to these findings is that the measured associations between sea urchin recruits and specific taxa were correlative, not causal, and further research is needed to understand the mechanistic relationships. However, the consistent correlations between specific community taxa and sea urchin recruits suggest important common mechanisms may be underlying these species relationships, and we can speculate as to these relationships with reasonably informed expectations in some cases.

Correlations with macroalgae

The encrusting green alga, *Codium*, occurred in dense patches in both kelp forests and barren grounds. Despite the potential for being overgrazed, *Codium* is one of the few macroalgae that persists and thrives in barren grounds. The association between sea urchin recruits and *Codium* could be indicative of several possible mechanisms. First, *Codium* could be a food source for sea urchins, as they have been documented to consume it; however, *Codium* is not a particularly nutritious resource for sea urchins (Trowbridge 2006, Suskiewicz & Johnson 2017). Alternatively, sea urchin recruits could instead be feeding on the biofilm that occurs on the surface of the *Codium* and not relying on the alga for nutrition (Zhang *et al.* 2014). *Codium* can also produce dimethylsulfoniopropionate (DMSP, Lyons *et al.* 2010) as a chemical defense strategy to deter grazing; however, DMSP can also act as a chemical attractant to sea urchin larvae (Van Alstyne *et al.* 2001, Van Alstyne & Puglisi 2007). It is unknown if the chemical compounds within *Codium,* such as DMSP, act as an attractant or deterrent to sea urchins, or if it perhaps changes dependent on sea urchin life stage. Finally, it is likely that sea urchin recruits use the folds and physical structure of *Codium* beds as a structural refuge from predators and larger conspecifics (Figure 4.6b).

The red alga, *Constantinea* is a perennial with an erect thallus and a branched cylindrical stipe emerging from a small discoid holdfast that grows up to a height of approximately 15 cm. The circular, cup-shaped blades grow through the winter each year to form an understory canopy over the benthos (Figure 4.6a). *Constantinea rosa-marina* was the only *Constantinea* species observed in this study, observed in both kelp forests and barren grounds. While it is unknown if this alga produces chemical defenses to deter grazing, the robust structure of the stipe may be a structural defense against grazing by sea urchins. *Constantinea* individuals are long-lived perennials, often surviving longer than 15 years (Klochkova and Pisareva 2009), and play an important ecological role by providing persistent sub-canopy habitat over the benthos, even when under intensive grazing pressure (Foreman 1977). The relationship between *Constantinea* and sea urchin recruits remains unclear, as it is not understood if the sea urchins are associated with the plant as a food source or as a structural refuge from predation or displacement by larger conspecifics.

Another red alga that was positively correlated with sea urchin recruits is *Schizymenia*, although once again the mechanistic basis of this association is not clear. *Schizymenia* is an ephemeral alga and does not feature any robust structure that could resist grazing from or harbor sea urchin recruits. The large, thin, leafy blades often cover patches of the benthos and perhaps sea urchin recruits can find refuge beneath the dense cover (Figure 4.6d) or use *Schizymenia* as a food source. However, some *Schizymenia* species produce compounds that have been extracted for use in antiretroviral therapy treatments in the biomedical field (Nakashima *et al.* 1987, Anand *et al.* 2016). It is unknown if these same compounds influence the palatability of *Schizymenia* to sea urchins.

The relationship between urchin recruits and the filamentous red alga *Polysiphonia* was paradoxically negative in barren grounds and positive in kelp forests. *Polysiphonia* can occur in large, bushy tufts that sweep across the benthos, and which can thus act as a physical deterrent to organisms that would be whipped away in the surge. The complex structure provided by the fine branching also could offer refuge for sea urchin recruits that seek shelter within the body of the plant. *Polysiphonia* also induces metamorphosis in larval sea urchins and act as a refuge for post-larval juveniles (Pearce & Scheibling 1991). In the kelp forest habitats, *Polysiphonia* may play this role for sea urchin recruits; whereas, in the barren grounds this function is reduced under higher grazing intensity. More research is needed on the relationship between sea urchin recruits and *Polysiphonia* in both habitats.

Pachyarthron and *Corallina* are branching geniculate coralline algae that create complex turf habitat over the benthos (Figure 4.6f). The negative relationships between these taxa and sea urchin recruits may be due to the physical structure of these upright corallines, which makes them more resistant to grazing. Higher biomass of these species was observed in barren grounds, where grazing intensity is likely much greater. The thick, calcified cell structure and robust branches may make these algae inedible for sea urchins. Their structure likely does not offer a refuge for sea urchin recruits as the rigidity may damage small sea urchins seeking shelter in the typical high surge environment found in the shallow water of the Aleutians. *Pachyarthron* was positively correlated with presence of large sea urchins, a trend that was likely the result of sea urchin grazing in the local area removing fleshy macroalgae and reducing competition for space among macroalgae. To the extent that the geniculate corallines are more likely to occur, where large sea urchins occur, it is possible that the lack of sea urchin recruits may not be due to the coralline directly, but rather to the presence of larger conspecifics.

Correlations with invertebrates

There were both positive and negative correlations between sea urchin recruits and several phyla of benthic invertebrates, potentially reflecting predator-prey interactions. The strong positive correlation between sea urchin recruits and Hydrozoan invertebrates in both habitats was likely indicative of sea urchins using hydroids as a refuge from other predators in the system, *e.g.*, larger conspecifics, sea stars, or other macroinvertebrates (Figure 4.6c). The hydroids observed in this study were erect with alternate branching, often occurring as a benthic canopy layer approximately 5 cm tall. Sea urchin recruits were frequently observed among the hydroids, potentially using the stinging nematocysts as a defensive refugia. Weak positive relationships between sea urchin recruits and the upright, fleshy bryozoan, *Alcyonidium*, and multiple genera of tunicates, Ascidiacea, could be due to both the biogenic structure offered by these taxa and their potential provisioning of a food source. Sea urchin recruits may be seeking refuge from other predators in the complex structure and also could be feeding on the biofilms or organisms themselves (Zhang *et al.* 2014).

Crabs are known to prey on small sea urchins, and in some cases can regulate their abundance and ecological effectiveness as a grazer (Steneck *et al.* 2013, Fagerli *et al.* 2014, Feehan *et al.* 2014). Our finding that sea urchin recruits showed strong negative correlations with *Pugettia* crabs fits with observations from other systems with *S. droebachiensis* in the Gulf of Maine and Norway (Steneck *et al.* 2013, Fagerli *et al.* 2014), and presents a potentially alternative pathway to demographic regulation of sea urchins in the absence of their keystone predator, the sea otter. However, while some *Pugettia* were observed and were negatively correlated with urchin recruits in barren grounds, they are probably not sufficiently abundant to control sea urchin demographics in such an urchin dominated habitat, although they could potentially alter grazing behavior to some extent (Hagen *et al.* 2002). *Pugettia* could have a much greater effect on sea urchin recruits in kelp forests, where sea urchins occur in lower densities, the crabs in higher densities, and where the crabs are able to prey on small, newly settled individuals (Steneck *et al.* 2013). Such regulation of small sea urchins by mesopredators can be critical in controlling demographics, even in the presence of sea otters, as evidenced by increases in urchins following loss of *Pycnopodia* due to the recent sea-star wasting epidemic in the North Pacific (Burt *et al.* 2018). We did observe *Pycnopodia* and many other sea stars during this study; however, they were often deeper than our sampling depth and did not generally occur in our surveys, and thus we were unable to detect any significant correlation with sea urchin recruits.

Sea urchin biomass was not significantly correlated to sea urchin recruits in this study; however, density of sea urchin recruits was inversely correlated with density of large sea urchins. There is evidence that large sea urchins will displace smaller conspecifics in pursuit of food (Narvaez-Diaz 2018) – and even cannibalize small sea urchins (LeGault & Hunt 2016). The dearth of sea urchin recruits at some islands, such as Attu and the Semichi islands, may be due to the preponderance of large sea urchins. Large sea urchins are quite mobile and will cover meters of the sea floor per day in search of food, while small urchins may opt for a more sedentary, cryptic lifestyle (Dumont *et al.* 2004). These ontogenetic shifts in behavior lead to differences in growth, where small sea urchins express slower growth due to fewer opportunities to feed on high quality food (Himmelman 1986).

In the central and western Aleutians, sea urchin recruitment was influenced by patterns of sea urchin size structure, in combination with the associated biological community. The findings of this study indicate species-interactions controlling sea urchin recruitment that are manifested in both alternate stable states, barren grounds and kelp forests. To our knowledge, this is the first study to demonstrate that there may be specific taxa that drive sea urchin recruitment, regardless of habitat. While patterns of community structure are obviously different between habitats, our findings suggest that within habitat differences in community structure, specifically the preponderance of the specific taxa identified in this study, could influence the ability for temperate reef systems to flip between alternate stable states by shaping patterns of sea urchin demographics.

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FIGURES

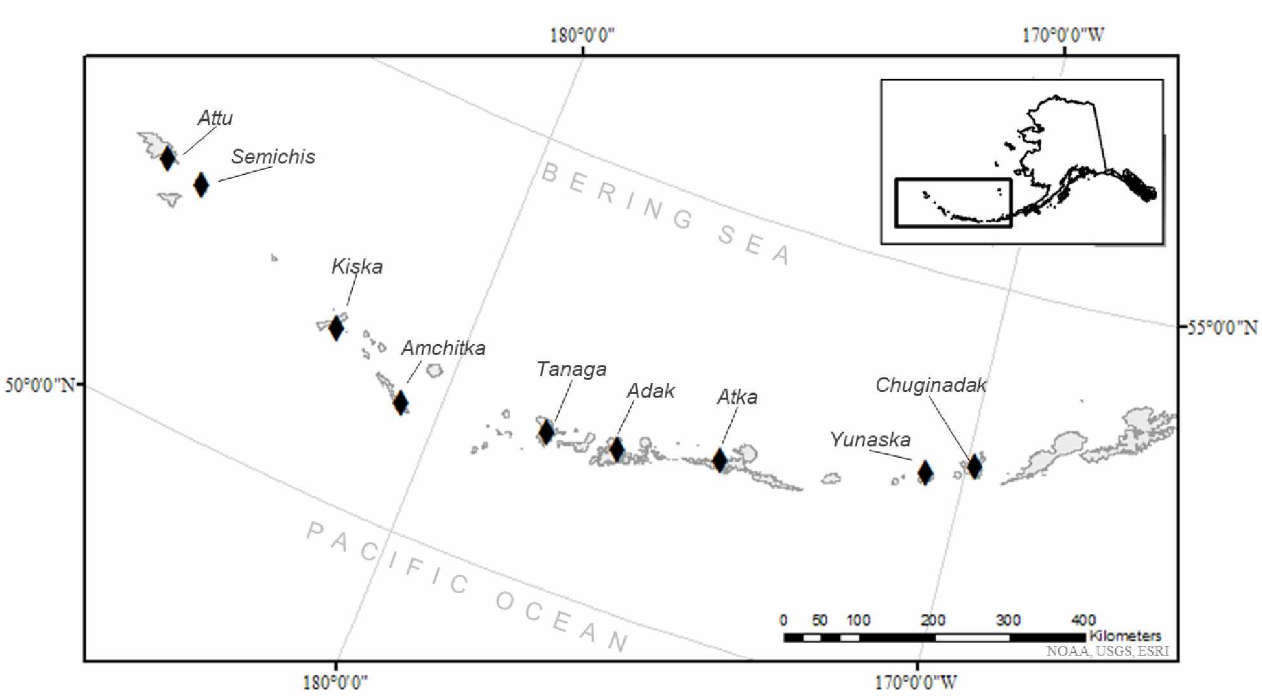

Figure 4.1. Map of the Aleutian Archipelago denoting study islands from west to east. Benthic community sampling islands are shown by the black diamonds.

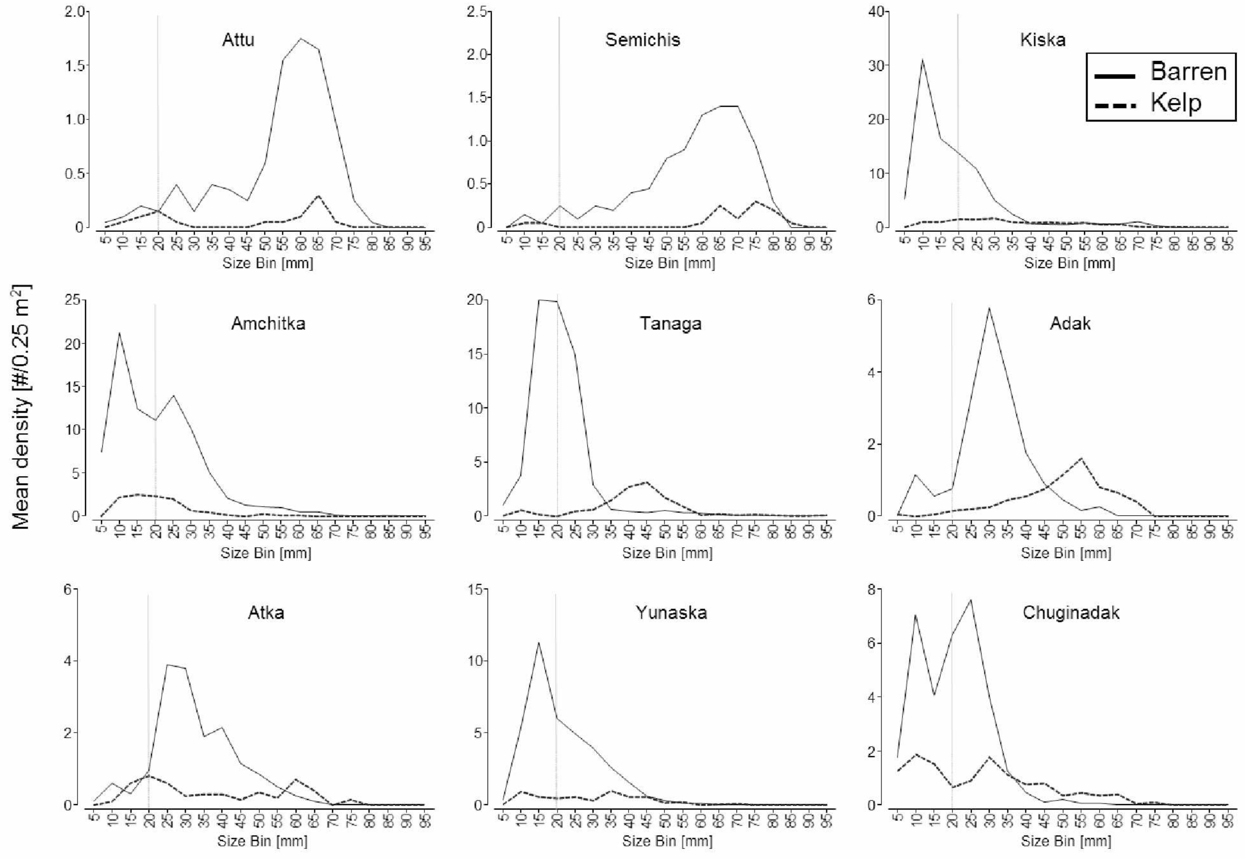

Figure 4.2. Mean size distributions showing summed densities of measured sea urchins in 5 mm size-bins, averaged between sites (n=2), by habitat: barren (solid line) and kelp (dashed line) for each island. The gray dotted line at 20 mm marks the cutoff for the recruit size class. Note differences in abundance among island by y-axis scale (range = <1–40).

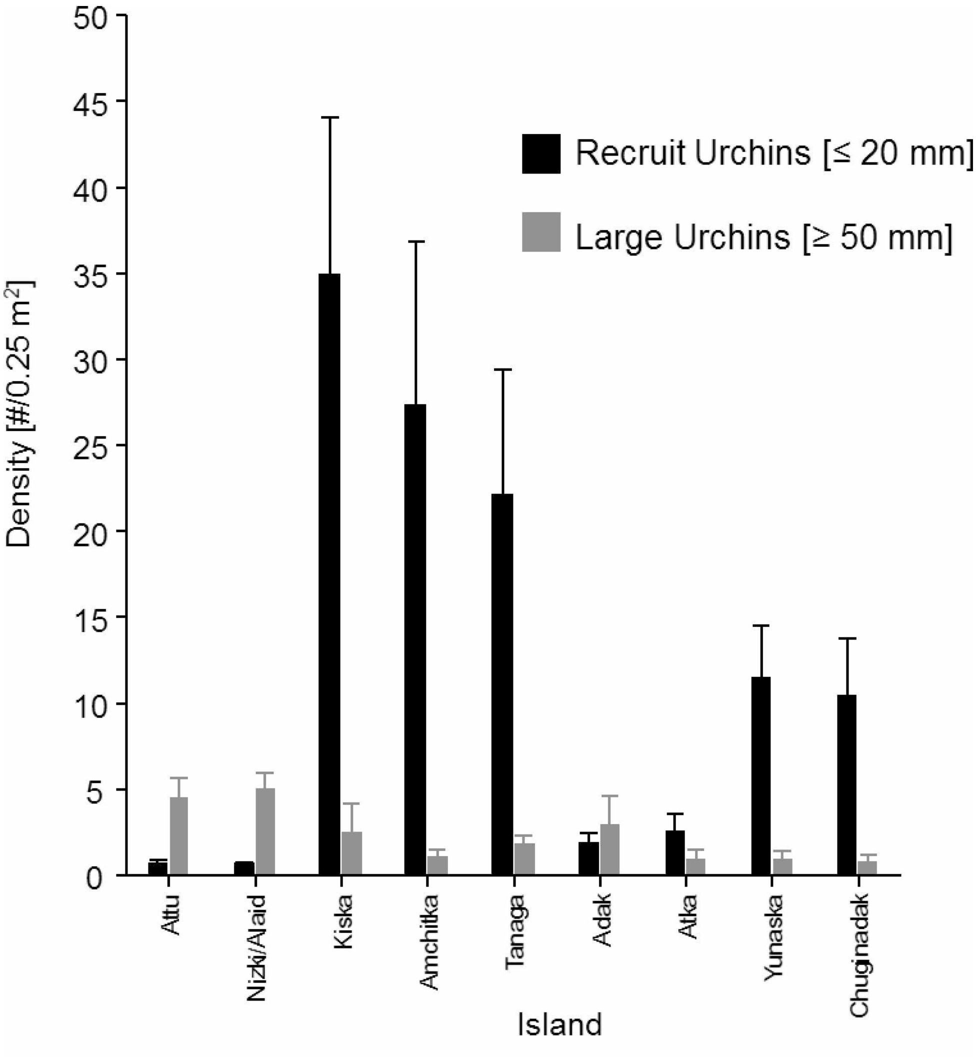

Figure 4.3. Mean density (# per quarter m^2) of recruit (black bar) and large (gray bar) sea urchin size classes averaged among sites by island (n=4, 2 of each habitat). Whiskers show 1 standard deviation.

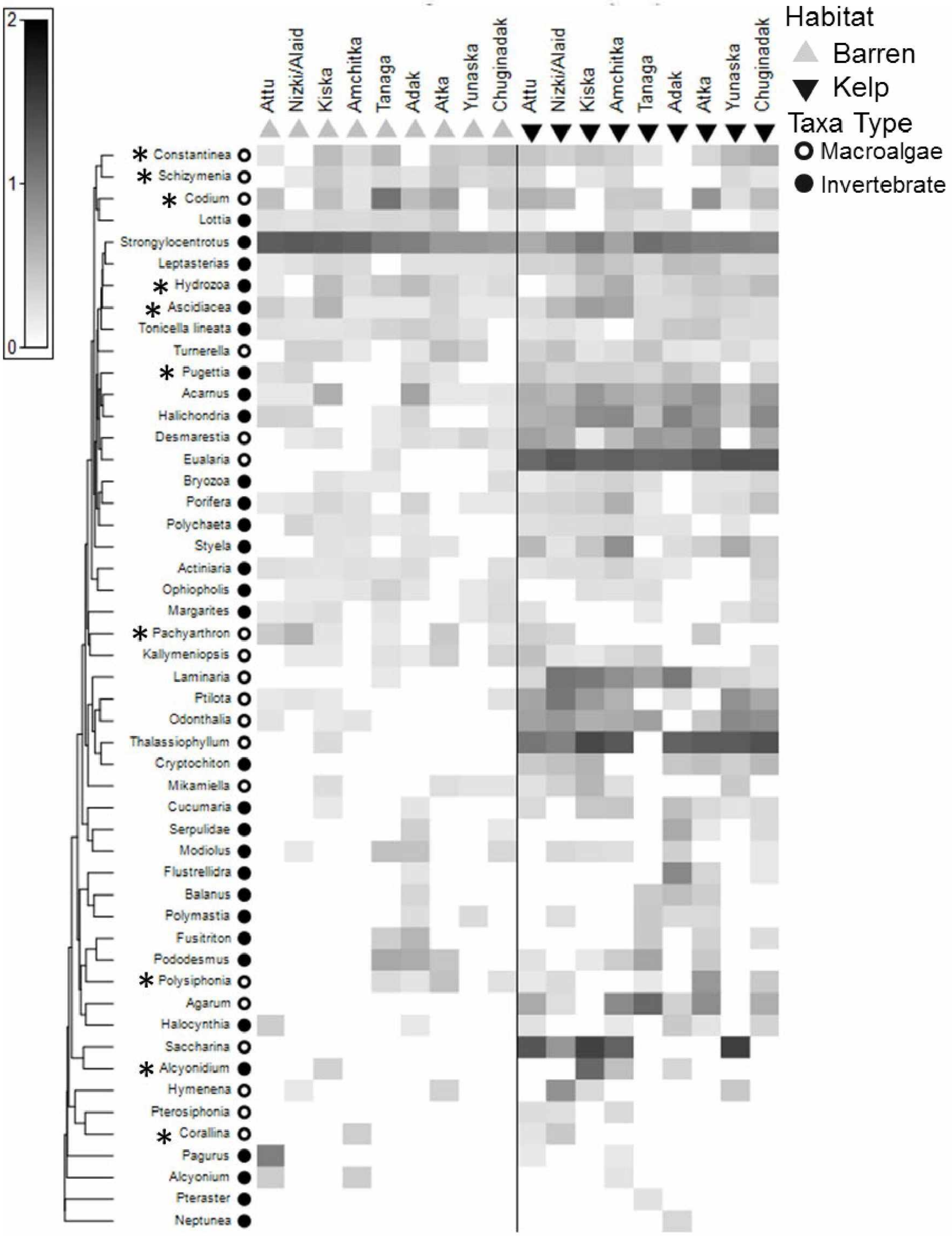

Figure 4.4. Shade plot of fourth-root transformed biomass (kg) for each of 50 taxa that were most important in distinguishing the benthic community in kelp forest and sea urchin barren habitats, shown by habitat (barren: up-triangle and kelp: down-triangle) and taxa type (open circles: macroalgae and closed circles: invertebrates). Clustering of taxa from a resemblance matrix of index of association shows correlations among taxa. Taxa that are significantly ($p<0.05$) correlated with sea urchin recruits in both habitats are denoted by an asterisk.

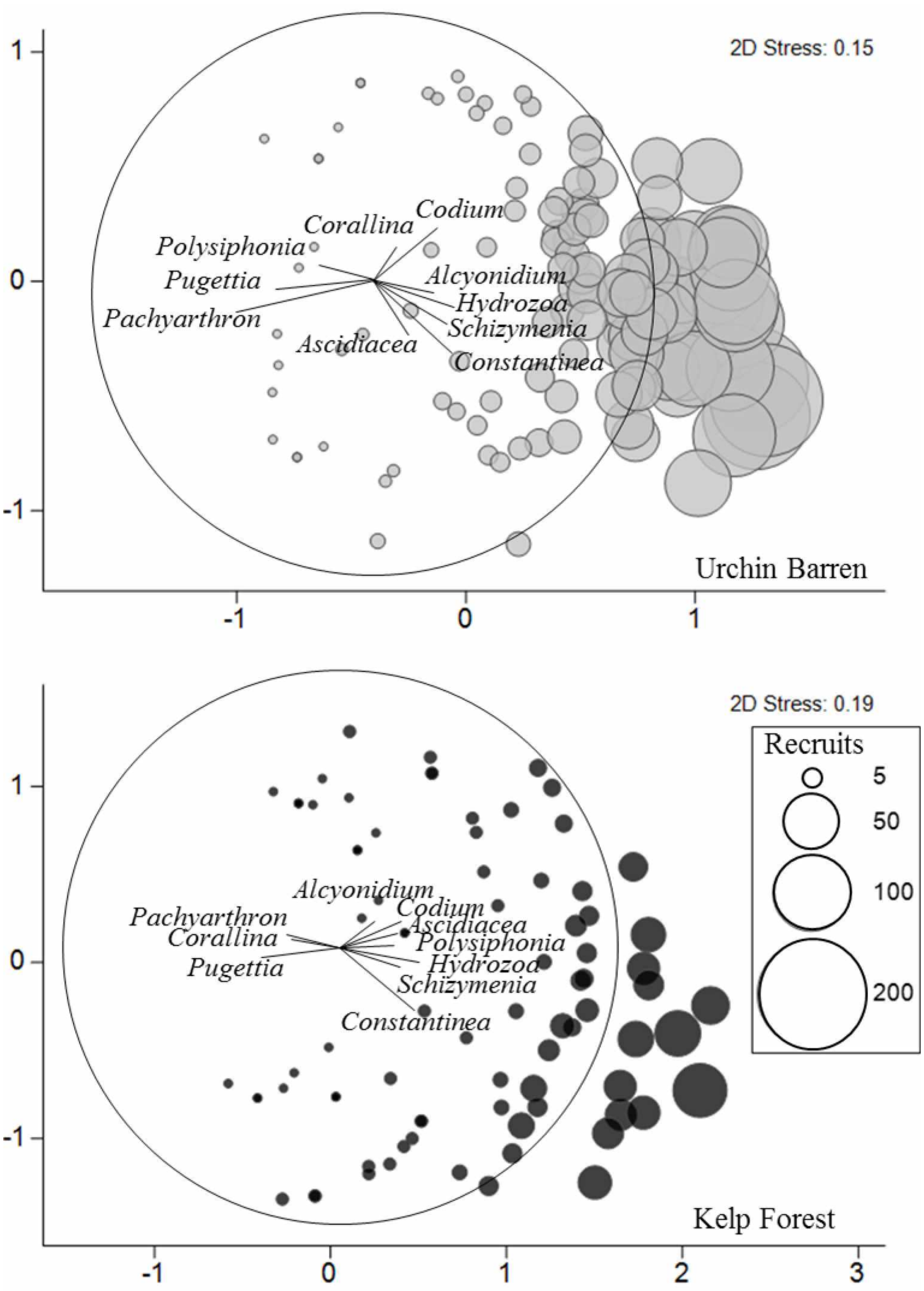

Figure 4.5. nMDS plot of similarity of sea urchin size structure (zero-corrected Bray-Curtis) by quadrat for barren ground (top) and kelp forest (bottom) habitats. Bubble plot shows densities (0.25 m^{-2}) of sea urchin recruits (test diameter ≤ 20 mm). Vectors show the strength of correlations with taxa significantly correlated in both habitats by DistLM (Table 4.2) and the circle represents a unit of 1.0 correlation strength.

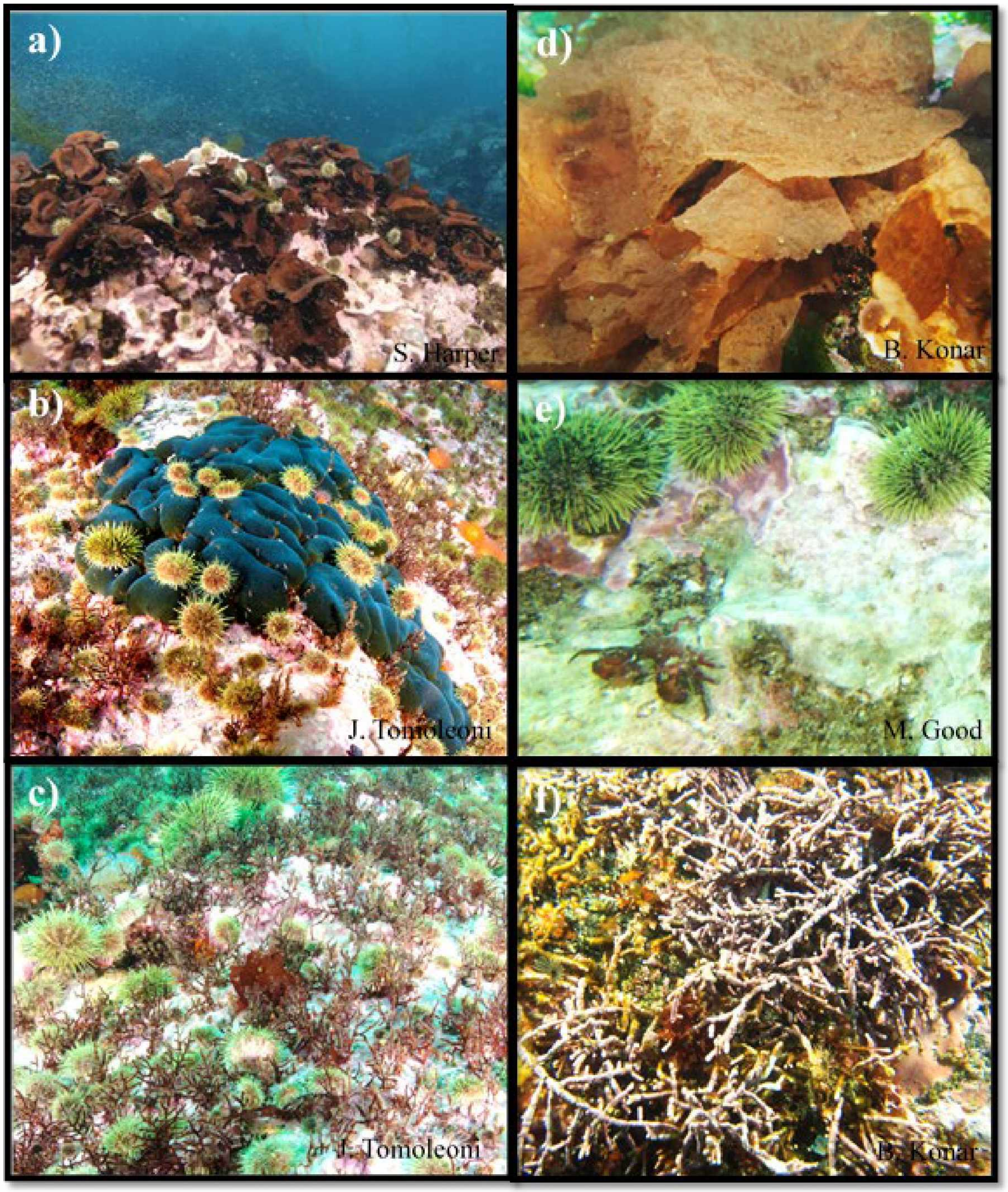

Figure 4.6. Images of some taxa that were significantly correlated with sea urchin recruits (≤ 20 mm): a) *Constantinea*, b) *Codium*, c) Hydrozoa, d) *Schizymenia*, e) *Pugettia* and large *Strongylocentrotus*, and f) *Pachyarthron*. Photo credit: a) Shawn Harper (http://www.seaweedsofalaska.com/species.asp?SeaweedID=218), b & c) Joseph Tomoleoni (USGS-Western Ecological Research Center), d & f) Brenda Konar (co-author, UAF), and e) Melissa Good (Alaska Sea Grant).

Table 4.1. Results from SIMPER analysis for dissimilarity of fourth-root transformed community biomass between barren ground and kelp forest habitats. Average fourth-root biomass of each taxa shows differences between habitats. The percent variation explaining the dissimilarity by each taxon is provided individually and cumulatively, up to a cut-off of 70% cumulative variation explained.

Taxa	**Average fourth-root biomass [g]**		**Contribution to explained variation**	
	Barren Ground	Kelp Forest	Individual %	Cumulative %
Thalassiophyllum	0.01	0.81	7.15	7.15
Eualaria	0.01	0.70	6.34	13.49
Saccharina	0.00	0.53	4.66	18.16
Strongylocentrotus	0.91	0.76	4.62	22.78
Odonthalia	0.01	0.47	4.32	27.10
Acarnus	0.08	0.44	3.88	30.98
Ptilota	0.01	0.36	3.23	34.21
Halichondria	0.03	0.36	3.13	37.34
Desmarestia	0.04	0.29	2.75	40.09
Codium	0.19	0.18	2.68	42.76
Laminaria	0.00	0.27	2.37	45.13
Ascidiacea	0.10	0.25	2.35	47.48
Hydrozoa	0.16	0.22	2.22	49.70
Styela	0.02	0.25	2.15	51.85
Constantinea	0.14	0.18	2.12	53.97
Leptasterias	0.05	0.21	1.96	55.93
Agarum	0.00	0.18	1.86	57.78
Pugettia	0.05	0.18	1.74	59.52
Tonicella	0.08	0.11	1.44	60.97
Pachyarthron	0.11	0.07	1.41	62.37
Musculus	0.02	0.14	1.31	63.68
Alcyonidium	0.02	0.15	1.26	64.94
Pododesmus	0.09	0.06	1.21	66.15
Lottia	0.12	0.04	1.20	67.35
Turnerella	0.06	0.09	1.19	68.54
Polysiphonia	0.04	0.10	1.18	69.73
Henricia	0.01	0.12	1.08	70.81

Table 4.2. DistLM results for community biomass of taxa that were determined to be significantly correlated (p-value < 0.05) with sea urchin recruits in both barren ground and kelp forest habitats, out of the full community (n = 170 taxa). The proportion of explained variation (Prop. Exp. Var.) shows the contribution of each taxa to the amount of explainable observed variation for each habitat, independently.

Taxa	**Kelp Forest**			**Barren Ground**		
	pseudo-F	*p-value*	Prop. Exp. Var.	*pseudo-F*	*p-value*	Prop. Exp. Var.
Alcyonidium	4.038	0.008	2.22%	4.338	0.003	2.38%
Ascidiacea	6.915	0.001	3.74%	2.816	0.017	1.56%
Codium	3.031	0.020	1.67%	4.516	0.001	2.47%
Constantinea	7.569	0.001	4.08%	3.870	0.006	2.13%
Corallina	3.469	0.011	1.91%	3.098	0.009	1.71%
Hydrozoa	6.960	0.001	3.76%	5.153	0.001	2.81%
Pachyarthron	2.965	0.022	1.64%	17.818	0.001	9.10%
Polysiphonia	3.160	0.014	1.74%	2.641	0.016	1.46%
Pugettia	3.673	0.012	2.02%	9.075	0.001	4.85%
Schizymenia	4.702	0.001	2.57%	4.907	0.002	2.68%

CHAPTER 5: CONCLUSION

Sea urchin demographics have typically been thought to be structured by the presence or absence of top-down control by keystone predators (Estes *et al.* 2016, Filbee-Dexter & Scheibling 2014). When predators are not sufficiently abundant to control sea urchin demographics, the system can become overrun with highly abundant and large urchins (Estes *et al.* 2010); however, the resulting patterns vary spatially due to variability in environmental conditions, and the local biological communities that are associated biogeographic patterns as documented across the Aleutian Archipelago (Konar *et al.* 2017, Estes & Duggins 1995). Predicted climate change stands to affect sea urchin demography; however the extent to which these effects will permeate to the ecosystem scale remains to be seen. The Aleutian Archipelago has provided an ideal natural laboratory to understand how an ecosystem responds to, and functions in the absence of, the keystone predator, the sea otter (*Enhydra lutris*). The manuscripts contained within my dissertation (Chapters 2, 3, & 4) contribute to a recent wave of knowledge that examined various aspects of nearshore ecosystem function that included: biogeographic breaks (Konar *et al.* 2017), benthic habitat and biodiversity (Metzger *et al.* 2019), benthic productivity and community structure (Edwards *et al.* 2020), interactions between sea urchins and the green encrusting macroalgae, *Codium* spp. (Gabara *et al.* in review), climate change effects on interactions between sea urchins and crustose coralline algae (Rasher *et al.* in review), and continued trends in the abundance and distribution of sea otters (Tinker *et al.* in prep). Sea urchins, and the factors that shape their demographics, are a common thread amongst all of these articles. My dissertation provides detailed insights into drivers of patterns of sea urchin demography across space and time, while taking into account the effects of predicted climate change and the biological community, from novel perspectives.

In my second chapter, I found that with the keystone predator, sea otters, rendered functionally extinct, the influence of environmental factors at local, island, and even regional scales became more evident. While these drivers may not have the same magnitude of effect that sea otters exert, they provide insights as to what factors are important in regulating sea urchins in the absence of sea otters. These insights may prove to be critical for understanding ecosystem change in a sea urchin dominated benthic system. Particularly where the keystone predator has been removed and shows little to no sign of recovery, as has been the case for much of the Aleutian Archipelago over the previous two and half decades to date. Some of the environmental variables that were static through time, such as island size or bathymetry, are likely important drivers of sea urchin demographics, whether or not sea otters are functionally present in the system. However, the influence of these static environmental variables on variability in sea urchin demographics only became apparent once sea otters were no longer present. This pattern fits with similar observations of the relative control between top-down and bottom-up influences in terrestrial systems (Pasanen-Mortensen *et al.* 2017). Of the influences examined that changed over time, temperature and recruitment were particularly important in structuring sea urchin demographics.

Chapter 3 presented evidence that the direct effects of ocean acidification on *Strongylocentrotus polyacanthus* must be considered in the context of temperature, and that ocean warming is likely to also influence sea urchin survival, calcification, and reproductive potential. My results showed that *S. polyacanthus* responses to acidification were non-linear, exhibiting a quadratic functional response. This non-linear response to acidification is similar to that reported for other sea urchin species, as reviewed in Ries *et al.* (2009). My experiment examined the direct responses of adult sea urchins to temperature and $p\text{CO}_2$ over 108 days, finding significant impacts to physiology and survival over this time frame. However, there is also recent evidence that adult sea urchins are capable of acclimating to acidified conditions over longer time periods (Dupont *et al.* 2013). While acclimation of adult sea urchins to laboratory conditions is likely, it has also been shown that survival of offspring can be impacted (Karelitz *et al.* 2020). Climate change effects are therefore most likely to affect sea urchins through effects on early life history, during larval life stages (Byrne *et al.* 2013). Effects on early-life history processes, coupled with increased stress on reproductive adults, could influence some of the positive feedback mechanisms that maintain sea urchin barrens, such as high reproductive potential/output and high survival (Ling *et al.* 2019). *In situ* conditions are expected to be quite variable across space and time; however, changes to the magnitude of variability or severity in local environmental patterns could further stress reproductive sea urchins, and thereby affect key demographic processes, as witnessed elsewhere (Norderhaug *et al.* 2016, Nyhagen *et al.* 2018).

Recognizing that recruitment can significantly influence sea urchin demography, my fourth chapter examined biological factors that might affect sea urchin recruitment in both sea urchin barrens and kelp forest habitats. My results showed that small sea urchin recruits were associated with specific macroalgal and invertebrate taxa, regardless of habitat type. The fact that the same species emerged as significant correlates in both habitats suggests that the surrounding biological community influences patterns of sea urchin recruitment. An important caveat to these findings is that the measured associations between sea urchin recruits and specific taxa were correlative, not causal, and further research is needed to understand the mechanistic relationships. Nonetheless, it is probable that positive associations with certain taxa reflect some feature of the interaction that acts to benefit the newly settled sea urchin, either by offering refuge or food (Pearce & Scheibling 1991), or by chemical attraction (Van Alstyne & Puglisi 2007). Similarly, it is reasonable to hypothesize that negative associations are the result of displacement (Narvaez-Diaz 2018), physical or chemical deterrents (Hagen *et al.* 2002, Gagnon *et al.* 2004), predation (Feehan *et al.* 2014, Burt *et al.* 2018), or even cannibalism (LeGault & Hunt 2016) by larger conspecifics. If the surrounding community structure were to contain higher or lower proportions of the taxa correlated with sea urchin recruits, then it could potentially influence the recruitment of sea urchins into the system.

Together, my dissertation provides multiple perspectives into the factors that shape contemporary patterns of sea urchin ecology across the Aleutian Archipelago and provide insights into the processes that can lead to change on temperate rocky reef habitats. In the current ecosystem state, where sea otters do not occur at densities necessary to regulate sea urchins, greater spatiotemporal variability in sea urchin demographics can be expected. It is likely that unless top-down predatory control of urchin is reestablished, sea urchin barrens will continue to predominate the system. Although they are influenced by other environmental factors besides sea otters, sea urchins occur at such high densities at most islands that only a catastrophic mortality event would be sufficient to allow recruiting kelps to survive and cause a flip back to a kelp forest state. Even a moderate sea urchin mortality event due to environmental factors would likely not be sufficient to slow the grazing and recruitment of sea urchins in the system, due to the positive density-dependent feedbacks from hysteresis (Ling *et al.* 2019). However, despite the fact that regulation by environmental forces is far weaker than the top-down regulation exerted by the now-absent keystone predator, understanding these environmental drivers is nonetheless important for informing a coherent ecosystem management strategy for the Aleutian

Archipelago. For example, part of the Southwest sea otter recovery plan (U.S. Fish and Wildlife Service 2013) includes an ecological recovery criterion (Estes *et al.* 2010) that assesses the ecological state of coastal rocky reefs across the Aleutian Archipelago relative to the state if sea otters were functionally controlling sea urchins and allowing a kelp forest to flourish. If, in the absence of sea otters, the biological community at some islands varies due to other factors, then understanding these factors may allow management towards more resilient community states, which will be critically important in a time of rapid environmental change. Findings from my dissertation can be used to understand factors that could shape ecological transitions across the Aleutian Archipelago and other rocky nearshore ecosystems at temperate latitudes, globally. Results from my dissertation will help support managers and researchers seeking to better understand the influence of sea urchins on rocky reef habitats as important drivers of ecological outcomes. Where keystone predators have been lost and sea urchin barrens expanded throughout the north Pacific, it remains to be seen if a return to kelp forest state can be achieved by environmental controls or the remaining biological community.

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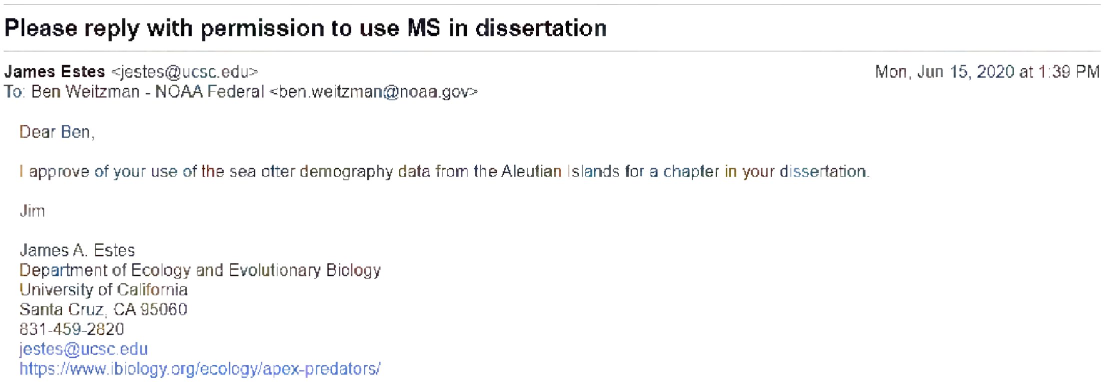
APPENDICES

Appendix A. Letters from non-committee co-authors: J. Estes, M. Edwards, M. Kenner, and D. Rasher authorizing the use of a manuscript prepared for publication as Chapter 2 in B. Weitzman's dissertation.



Please reply with permission to use MS in dissertation

James Estes <jestes@ucsc.edu>
To: Ben Weitzman - NOAA Federal <ben.weitzman@noaa.gov>

Mon, Jun 15, 2020 at 1:39 PM

Dear Ben,

I approve of your use of the sea otter demography data from the Aleutian Islands for a chapter in your dissertation.

Jim

James A. Estes
Department of Ecology and Evolutionary Biology
University of California
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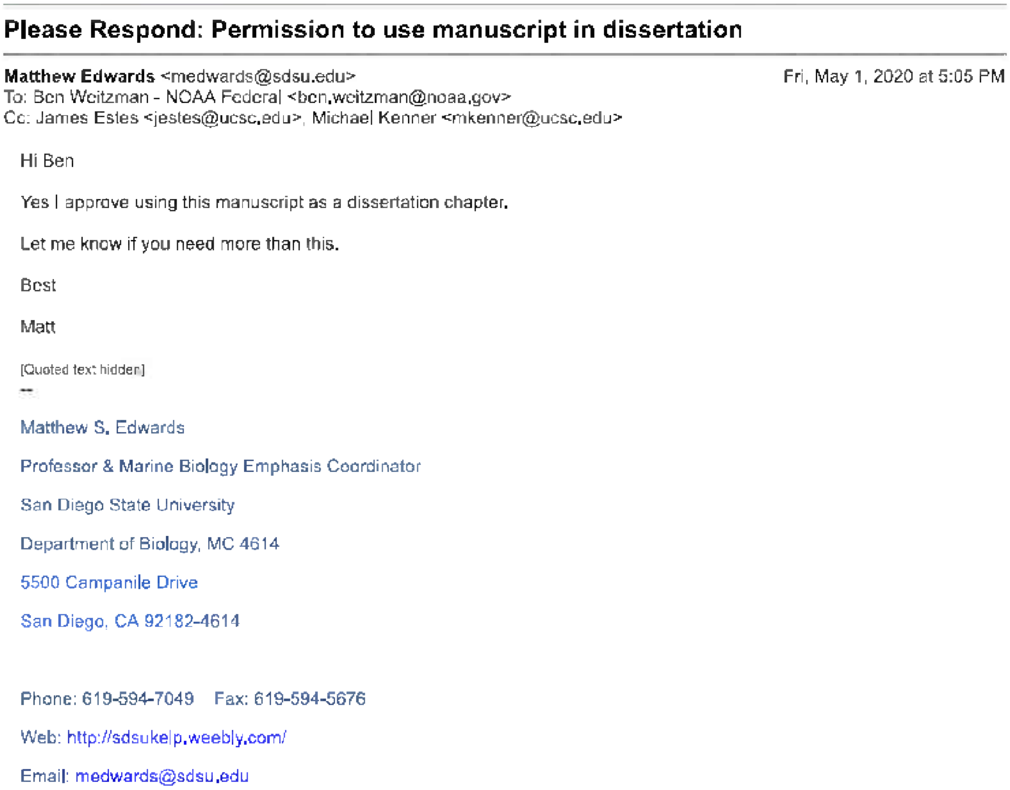

Please Respond: Permission to use manuscript in dissertation

Matthew Edwards <medwards@sdsu.edu>
To: Ben Weitzman - NOAA Federal <ben.weitzman@noaa.gov>
Cc: James Estes <jestes@ucsc.edu>, Michael Kenner <mkenner@ucsc.edu>

Fri, May 1, 2020 at 5:05 PM

Hi Ben

Yes I approve using this manuscript as a dissertation chapter.

Let me know if you need more than this.

Best

Matt

[Quoted text hidden]
--

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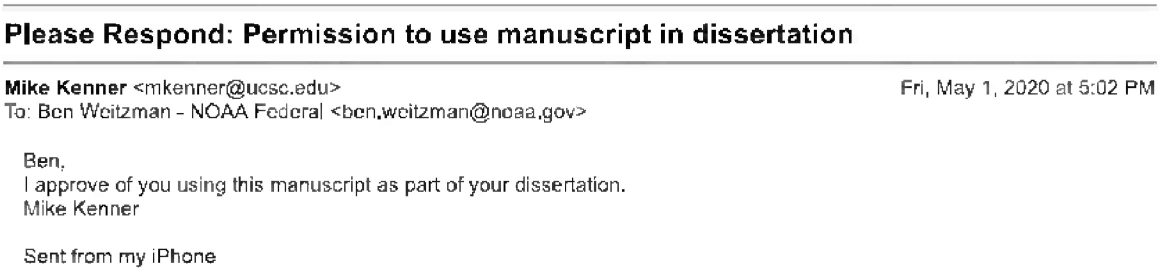
Appendix A continued



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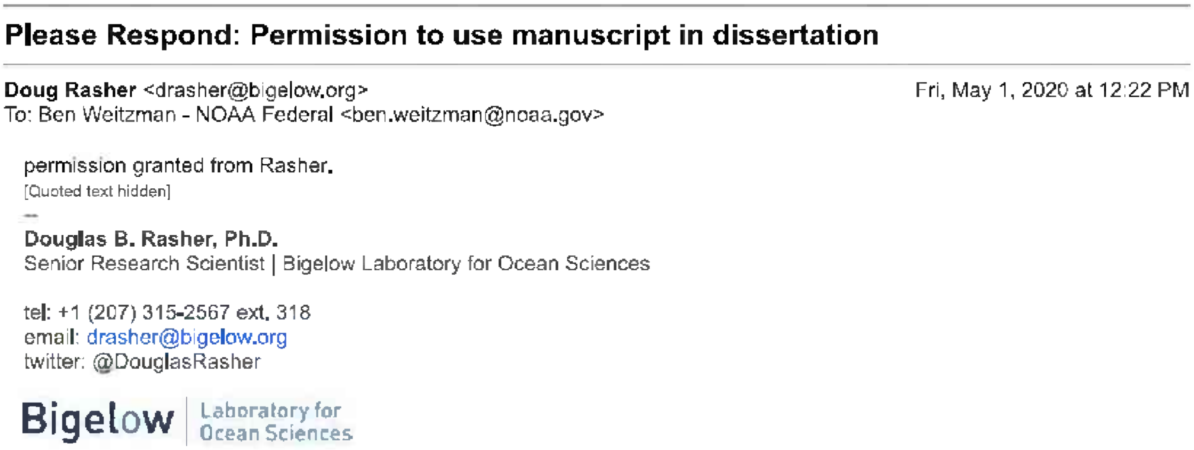
Mike Kenner <mkenner@ucsc.edu> Fri, May 1, 2020 at 5:02 PM
To: Ben Weitzman - NOAA Federal <ben.weitzman@noaa.gov>

Ben,
I approve of you using this manuscript as part of your dissertation.
Mike Kenner

Sent from my iPhone



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Doug Rasher <drasher@bigelow.org> Fri, May 1, 2020 at 12:22 PM
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permission granted from Rasher.
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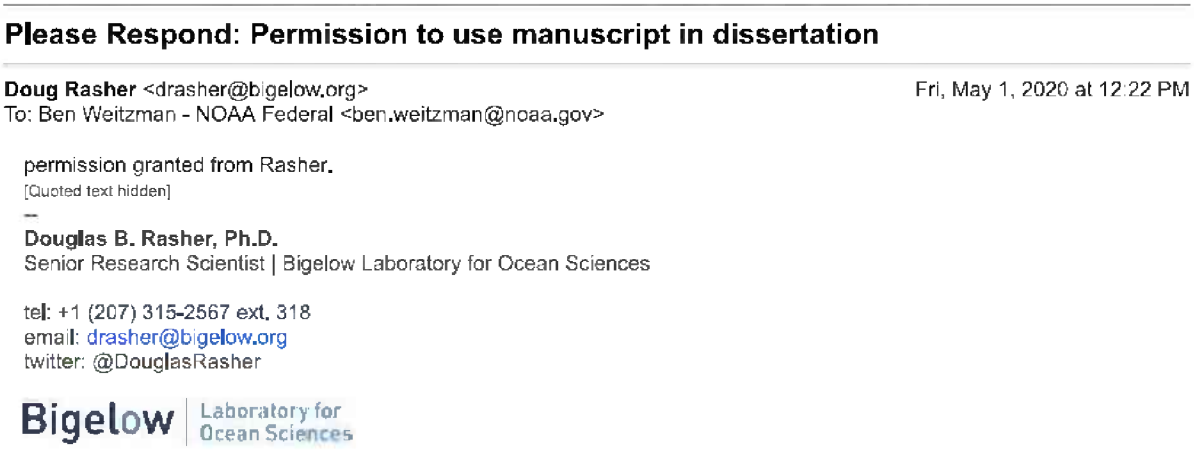
Appendix B. Letters from non-committee co-authors: D. Rasher, K. Lawton, I. Westfield and J. Ries authorizing the use of a manuscript prepared for publication as Chapter 3 in B. Weitzman's dissertation.



Please Respond: Permission to use manuscript in dissertation

Doug Rasher <drasher@bigelow.org> Fri, May 1, 2020 at 12:22 PM
To: Ben Weitzman - NOAA Federal <ben.weitzman@noaa.gov>

permission granted from Rasher.
[Quoted text hidden]
--
Douglas B. Rasher, Ph.D.
Senior Research Scientist | Bigelow Laboratory for Ocean Sciences

tel: +1 (207) 315-2567 ext. 318
email: drasher@bigelow.org
twitter: @DouglasRasher

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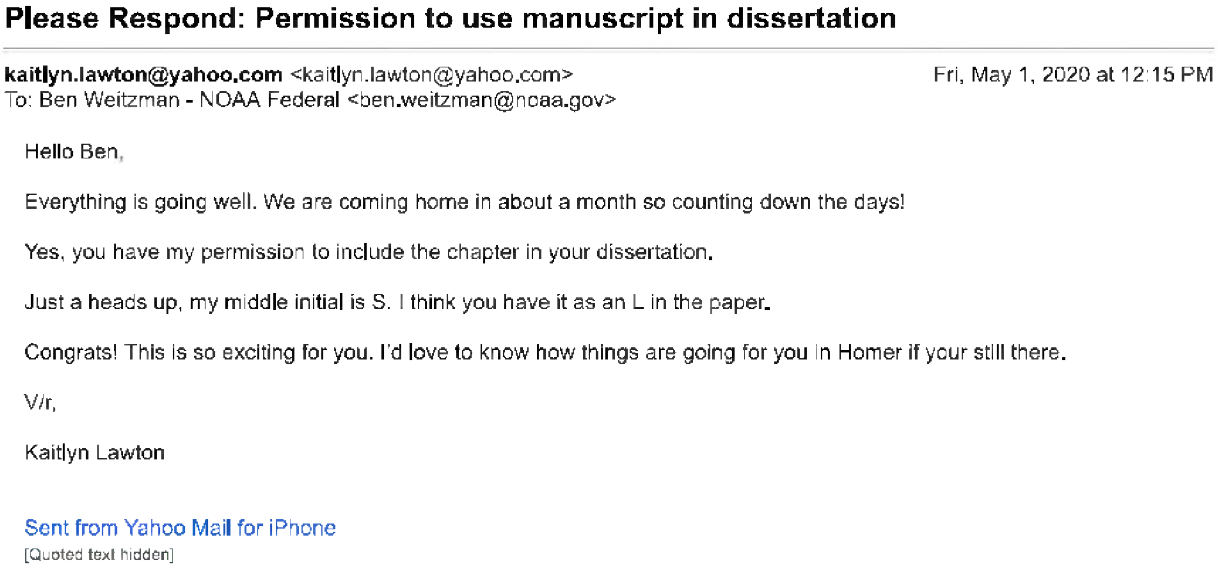

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kaitlyn.lawton@yahoo.com <kaitlyn.lawton@yahoo.com> Fri, May 1, 2020 at 12:15 PM
To: Ben Weitzman - NOAA Federal <ben.weitzman@noaa.gov>

Hello Ben,

Everything is going well. We are coming home in about a month so counting down the days!

Yes, you have my permission to include the chapter in your dissertation.

Just a heads up, my middle initial is S. I think you have it as an L in the paper.

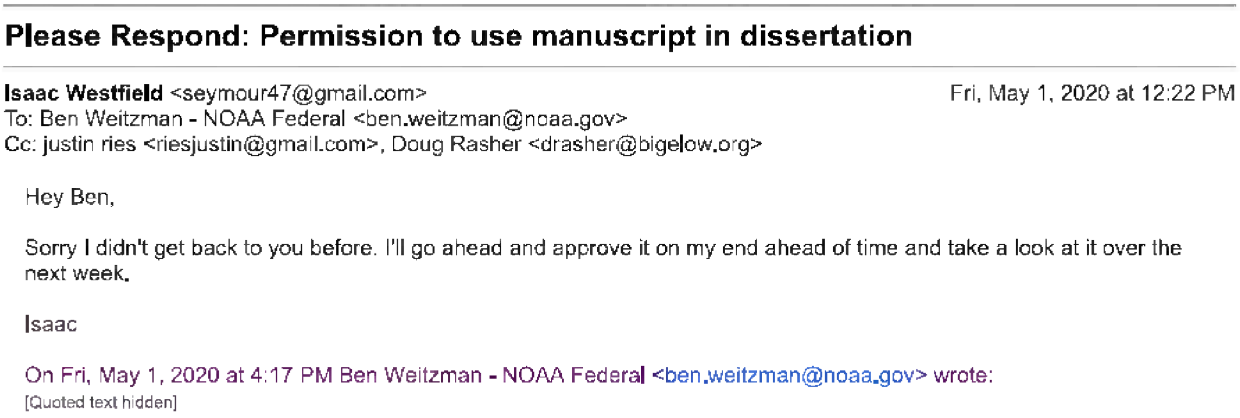
Congrats! This is so exciting for you. I'd love to know how things are going for you in Homer if your still there.

V/r,

Kaitlyn Lawton

Sent from Yahoo Mail for iPhone
[Quoted text hidden]

Appendix B continued



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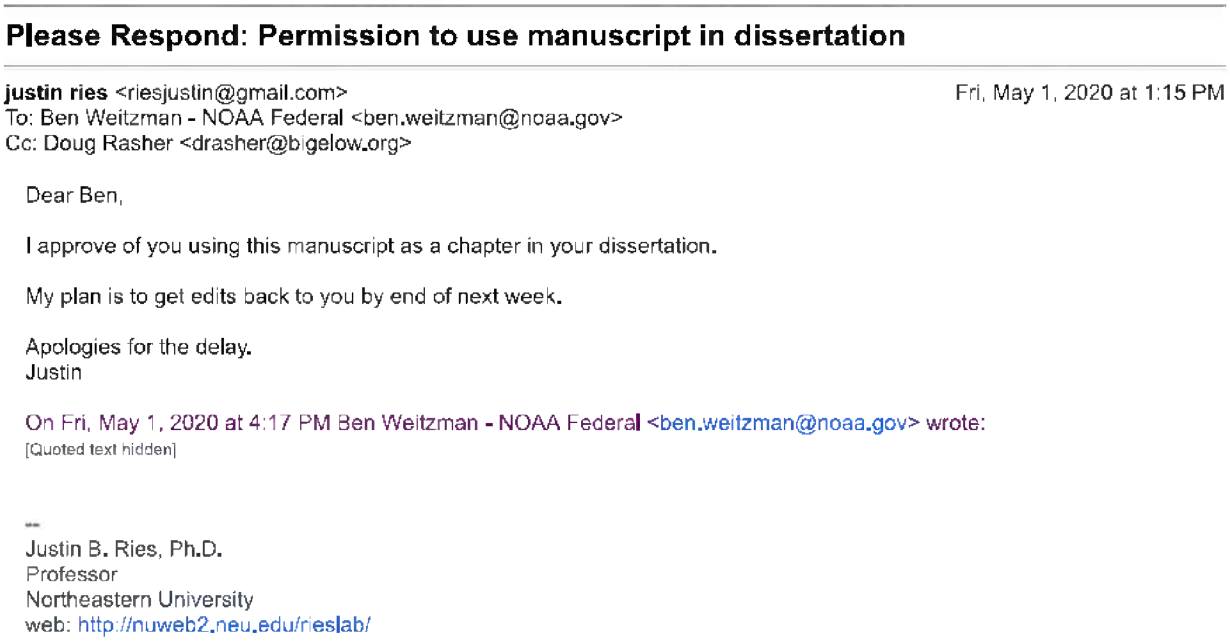
Isaac Westfield <seymour47@gmail.com> Fri, May 1, 2020 at 12:22 PM
To: Ben Weitzman - NOAA Federal <ben.weitzman@noaa.gov>
Cc: justin ries <riesjustin@gmail.com>, Doug Rasher <drasher@bigelow.org>

Hey Ben,

Sorry I didn't get back to you before. I'll go ahead and approve it on my end ahead of time and take a look at it over the next week.

Isaac

On Fri, May 1, 2020 at 4:17 PM Ben Weitzman - NOAA Federal <ben.weitzman@noaa.gov> wrote:
[Quoted text hidden]



Please Respond: Permission to use manuscript in dissertation

justin ries <riesjustin@gmail.com> Fri, May 1, 2020 at 1:15 PM
To: Ben Weitzman - NOAA Federal <ben.weitzman@noaa.gov>
Cc: Doug Rasher <drasher@bigelow.org>

Dear Ben,

I approve of you using this manuscript as a chapter in your dissertation.

My plan is to get edits back to you by end of next week.

Apologies for the delay.
Justin

On Fri, May 1, 2020 at 4:17 PM Ben Weitzman - NOAA Federal <ben.weitzman@noaa.gov> wrote:
[Quoted text hidden]

--
Justin B. Ries, Ph.D.
Professor
Northeastern University
web: http://nuweb2.neu.edu/rieslab/