

Exxon Valdez Oil Spill
Long-term Monitoring Program (Gulf Watch Alaska) Final Report

Long-term Monitoring: Nearshore Benthic Ecosystems in Kachemak Bay

Exxon Valdez Oil Spill Trustee Council Project 16120114-L
Final Report

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May 2018

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Study History: The ecological aftermath of the 1989 *Exxon Valdez* oil spill in Prince William Sound, Alaska, prompted a need for a better understanding of the marine ecosystem to be able to discern the effects of such spills and to gauge the recovery of the ecosystem. In Prince William Sound, approximately 21 million liters of crude oil came ashore, impacting the nearshore habitats and their associated food webs. Several research projects were funded by the *Exxon Valdez* Oil Spill Trustee Council to improve the ecological understanding of nearshore communities and to determine their recovery. Upon recognition that a larger geographic context of the ecosystem was needed to understand the nearshore processes and recovery in Prince William Sound, work within the Census of Marine Life Natural Geography In Shore Areas project was funded in 2002 (1 January 2003 - 30 June 2005) to assess nearshore subtidal and intertidal biodiversity in three regions of the Gulf of Alaska: Prince William Sound, Kachemak Bay, and Kodiak Island (Gulf Ecosystem Monitoring project G040666). Sampling protocols were based on established protocols by the Natural Geography In Shore Areas project (Rigby et al. 2007), and the work led to several peer-reviewed publications on Gulf-wide nearshore biodiversity (Chenelot et al. 2007, Hondolero et al. 2007, Konar and Iken 2009, Konar et al. 2009) as well as multiple global nearshore biodiversity assessments (Konar et al. 2010, Iken et al. 2010, Benedetti-Cecchi et al. 2010, Cruz-Motta et al. 2010, Pohle et al. 2011, Miloslavich et al. 2013).

When the *Exxon Valdez* Oil Spill Trustee Council decided in 2012 to embark on a long-term monitoring program in the Gulf of Alaska (from here on referred to as Gulf Watch Alaska), nearshore systems (benthic and upper trophic level) were identified as an integral part of this program. Kachemak Bay (this project) was included as a location that serves as a downstream reference site to sites in the Prince William Sound focus area. Similarly, nearshore sites in Kenai Fjords National Park and Katmai National Park and Preserve were included for large-scale spatial coverage of nearshore systems, building on previous work by the National Park Service (see Coletti et al. 2018 report on Restoration Project 16120114-R). By integrating standard operating procedures across investigator groups and regions, we have now built a system-wide nearshore monitoring group within the central Gulf of Alaska as part of the Gulf Watch Alaska. Results from Kachemak Bay are reported here separately, but the cohesive nature of the monitoring is evidenced by joint peer-reviewed publications (e.g., Konar et al. 2016) and presentations at scientific conferences. We have further integrated with restoration project 16120114-R (Nearshore Benthic Systems in the Gulf of Alaska) into a single project allowing for more collaborative work to continue into the next 5 years of the Gulf Watch Alaska (2016-2021).

Because of the role sea otters play in the north Pacific as keystone predators, Gulf Watch Alaska has supported sea otter work in Kachemak Bay since 2012. Sea otters are, therefore, an integral part of the Gulf Watch Alaska across all Gulf of Alaska regions monitored. In

Kachemak Bay, no previous sea otter work has been funded by the *Exxon Valdez* Oil Spill Trustee Council. Previous sea otter work in Kachemak has mostly been conducted by the U.S. Fish & Wildlife Service and the U.S. Geological Survey through different funding mechanisms. Monitoring of sea otter relative abundance and distribution has been sporadic but ongoing since the mid-1970s (Gill et al. 2009), and the population was last surveyed in 2012 by the U.S. Geological Survey in collaboration with U.S. Fish and Wildlife Service. Beginning in 2006, monitoring for sea otter and other marine mammal mortality became more established and monitoring effort became more consistent in Kachemak Bay through a Prescott grant awarded to the Alaska Sea Life Center to coordinate network volunteer responses to marine mammal morbidity and mortality in this region. Visual observations of sea otter foraging and scat data time series began in 2008 as part of a study associated with an Unusual Mortality Event in 2006 (Doroff et al. 2012). The GWA now affords the opportunity to better integrate work on sea otters in Kachemak Bay with that in other Gulf of Alaska regions to produce a more holistic view of sea otter performance.

Abstract: The nearshore system, from benthic to upper trophic levels, was examined in Kachemak Bay, Alaska as part of the Gulf Watch Alaska Long-term Monitoring Program from 2012 to 2016. Important habitat types (rocky intertidal, seagrass beds, soft-sediment gravel beaches) and quantitative information on key biotic elements of these habitat types (macroalgae, mussels, sea stars, seagrass, clams, sea otters) were collected and data made publicly accessible. All habitat types and elements were characterized by high spatial and temporal variability. We found that the influence of some static environmental drivers, those that do not appreciably change over the course of several years, play a minor role in distinguishing regional patterns in rocky intertidal communities. Sea star wasting was discovered in 2015 in Kachemak Bay and we assume that the higher than usual temperature conditions in the Gulf of Alaska contributed to the spread of the disease. Similarly, despite seemingly stable population numbers, we observed high sea otter mortality in 2015, possibly linked to increases in disease and/or increases in harmful algal blooms at the bottom of the food web because of the unusually warm conditions. Long-term declines in some of the sea otter prey items, especially large clams, also raises concerns.

Key words: Biodiversity, clams, diet, environmental drivers, Gulf of Alaska, intertidal, invertebrates, Kachemak Bay, macroalgae, monitoring, mussels, sea otters

Project Data: Data collected during this first 5-year period of the Gulf Watch Alaska are published through the Alaska Ocean Observing System Gulf of Alaska Data Portal (<http://portal.aaos.org/gulf-of-alaska.php#metadata/a51209ad-e2fd-4292-b9ef-4e6f45b5f15a/project>) and on DataONE (DOI: [10.24431/rw1k1o](https://doi.org/10.24431/rw1k1o) and [10.24431/rw1k1e](https://doi.org/10.24431/rw1k1e)). Contact is Carol Janzen, 1007 W. 3rd Ave. #100, Anchorage, AK 99501, 907-644-6703, janzen@aaos.org. Data are in .csv format and appropriate metadata were subjected to QA/QC and then published for public access. There are no limitations on the use of the data, however, it is requested that the authors be cited for any subsequent publications that reference this dataset. It is strongly recommended that careful attention be paid to the contents of the metadata file associated with these data to evaluate data set limitations or intended use. These data include:

1. **Rocky intertidal community data:** Percent cover and counts of macroalgae and invertebrates, 5 files: 1 file per year (2012-2016), each file includes data for 5 sites (Bluff Point, Bishop's Beach, Cohen Island, Outside Beach, Port Graham: 2012-2013) or 6 sites (Bluff Point, Bishop's Beach, Cohen Island, Outside Beach, Port Graham, Elephant Island: 2014-2016)
2. **Rocky intertidal swath count data:** Counts of sea stars and anemones, 1 file: contains data for all years for 5 sites (Bluff Point, Bishop's Beach, Cohen Island, Outside Beach, Port Graham: 2012-2013) or 6 sites (Bluff Point, Bishop's Beach, Cohen Island, Outside Beach, Port Graham, Elephant Island: 2014-2016)
3. **Rocky intertidal substrate composition data:** Percent cover of substrate grain size in rocky intertidal, 3 files: 1 file per year (2014-2016), each file including data for 6 sites (Bluff Point, Bishop's Beach, Cohen Island, Outside Beach, Port Graham, Elephant Island: 2014-2016)
4. **Rocky low intertidal temperature data:** Temperature measurements in low rocky intertidal, 13 files: 1 file per site (Bluff Point 2012, 2013; Bishop's Beach 2014, 2015; Cohen Island 2013, 2014, 2015; Outside Beach 2013, 2014, 2015; Port Graham 2013, 2014, 2015)
5. **Limpet size-frequency data:** Size-frequency distribution of *Lottia persona* in rocky intertidal, 4 files: 1 file per year (2012-2015), each file including data for 5 sites (Bluff Point, Bishop's Beach, Cohen Island, Outside Beach, Port Graham: 2012-2013) or 6 sites (Bluff Point, Bishop's Beach, Cohen Island, Outside Beach, Port Graham, Elephant Island: 2014-2015)
6. **Mussel size-frequency data:** Size-frequency distribution of *Mytilus trossulus* in rocky intertidal, 5 files: 1 file per year (2012-2016), each file including data for 3 sites (Cohen Island, Outside Beach, Port Graham: 2012-2014) or 6 sites (Bluff Point, Bishop's Beach, Cohen Island, Outside Beach, Port Graham, Elephant Island: 2015-2016)
7. **Seagrass shoot density data:** Seagrass shoot counts, 5 files: 1 file per year (2012-2016), each file including data for 4 sites (Jakolof Bay, Herring Island, Petersen Bay, Homer Spit)
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10. **Sea otter indirect foraging observations:** Data on foraging subtidal pit abundance

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EXECUTIVE SUMMARY

This report covers the first five years (2012 – 2016) of the investigations of the nearshore ecosystem in Kachemak Bay, Gulf of Alaska under the Gulf Watch Alaska Long-term Monitoring Program, funded by the *Exxon Valdez* Oil Spill Trustee Council. The nearshore environment is distinct by its influences from both marine and terrestrial realms, which creates highly productive systems that support many upper trophic-level organisms. In addition, the nearshore environment also is particularly vulnerable to effects from climate changes as well as human-induced disturbances, such as oil spills.

We investigated a variety of nearshore benthic habitats, including rocky intertidal coastlines, seagrass beds, and soft-sediment gravel beaches. These habitats are abundant, highly productive, support complex food webs, and some can serve as nursery habitat for juvenile stages of important fisheries species. Within these habitats, we assessed key taxa with high ecological value and that are food for upper trophic levels such as sea otters, sea ducks, and sea stars. The main goal of the study was to assess patterns in variability (trends) of these habitats as well as trends in key elements of these systems so that underlying causes of variation can be identified. Of particular importance is to be able to distinguish between natural, climate-related drivers and human-induced perturbations of the nearshore system. As such, this project represents the first 5-year phase of a planned 20-year endeavor.

The intertidal monitoring work showed high variability across space (sites) and time (years) in several metrics, such as rocky intertidal community, seagrass cover, clam species composition, for all habitats investigated. In the rocky intertidal, patterns in variability also differed by intertidal height stratum, confirming our earlier results that these strata may respond to different drivers and need to be investigated separately. To begin to understand these patterns in variability, we examined static attributes as possible drivers across rocky intertidal sites. We found that static habitat attributes were not strong drivers of rocky intertidal community composition on a regional scale. Despite overall high variability among sites, there seemed to be some common trends across sites with regards to change in community composition for the latter years (especially 2015 and 2016). We assume that these observed trends may be related to the unusually warm water conditions measured during these years and this will be a focus of study for the coming years. In addition, we attribute the recent appearance of sea star wasting disease in 2015 in Kachemak Bay to these warmer temperatures. Possible effects on overall rocky intertidal community structure from likely changes in the sea star assemblages will be monitored closely over the coming years.

Mussel populations, one key element of rocky intertidal systems and important food for upper trophic levels, had annual settlement events at established sites in Kachemak Bay. Our observations indicate, however, that size of the settlement peak differed by site. Mussel populations measured at all sites were dominated by individuals less than 33 mm shell length, which likely represents a maximum age of about 3 years.

Other intertidal habitats, such as seagrass beds and clam gravel beaches, also experienced high variability in representative metrics of key species. Seagrass shoot counts varied greatly over the study years and with no consistent trends across sites. A long-term survey conducted since 2003 at one of our sites showed a nearly 95% decline in shoot density over a 10-year period before recovery in the last two years. Sedimentation may play a role in this variability.

Variability in clam composition was high although certain species were consistently present at certain sites. Apparent declines in *Saxidomus gigantea* are of concern for higher trophic levels as this species is a favorite prey of sea otters in Kachemak Bay. Other most common sea otter prey items in Kachemak Bay were mussels and crabs, based on winter scat analyses. In the next five years of Gulf Watch Alaska, we will be expanding sea otter foraging studies to include observations in summer 2017.

During 2012, the sea otter population estimate for the Kachemak Bay was close to 6,000 animals from an aerial-based survey; no other surveys occurred since and during the GWA monitoring period. A new population survey in Lower Cook Inlet, including Kachemak Bay, is planned for summer 2017. In 2015, we observed a high mortality event of mostly adult male sea otters, although this gender focus may be biased by the specific study area. Many deceased animals showed signs of Strep Syndrome conditions. The relationship between warm water events and sea otter mortality are not fully understood but a link via bioaccumulated toxins in their prey may play a role. The warm water conditions such as we experienced since 2015 coincided with a prevalence of harmful algal blooms in the bay, which cause toxins to accumulate in filter feeding benthic taxa such as mussels and clams, both of which are important sea otter prey items.

In summary, this first 5-year phase of the long-term monitoring in Kachemak Bay has provided us with important insight into the patterns of variability of several elements within the nearshore food web. The next five years will provide us with a longer time series for the currently measured metrics and will allow us to test the influences of more variable environmental drivers. In that regard, the recent unusual warming event may have created a “natural experiment” that will allow us to observe responses across trophic levels of the nearshore food web to this extreme event.

INTRODUCTION

More than twenty-five years ago the *Exxon Valdez* oil spill resulted in almost 42 million liters of crude oil being discharged in Prince William Sound (Spies et al. 1996). Approximately half of the oil came ashore and was deposited in the nearshore environment (Wolfe et al. 1994). The impacts on the invertebrate and macroalgal foundation species were tremendous and dramatic losses were experienced by upper trophic level birds and marine mammals (Dean et al. 1996, Peterson 2000, Peterson et al. 2003). One of the issues in evaluating the severity of the impacts of the spill and the subsequent recovery of the environment was the lack of information on the community structure of the various habitats in the coastal ecosystem in the Gulf of Alaska. Specifically, species composition and proportional abundance were unknown for many habitats, including rocky intertidal systems and seagrass beds. One of the problems in assessing ecosystem injury from a

human-induced impact, such as an oil spill or warming trends, is the naturally high variability in marine systems, and in nearshore systems in particular (Coletti et al. 2016). A long-term monitoring approach is needed to understand the multiple temporal and spatial scales of variability for the diverse nearshore ecosystem components. The current Gulf Watch Alaska (GWA) Program accomplishes this by incorporating multiple habitats and regions with replication at various scales from lower to higher trophic levels. For the nearshore component, the GWA complementary work is conducted in Prince William Sound, Kenai Fjord National Park, Katmai National Park and Preserve, and Kachemak Bay (this project).

At the center stage of the nearshore component of the GWA are rocky intertidal systems because of their importance to management and local subsistence communities, their overall abundance in the central Gulf of Alaska, their high diversity, and their support of nearshore food webs that include shore birds, diving ducks, and sea otters (Coletti et al. 2016). We have a general understanding that bottom-up and top-down factors influence rocky intertidal communities, and that these factors can act on multiple temporal and spatial scales (Menge et al. 1997, Okuda et al. 2004, 2009, Iken et al. 2010, Konar et al. 2010), but we lack a specific understanding for the Gulf of Alaska (although see Konar et al. 2009). Understanding the important drivers for the Gulf of Alaska rocky intertidal communities, and the scale of their effects, will allow for the interpretation of community changes. In other words, this information will aid in determining if these community changes are part of natural variability, part of a long-term climate change response, or part of an outcome of a sudden impact such as a spill or pollution point source.

Focusing attention on biological drivers in the system, such as apex predators, in concert with environmental drivers, can help explain intertidal community trends (Sanford 1999). For example, sea stars are ecologically important in intertidal systems and have been shown to be apex species (reviewed in Menge 2000). They can be predators, grazers and/or scavengers and, thus, play a key role in trophic interactions. While understanding sea stars and their role in the rocky intertidal system of the Gulf of Alaska is generally important, this has become ever more pressing with the outbreak of sea star wasting disease in the East Pacific and its recent extension into the Gulf of Alaska. In other regions of the North Pacific, sea star wasting disease has decreased sea star populations, which could have ramifications on the rest of the community. Recognizing trends in sea star populations and their intertidal communities can only be accomplished through long-term observations, such as that being done through the GWA.

Another key component of rocky intertidal communities are mussels (*Mytilus trossulus*), which act as primary space competitors and increase overall diversity and productivity of these intertidal regions (Seed 1996, Arribas et al. 2014). They also are an essential trophic link between offshore primary production and the nearshore food web, where they serve as prey for higher trophic levels, including sea otters, sea ducks, shorebirds, sea stars, and other invertebrate predators (Dolmer 2000, Singh et al. 2013, Varennes et al. 2015). Yet, the dynamics that drive mussel populations at local and regional scales in the Gulf of Alaska are not well understood. Within the GWA, declines in overall mussel abundance have been found across monitored regions with recovery beginning in 2013 (Bodkin et al. 2017).

While the decline and the subsequent recovery seemed to be temporally linked across regions, the magnitude varied across sites. It is possible that local or regional differences in larval supply, settlement, and survival may be contributing to this variation. A better understanding of recruitment dynamics will allow us to determine how environmental drivers across the Gulf of Alaska influence the distribution of these important species.

In addition to rocky intertidal habitats, seagrass beds are essential coastal ecosystems. They stabilize coastal shore sediments, are highly productive, create habitat for a high diversity of associated flora and fauna, are nursery grounds for some invertebrates and fish, and play important roles in the global carbon cycle (Duffy 2006). Alaskan seagrass beds provide essential habitat functions to a variety of commercially and ecologically important fish and shellfish species (Dean et al. 2000, Murphy et al. 2000) with a need for monitoring and management of this critical habitat (Beck et al. 2001). The effects that the *Exxon Valdez* oil spill had on seagrass beds in Prince William Sound illustrate the need for continued monitoring of this resource (Dean et al. 1998).

Infaunal clam species in the intertidal zone are ecologically important organisms in soft-sediment habitats. Through their particle feeding action, clams are often important links between pelagic and benthic productivity (Fr  chette et al. 1993). In areas where tides are extreme with high resuspension of sediments, such as Kachemak Bay, clams are often supported by high food concentrations. These clams serve as a common food source for many marine species, including sea stars, crabs, sea otters, and shore birds (Kvitek and Oliver 1992). For example, in lower Cook Inlet and Kachemak Bay, sea otters depend primarily on clams (mostly *Saxidomus gigantea*) as a food source. Top-down effects of these predators can locally structure and control infaunal clam communities (Kvitek et al. 1992) as sea otters are considered a key stone species for the nearshore habitat (Estes and Palmisano 1974). Alternately, or in addition, bottom-up effects including nutrient availability, food abundance, and the replenishment of benthic communities via larval settlement can influence clam community composition. We are uncertain of how ocean acidification, warming trends, and fresh water flux will impact the recruitment and maintenance of clam populations in Alaska. In some locations, clam populations have declined significantly for the razor clam (*Siliqua patula*), the butter clam (*Saxidomus giganteus*), and the little neck clams (*Leukoma staminea*) over the past two decades (Brooks 2001, 2004, Brooks et al. 2001, Salomon et al. 2007, Seaman 2012; Glen Seaman and Patrick Norman pers comm). The value of clams as a recreational and subsistence resource in the Gulf of Alaska makes them an important monitoring and management target as evidenced by Alaska Department of Fish and Game (ADF&G) emergency clam harvest closures in 2013, 2014, and 2015 (ADF&G website).

Sea otters are an upper trophic level species that depends on these nearshore food webs, and they provide vital ecosystem functions and serve as an indicator of climate change stressors. For example, a strong driver of sea otter population dynamics is the first-year survival of dependent/independent pups (Monnet and Rotterman 1995, Ballachey et al. 2003). Severe or persistent storm events that can become more prominent with climate changes can cause mother/pup separations, which is lethal for a small, dependent pup. Sea otters also have very high metabolic rates, which are an adaptation to living in cold Pacific

waters, and otter physiological performance can be influenced by variations (especially shortages) in their prey resources. Warm water anomalies like the recently observed “blob” in the Gulf of Alaska (DiLorenzo and Mantua 2016) can initiate toxic algal blooms in coastal waters (McCabe et al. 2016). Sea otters can detect some toxins accumulated in their prey such as paralytic shellfish poisoning (PSP) (Kvitek et al. 1991); however, PSP may restrict forage availability and it is unclear if sea otters can detect all toxins produced and accumulated (Kvitek and Bretz 2004). In an analysis of data from marine mammal stranding networks, mortality events due to biotoxins have become more prevalent (Gulland and Hall 2007). To date, we have found non-lethal amounts (by health and human services standards) of both dioxin and saxitoxin in stranded sea otters and other marine mammals in coastal waters of Alaska (Lefebvre et al. 2016), but continued monitoring of key species such as sea otters is needed to fully assess the potential effects of the recent warm water anomaly. The overall goal of the GWA program is to address population status, numeric equilibrium of sea otters and their prey resources, throughout all GWA study areas by aerial-based population surveys and metrics of caloric gain per individual foraging dive. Increasing data for both abundance surveys and individual foraging dives in the next 5-year phase of the program will strengthen our ability to compare and contrast metrics from Kachemak Bay to all other sites.

OBJECTIVES

The overarching objectives of this study were to continue monitoring in the nearshore ecosystem in Kachemak Bay, including sea otters as higher trophic level users of the nearshore environment, and to identify potential environmental variables that relate to the biological ecosystem components.

The **specific objectives** for work in Kachemak Bay were:

1. Determine trends in abundance and distribution of rocky intertidal plants and invertebrates and of seagrass beds.
2. Determine trends in the abundance and size frequency of clams (gravel beaches) and mussels (rocky beaches).
3. Determine trends in selected environmental variables and relate to biological measurements.
4. Determine trends in sea otter abundance.
5. Determine the diet and dietary shifts of sea otters.
6. Determine trends in sea otter mortality.
7. Determine trends in marine debris.

METHODS

Site description

Kachemak Bay, Alaska is located within the north-central part of the Gulf of Alaska at 60° N and 151° W. The bay is divided into an inner and outer bay at the Homer spit, which extends several kilometers into the bay. The outer bay is largely free of glacial influence, whereas several points of glacial discharge from the Harding Icefield enter the inner bay.

Oceanic water from the Alaska Coastal Current enters the bay along the southern shore and rotates counter-clockwise to then exit along the northern shore (Schoch and Chenelot 2004). The outer, southern shore of the bay is free of glacial sediments while the inner bay has a gradient of sedimentation along the coast with lower light and salinity and greater inorganic sedimentation at the head of the bay (Abookire et al. 2000, Spurkland and Iken 2011). Some freshwater and glacial sediment is also circulated back toward the mouth of the bay and to the outer, northern side of the bay by currents (Gatto 1982). Intertidal monitoring sites for the GWA are located on both the southern and northern portions of the bay to ensure that sites are representative of the environmental conditions of the entire bay (Fig. 1, Table 1).

Table 1. Intertidal sites sampled for various monitoring tasks and the years during which this monitoring was conducted. Site abbreviations are used throughout figures of this report. SFD is size-frequency distributions.

Monitoring metric	Site	Code	Longitude	Latitude	Years sampled
rocky intertidal	Bishop's Beach	BB	59.642783	-151.601783	2012-2016
rocky intertidal	Bluff Point	BP	59.656700	-151.671167	2012-2016
rocky intertidal	Cohen Island	CI	59.539133	-151.476950	2012-2016
rocky intertidal	Outside Beach	OB	59.464233	-151.708500	2012-2016
rocky intertidal	Port Graham	PG	59.373333	-151.894167	2012-2016
rocky intertidal	Elephant Island	EI	59.513961	-151.505881	2014-2016
mussel SFD	Bishop's Beach	BB	59.642783	-151.601783	2015-2016
mussel SFD	Bluff Point	BP	59.656700	-151.671167	2015-2016
mussel SFD	Cohen Island	CI	59.539133	-151.476950	2012-2016
mussel SFD	Outside Beach	OB	59.464233	-151.708500	2012-2016
mussel SFD	Port Graham	PG	59.373333	-151.894167	2012-2016
mussel SFD	Elephant Island	EI	59.513961	-151.505881	2015-2016
soft sediment clams	Bear Cove	BC	59.721900	-151.052700	2013, 2015
soft sediment clams	China Poot Bay	CP	59.568800	-151.301733	2013, 2015
soft sediment clams	Jakalof Bay	JB	59.457383	-151.527400	2013, 2015
soft sediment clams	Port Graham	PG	59.343450	-151.816900	2013, 2015
seagrass beds	Jakolof Bay	JB	59.449000	-151.499000	2012-2016
seagrass beds	Herring Island	HI	59.464517	-151.709000	2012-2016
seagrass beds	Petersen Bay	PB	59.582083	-151.264000	2012-2016
seagrass beds	Homer Spit	HS	59.648533	-151.436500	2012-2016

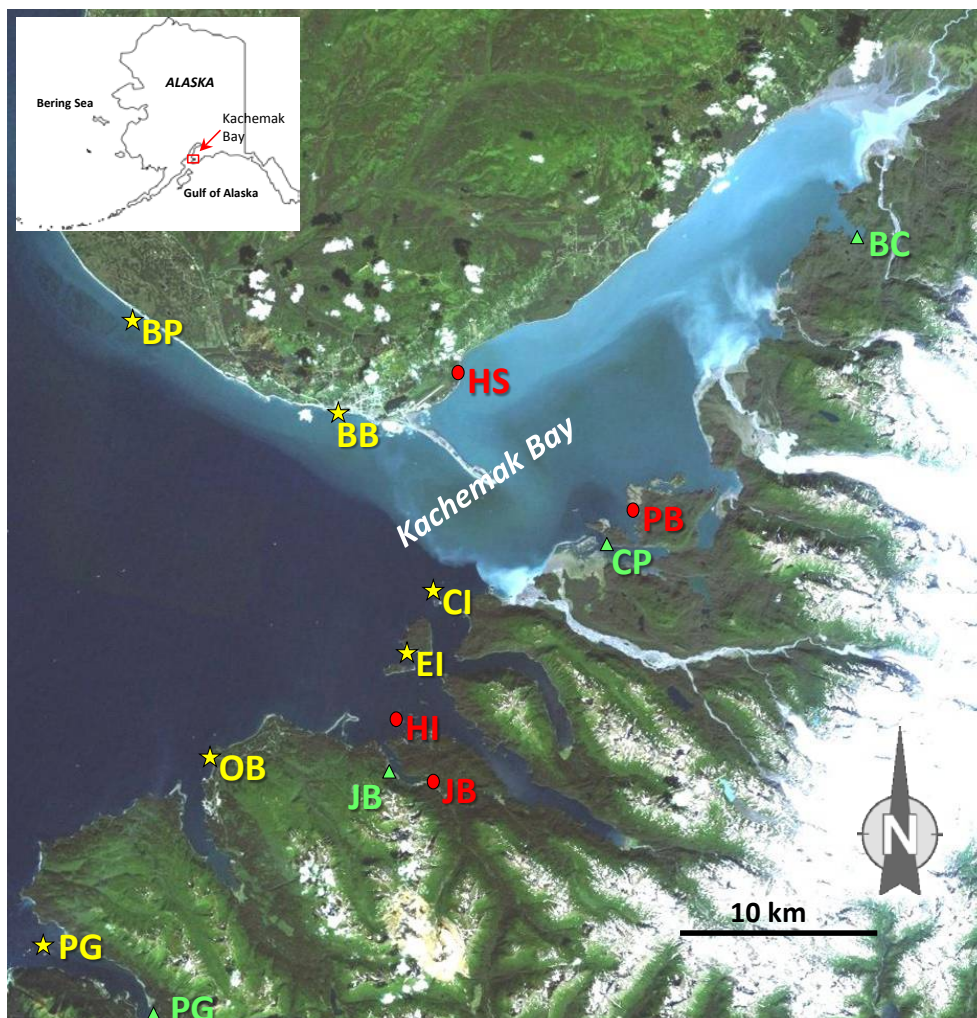


Figure 1. Gulf Watch Alaska Long-term Monitoring sampling sites in Kachemak Bay: yellow stars: rocky intertidal and mussel sites; red circles: seagrass sites; green triangles: soft-sediment clam sites. Site codes as in Table 1. Inset shows the location of Kachemak Bay in Alaska.

Standard operating procedures

All sampling procedures followed established Standard Operating Procedures (SOP), which are accessible through the Alaska Ocean Observing System (AOOS) Ocean Workspace and are outlined in the metadata associated with the respective data files.

Rocky intertidal communities

Rocky intertidal communities were sampled at six sites within Kachemak Bay. Sites were selected based on existing historical data, comparable exposure, and availability of continuous rocky substrate to accommodate sampling. Two sites (Bishop's Beach and Bluff Point) were located on the north side of the bay while the remaining sites (Port Graham, Outside Beach, Elephant Island and Cohen Island) were on the south side. At each site, 10 replicate 1 m² quadrats were sampled at random positions along a 50 m permanent transects in each of the high (approximately 7 m), mid (approximately 4 m), and low

(approximately 0 m) intertidal strata, and at 1 m deep subtidal strata (relative to mean lower low water (MLLW), some variation depending on site). Within each of the 10 replicate quadrats along each transect, percent cover of all macroalgae and sessile invertebrates was identified to the lowest possible taxonomic unit and their abundance estimated to the nearest 1%. All mobile invertebrates larger than 2 cm were identified to the lowest possible taxonomic unit and counted. Quadrat substrate composition was assessed by grain size categories: <1 mm Mud/Sand, 1 mm to <50 mm Gravel, 50 mm to <300 mm Cobble, 300 mm to <1 m Boulder, 1 m diameter or greater Rock.

In addition, counts of larger mobile invertebrates (primarily sea stars and large anemones) were taken along 1 m on both sides of each transect, resulting in a 2 x 50 m transect (=100 m²) at each tidal height. When sea star wasting became a possible concern, we began recording sea stars that exhibited signs of this disease along each transect and also generally at the site. We randomly collected and measured the length of approximately 120 *Lottia persona* (limpet) at each site for size frequency distribution because they are an important prey for nearshore predators such as the black oystercatcher.

A HOBO temperature logger was placed on an eye bolt epoxied to a rock at the end of the low transect at each site, which measured temperature at 30 min intervals over the course of a year. Loggers were exchanged each year or replaced if a logger was lost.

Intertidal mussel size-frequency distributions

Mussels were collected from a bed adjacent to each of the rocky intertidal sites. A permanent marker was epoxied onto the rock at one end of each of these mussel beds. A 50 m tape was then stretched along the shoreline parallel to the water edge across the bed. Ten vertical transects originating from this parallel transect were placed at random (between 0 and 5 m from starting point) and then in 5 m intervals from the initial random location. The length of each vertical transect from the upper to the lower end of the bed was recorded to gain an understanding of total mussel bed size. At a randomly selected distance corresponding to the vertical transect length, a 25 x 25 cm quadrat was placed to the right of the transect line. Within this quadrat, percent cover of taxa was determined and all mussels were removed and placed in a zip-lock bag. If there were no mussels in the core, a zero value was recorded. Each mussel was counted and its length measured.

Infaunal clams

Clams were sampled in odd years; in 2013 and 2015 during this reporting period. Following established SOPs (Weitzman et al. 2017) for soft sediment/gravel sites, we placed a 50 m transect at the zero tidal elevation. Along each transect, we sampled 10 randomly placed 0.25 m² quadrats down to a depth of 25 cm. All sediments collected from these quadrats were individually sieved over a 10 mm sieve and all clams were identified to the lowest possible taxonomic unit, counted, and shell lengths measured.

Seagrass beds

At each seagrass (*Zostera marina* = eelgrass) site, a 50 m transect was placed in the center of each bed. Along each transect, ten 0.25 m² quadrats were sampled and percent cover of seagrass, open substrate, macroalgae and sessile invertebrates determined to the nearest 1% at the lowest possible taxonomic level. We also counted all seagrass shoots within each

quadrat and identified all mobile invertebrates larger than 2 cm. The areal extent of each seagrass bed was determined by measuring width across the 50 m transect at the start and every subsequent 10 m.

Sea otters

Sea otter diet

Sea otter diet was assessed from scat collections, which are limited in our study area to the winter months when sea otters haul-out more frequently and in greater concentrations (Doroff and Badajos 2010, Doroff pers obs). In March 2008, we began a pilot study to assess the feasibility of determining sea otter diet by scat collection in Kachemak Bay. Nine locations were assessed, and of those, a site in Little Tutka Bay where sea otters (females, females with pups, and an occasionally territorial male, G. Christen pers comm) haul-out on floating docks was selected as a long-term monitoring location used in this study (Fig. 2).

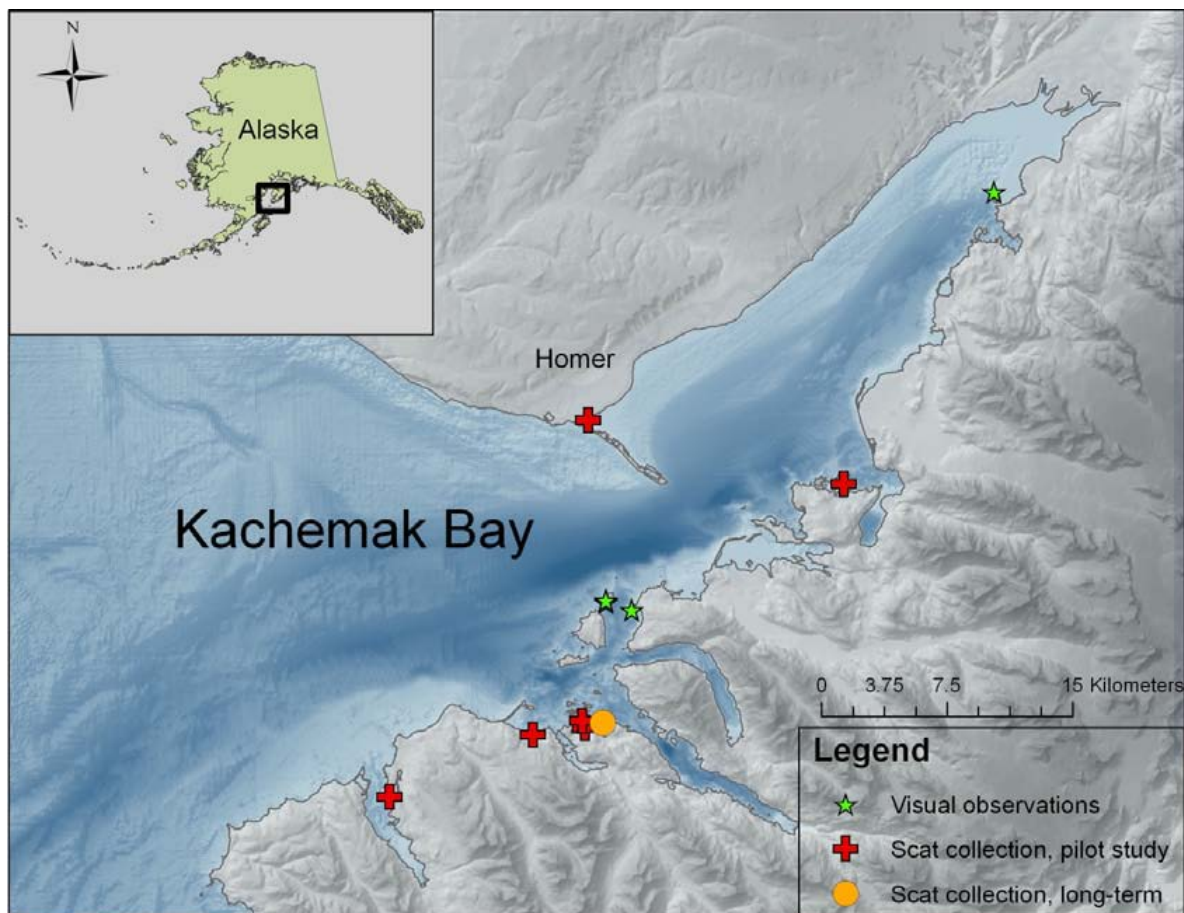


Figure 2. Sea otter scat collection sites in Kachemak Bay, southcentral Alaska. A single site in Little Tutka Bay (orange circle) was selected as our long-term monitoring location from multiple pilot collection sites in 2008 (red crosses). Diet also was assessed by visual observation in 2008 at three locations (green stars).

We collected monthly sea otter scat samples in Little Tutka Bay, located along the south shore of Kachemak Bay, during the winter months of 2012-2016 through citizen science

and collaboration with local land/dock owners (see Doroff et al. 2012 for sample collection and methods). We began sample collections for sea otter scat in 2008 and have processed 409 samples since then. During the winters 2012-2016, 117 samples were processed for this project and sample collection is ongoing for winter 2016.

Scat sampling and analysis methods followed Watt et al. (2000). Scats were collected each week during the winter haulout months, the exact time frame of which differs each year. Scat samples were washed with fresh water through a high-pressure hose using nested sieves of 2 mm and ≤ 1 mm mesh. Air-dried samples were sorted by hand to the nearest discernable taxonomic level and placed in Ziploc bags for further analysis. The relative importance of each prey type was determined by the frequency of occurrence and the percent volume for each sample. The frequency of occurrence was expressed as the presence of a prey type in a scat. The percent volume of each prey type was estimated and ranked as follows, using a 1-6 point index method where: 1= $<5\%$, 2=5-25%, 3=26-50%, 4=51-75%, 5=76-95%, 6= $\geq 95\%$. We ranked each prey type, which occurred in the scat. To summarize mean percent volume, we used the median value of each category.

As a second line of evidence of sea otter foraging, we analyzed foraging pits in the shallow subtidal region in Kachemak Bay. Natural and experimentally dug pits were marked and pit dimensions observed over time to assess if sea otter pits can be distinguished from sea star pits to assign predation to one of these main predators. The details of this study are reported in Traiger et al. 2016 (Appendix 1).

Sea otter abundance and mortality patterns

The U.S. Fish and Wildlife Service (USFWS) has the trust responsibility for the management of sea otters in the United States. The Marine Mammals Management Office of the USFWS in collaboration with the U.S Geological Survey (USGS) are the two agencies that provide population survey information for northern sea otters in Alaska. Sea otter surveys were not funded as part of GWA for Kachemak Bay; instead, assessment of the sea otter population in Kachemak Bay and lower Cook Inlet were to be based on the agency data for 2012-2016. Lower Cook Inlet is part of the Southcentral and Southwestern sea otter population stocks as defined by the USFWS; the Southwestern stock is listed as Threatened under the Endangered Species Act (includes Kamishak Bay in Cook Inlet) and the Southcentral stock is not listed (includes Kachemak Bay). Surveys of the Southwestern stock remain a high priority area for sea otter abundance surveys and the Kachemak Bay area is less of a priority. Survey methods for this region are documented in Gill et al. (2009).

The Alaska Marine Mammal Stranding Network (AMMSN) in Homer, in collaboration with the USFWS Marine Mammals Management Office, collects year-round data on sea otter carcass deposition and causes of mortality, and manages live animal strandings. We report on these data for the GWA period from 2012-2016. The AMMSN is voluntary and local stranding coordinators were assisted by multiple University of Alaska, Kachemak Bay Campus undergraduate student interns. We present information from sea otter carcasses for which age class was recorded by the USFWS AMMSN.

Marine debris

Marine debris in Kachemak Bay was assessed by the Center for Alaska Coastal Studies (CACS), who works with community volunteers to collect and dispose of marine debris. Result presented here are work conducted by CACS.

Advancing technology

Intertidal monitoring projects such as the GWA are often limited in their practicality because traditional methods such as visual surveys or removal of biota can greatly limit the spatial extent for which data can be collected during the time constraints of a low tide cycle. Leveraged heavily on the Kachemak Bay nearshore monitoring work, we obtained additional funding from the Bureau of Ocean Energy Management/Coastal Marine Institute to test the use of a small unmanned aerial vehicle (sUAV) in rocky intertidal and intertidal seagrass surveys. This sUAV was used at one of our rocky sites (Outside Beach) and one seagrass site (Homer), and this work is being published as part of the GWA special issue in the peer-reviewed journal Deep-Sea Research Part II (Appendix 2).

RESULTS

Rocky intertidal communities

Based on previous work (e.g., Konar et al. 2009), we know that community structure at different intertidal height strata in rocky intertidal communities in the Gulf of Alaska is significantly driven by environmental variables associated with length of exposure and are themselves significantly different in terms of species composition, abundance and biomass. We, therefore, considered intertidal communities separately for the four intertidal strata in Kachemak Bay within the GWA. We used multivariate statistical analyses such as permutational analysis of variance (PERMANOVA) in the software package PRIMER-e v7 to assess effects of year and site on rocky intertidal community composition. Non-metric multidimensional scaling (MDS) was used to visualize these patterns.

Rocky intertidal communities in all strata had significant Year, Site, and Year x Site effects, explaining large portions of the variability in community composition. In the **high intertidal**, communities grouped strongly by year (Fig. 3a), which was supported by the results of a PERMANOVA as indicated by a much stronger Year than Site effect (Table 2). In contrast, in the **mid intertidal**, the factor Site had a slightly stronger influence than Year on the similarity of intertidal communities across years (Fig. 3b, Table 2). This was visible in the multi-dimensional scaling (MDS) (Fig. 3b) where sites were separated along the second MDS axis (top to bottom). Across years, sites (especially noticeable for Bishop's Beach and Bluff Point) followed a similar progression from left to right along axis 1 on the multidimensional plot during 2012 to 2015, and then a distinct return back along axis 1 in 2016 (Fig. 3b). Therefore, years mostly grouped along a similar location along axis 1 on the MDS. In the **low intertidal**, factors Year and Site were of similar importance in driving similarities of intertidal communities (Table 2). Grouping of sites by year was particularly obvious for 2016 (Fig. 3c). In the **-1 m subtidal** stratum, Year again was a slightly stronger driver of community similarity than Site (Table 2), again visible in the MDS stronger grouping by year than by site (Fig. 3d).

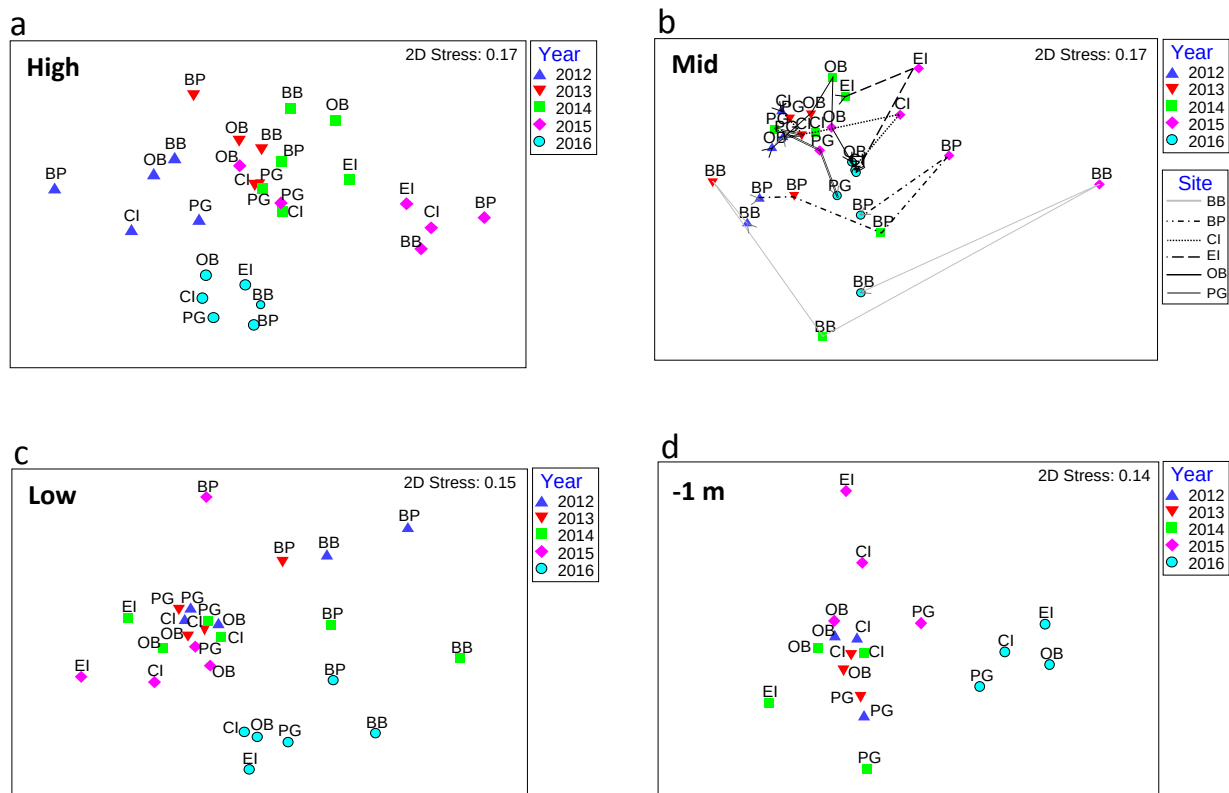


Figure 3. Multi-dimensional scaling plots of rocky intertidal community composition at sites in Kachemak Bay for 2012-2016 for the high intertidal (a), mid intertidal (b), low intertidal(c) and the -1 m stratum (d). See Table 1 for site names and locations.

Table 2. Permutational analysis of variance results on the effects of Year and Site on the rocky intertidal community composition by stratum.

<u>High Stratum</u>					
Source	df	SS	MS	Pseudo-F	P(perm)
Year	4	2.04E+05	51028	66.476	0.001
Site	5	96387	19277	25.113	0.001
Year x Site	18	1.10E+05	6099.1	7.946	0.001
Residual	251	1.93E+05	767.62		
Total	278	6.13E+05			
<u>Mid Stratum</u>					
Source	df	SS	MS	Pseudo-F	P(perm)
Year	4	1.42E+05	35568	39.216	0.001
Site	5	1.98E+05	39503	43.555	0.001
Year x Site	18	1.77E+05	9851.7	10.862	0.001
Residual	252	2.29E+05	906.97		
Total	279	7.50E+05			
<u>Low Stratum</u>					
Source	df	SS	MS	Pseudo-F	P(perm)
Year	4	1.14E+05	28440	34.004	0.001
Site	5	1.54E+05	30873	36.913	0.001
Year x Site	16	1.16E+05	7246.2	8.6637	0.001
Residual	231	1.93E+05	836.39		
Total	256	5.91E+05			
<u>-1 m Stratum</u>					
Source	df	SS	MS	Pseudo-F	P(perm)
Year	4	1.16E+05	29048	32.720	0.001
Site	4	92859	23215	26.149	0.001
Year x Site	10	79670	7967.0	8.974	0.001
Residual	171	1.52E+05	887.78		
Total	189	4.41E+05			

To examine trends in the sea star assemblages over time at each of the monitoring sites, we averaged the data from the swath surveys at the low intertidal and -1 m stratum over the years (including historical data since 2009). Overall, there were low densities in the early years. *Evasterias troschelii* was the most abundant species in early (2005-09) and late (since 2014) years, but experienced a drastic decline in 2012 and 2013 (Fig. 4). We also led an effort to investigate sea star patterns in comparison with other GWA regions (Konar et al. poster presentation at Alaska Marine Science Symposium in Jan 2017). *Evasterias troschelii* also was a dominant species in Katmai National Park and Preserve, while other species dominated in the other regions. In Kenai Fjords National Park, the assemblage was dominated by *Pisaster ochraceus* in most years, and this region had the overall highest sea

star abundances. Western Prince William Sound had the lowest number of sea star genera and also high variability in its two dominant species, *Pycnopodia helianthoides* and *Dermasterias imbricate* (also see Coletti et al. 2018).

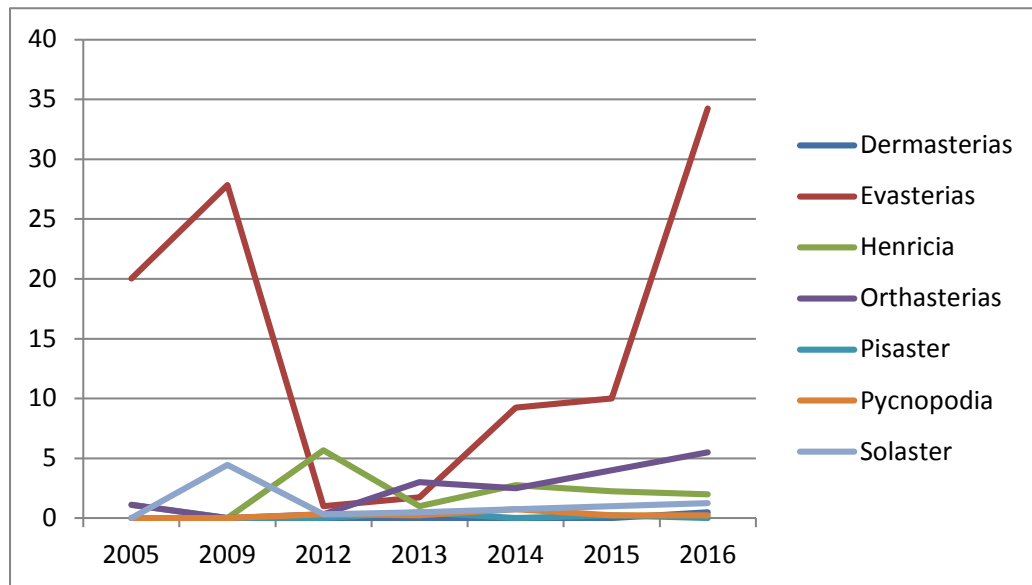


Figure 4. Sea star abundance in the combined low/-1 m strata in Kachemak Bay since 2005. Abundances are averaged across multiple sites in Kachemak Bay.

Considering the fast-spreading incidence of the sea star wasting disease throughout California and into southeast Alaska (<http://www.eeb.ucsc.edu/pacificrockyintertidal/data-products/sea-star-wasting/>), we took the opportunity in 2015 to survey sea stars during swath sampling in rocky intertidal regions for the incidence of sea star wasting disease. We observed a total of eleven sites (including our regular monitoring sites) and found up to 25% of stars diseased (at our clam monitoring site in China Poot, Fig. 5). The most commonly infected species was *Evasterias troschelii*, followed by *Pycnopodia helianthoides*. No wasting disease was observed during our regular surveys in 2014, but wasting continued to be observed in 2016.

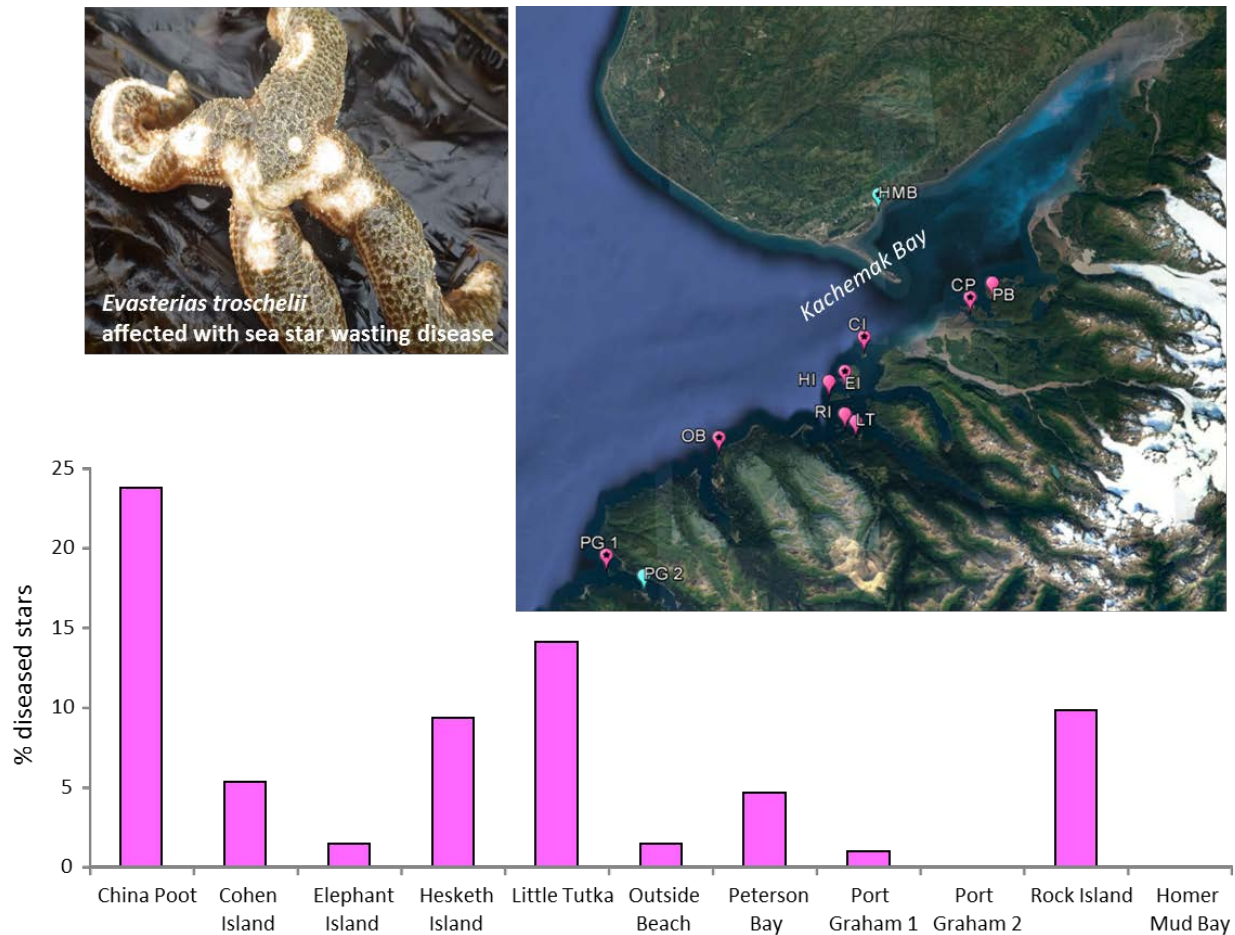


Figure 5. Abundance (%) of sea stars affected by sea star wasting disease at 11 sites in Kachemak Bay, including long-term monitoring sites within the GWA. These long-term rocky intertidal monitoring sites are marked on the top right map with black asterisk in the marker. Blue sites are those that did not have sea star wasting, pink sites had infected stars.

Intertidal mussel size-frequency distributions

Mussel size-frequency distributions were obtained from averaged quadrat samples per site, plotted in 1-mm increments, and patterns visually assessed. Mussel size-frequency distributions varied between sites and years for the same site, but a common pattern was that most mussels were in the smaller size groups (<5 mm). New settlement was usually highest in Port Graham and similar for Cohen Island and Outside Beach, although there was an unusually strong settlement event at Outside Beach in 2016 (Fig. 6). Although subsequent cohorts are not always distinct, 2-3 cohorts can be discerned (Fig. 7). Using a Bayesian approach (work is under development) we started to model mussel age from size cohorts. Assuming that these are annual cohorts, mussels in Kachemak Bay would live about 3 years.

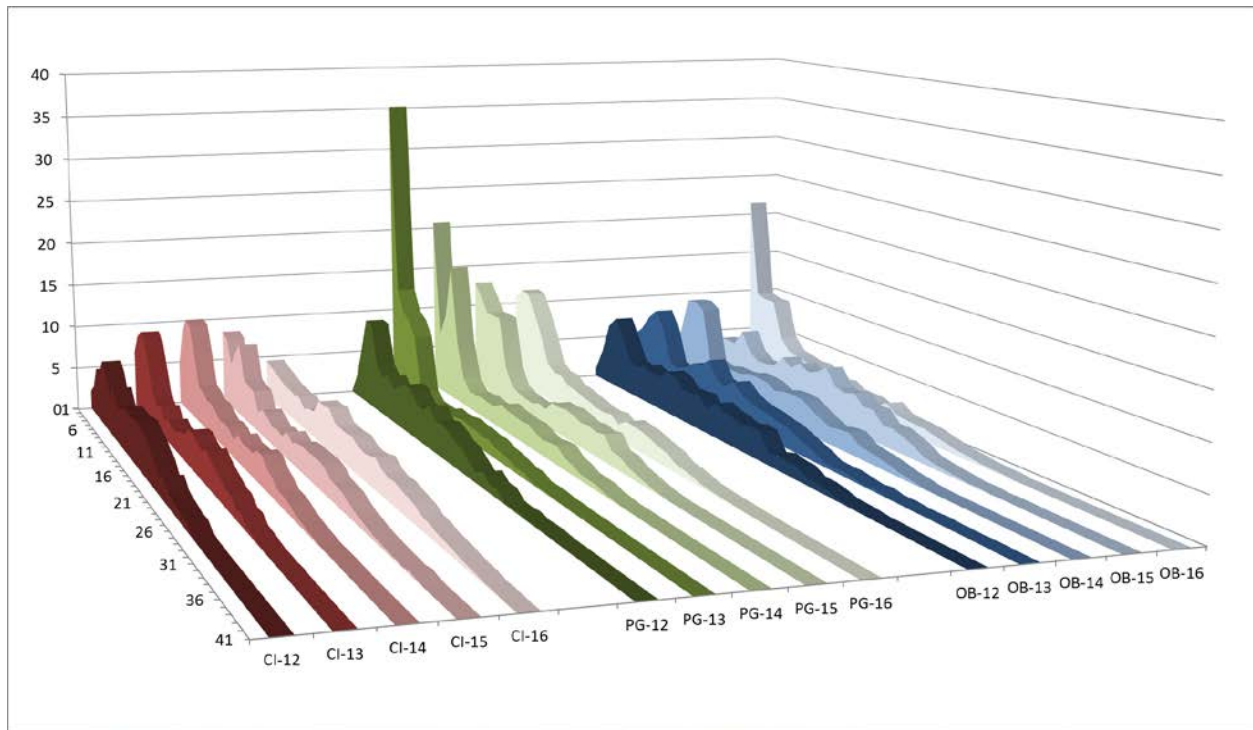


Figure 6. Mussel size-frequency over three sites: Cohen Island (CI), Port Graham (PG), and Outside Beach (OB) for years 2012-2016 by 1-mm size groups.

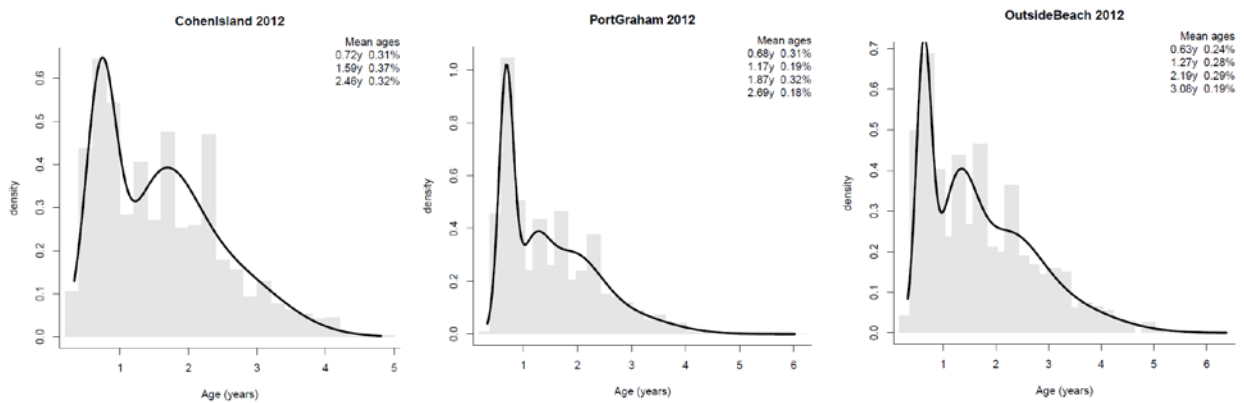


Figure 7. Cohort analysis of mussel size-frequency distributions in 2012 at three sites (Cohen Island, Port Graham, and Outside Beach) in Kachemak Bay. These indicate that mussels in Kachemak Bay generally don't live longer than 4 years.

We also led an effort to compare mussel size-frequency distribution in Kachemak Bay with that in other regions in the Gulf of Alaska (Iken et al. 2017, poster presentation at the

Alaska Marine Science Symposium in Jan 2017) using multivariate tools (PERMANOVA) to compare regional patterns. In this regional comparison (several sites averaged within a region), the overall size-frequency distribution patterns of mussels were relatively similar (PERMANOVA $p=0.075$; Fig. 8). Most mussels were ≤ 5 mm in size, followed by slowly declining numbers at larger sizes. In all years, Kachemak Bay had the highest proportion of newly settled mussels (≤ 5 mm), except for 2014, when Kenai Fjords National Park had the highest abundance of small mussels, with 67% of the mussels being ≤ 5 mm. In all years, abundance of newly settled mussels was always lowest in Western Prince William Sound ($<20\%$). Katmai National Park had generally the largest occurrence of larger mussels (>30 mm) of all regions in all years, with the largest mussel in this study found at 54 mm in 2015. However, there were significant differences in mussel size distribution among years (PERMANOVA $p=0.025$). Across regions, the proportion of mussels ≤ 5 mm was highest in 2014, except in Western Prince William Sound. This strong settlement cohort was particularly evident in subsequent years at Kenai Fjords National Park and Katmai National Park.

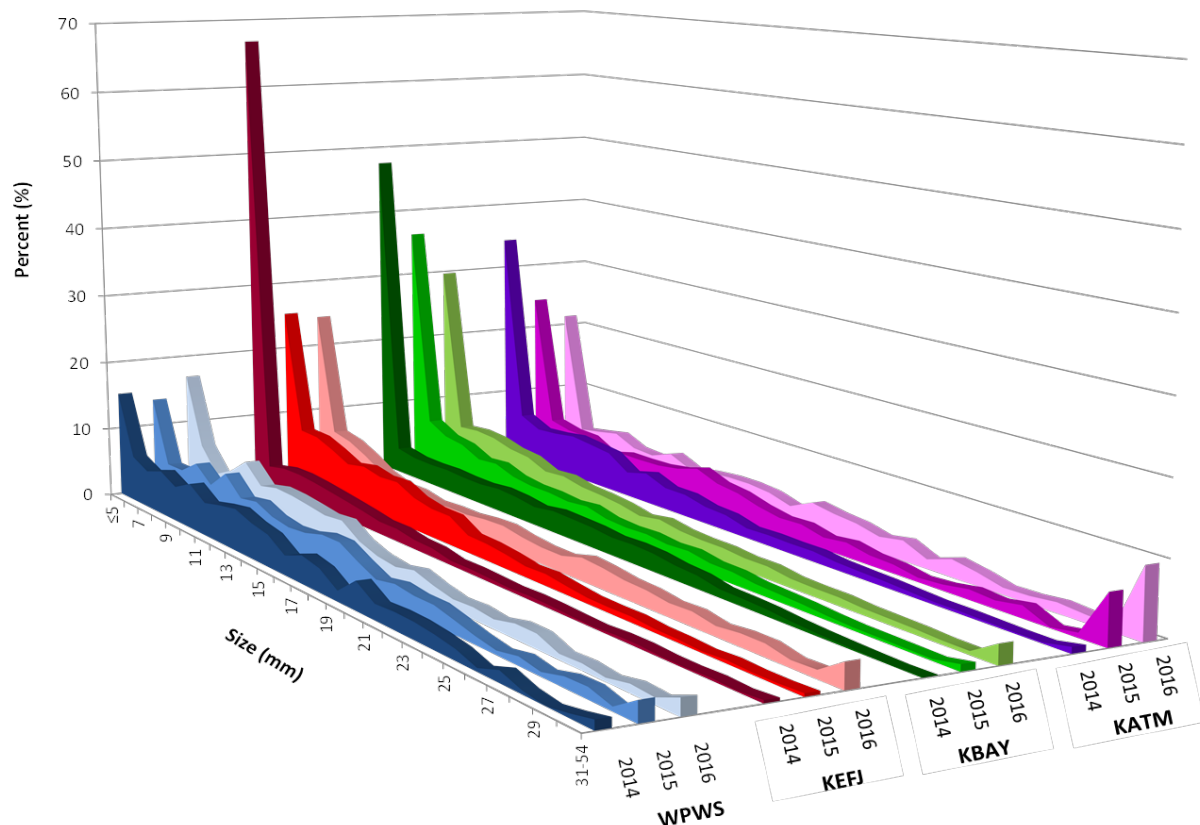


Figure 8. Mussel size-frequency distributions in four regions in the Gulf of Alaska (Western Prince William Sound [WPWS], Kenai Fjords National Park [KEFJ], Kachemak Bay [KBAY], and Katmai National Park [KATM]) over three years (2014-2016). Data from several sites per region were averaged. Size groups ≤ 5 mm and >30 mm were grouped.

Infaunal clam density trends

We sampled clams in 2013 and 2015; hence, the observation period is not long enough to discern any long-term trends or to apply statistical analyses. Over the two years, we did not observe any consistent patterns in total average clam density across sites. Clam densities increased at Jakolof Bay and Port Graham and decreased at China Poot and Bear Cove. The most common clam taxa were *Macoma* spp. (mostly, *M. nasuta*, *M. inquinata*, *M. calcareo*), *Saxidomus gigantea*, and *Leukoma staminea*. Distribution of clam species across sites differed with some consistent patterns over the two sampling years (Fig. 9): *Saxidomus gigantea* was the most abundant taxon at China Poot but did not occur at Port Graham. *Leukoma staminea* occurred at all sites except Port Graham but was most abundant in both years at Bear Cove. *Macoma* spp. is the only taxon that occurred at all sites. Overall number of clam species found was lowest in Port Graham and similar at the other sites.

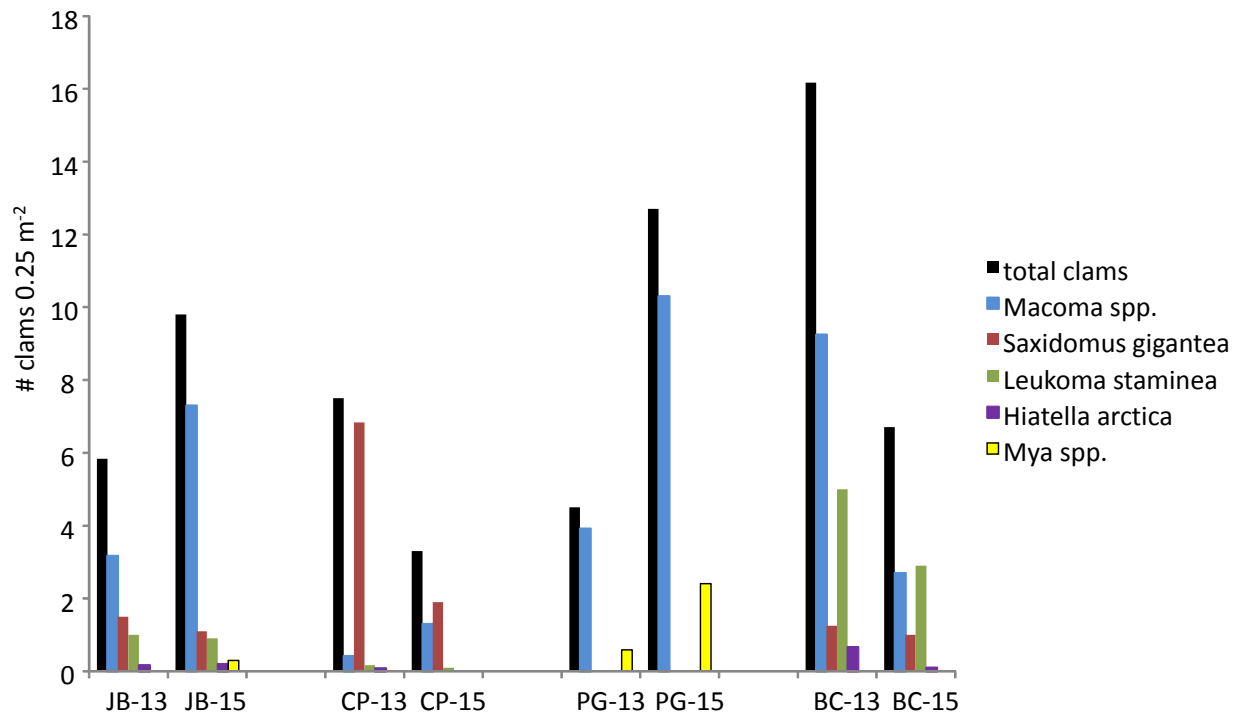


Figure 9. Clam abundance and species distribution at four sites in Kachemak Bay: Jakolof Bay (JB), China Poot (CP), Port Graham (PG), and Bear Cove (BC) over two sampling years (2013 and 2015).

Seagrass shoot density trends

Seagrass shoot density varied strongly between years at some of the sites and less so at others (Fig. 10). In Jakolof Bay, we observed a drastic decline in shoot density between

2012 and 2014 from approximately 40 to less than 10 shoots 0.25 m^{-2} . This seagrass bed then showed a marked recovery to > 75 shoots 0.25 m^{-2} in 2015 and 2016. The decline in the first three GWA years is part of a longer-term trend we have been observing in Jakolof Bay since 2003, when shoot densities at that site were as high as 169 shoots 0.25 m^{-2} at the onset of the decline (Fig. 11).

The opposite trend was observed at Herring Island, where shoot counts were high in 2012 and 2014 (> 75 shoots 0.25 m^{-2}) but then dropped to less than half those densities in 2015 and 2016 (Fig. 10). Shoot densities at the other two sites, Petersen Bay and Homer Spit, were more even across years, although both sites had lowest shoot densities in 2016.

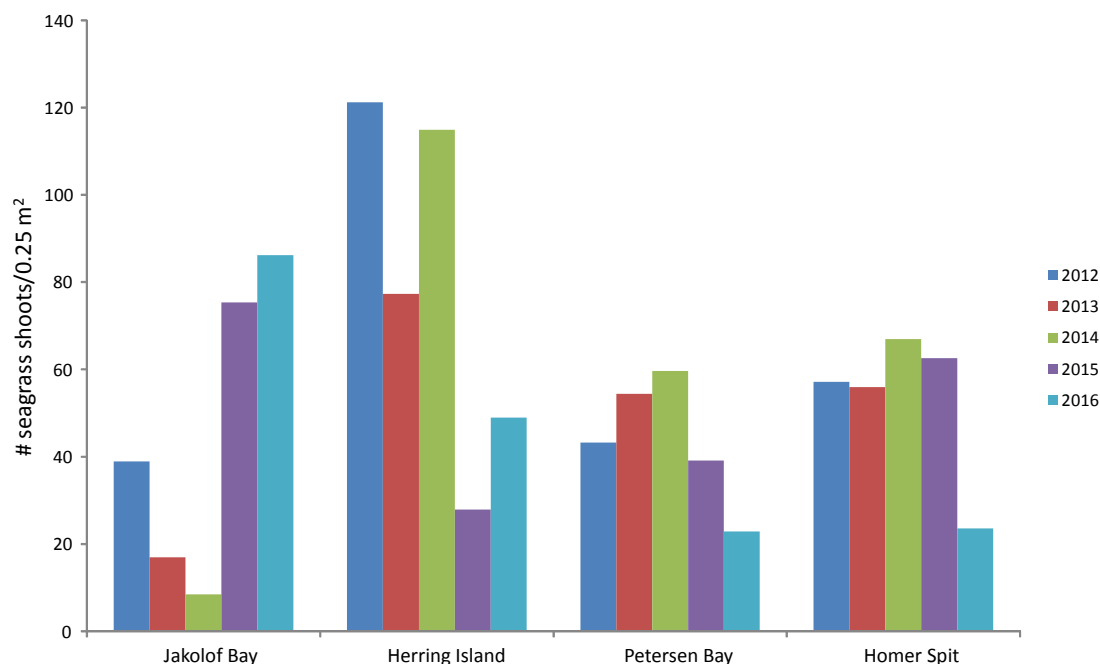


Figure 10. Seagrass shoot density at four sites in Kachemak Bay from 2012 to 2016.

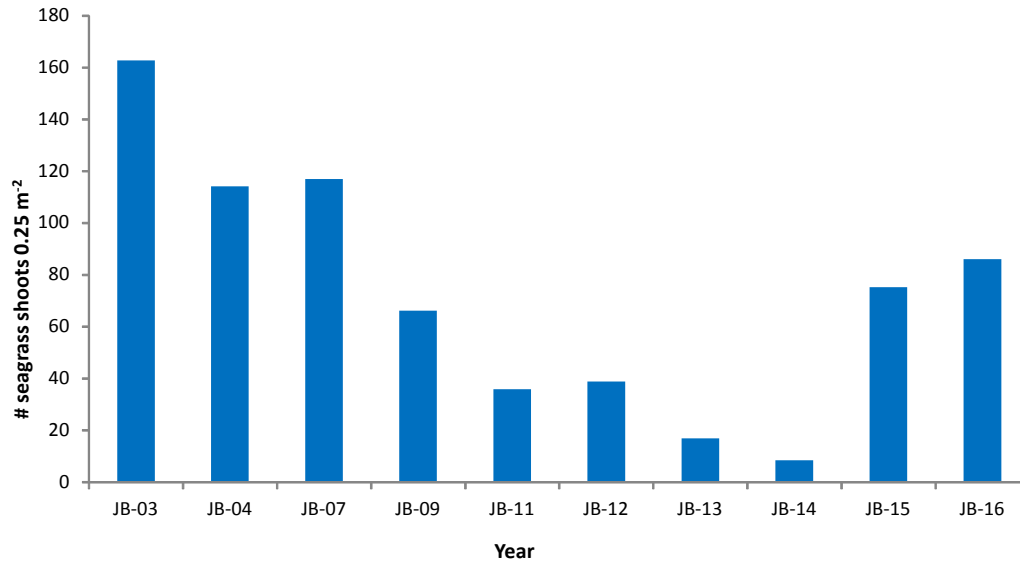


Figure 11. Long-term trend in seagrass shoot density at Jakolof Bay from 2003 to 2016, based on historical collections at that site.

Environmental variables and their relation to rocky intertidal communities

Temperature records taken in the low intertidal at rocky sites are incomplete because of loss of loggers. We assembled temperature records for the northern shore of Kachemak Bay from composites of loggers at Bishop's Beach and Bluff Point, and used temperature records at Outside Beach (since 2013 only) as representative of temperatures at the southern shore of the bay (Fig. 12a). General temperature profiles were colder on the north than the south shore, especially in winter. However, on both shores we observed a distinct warming of both summer and winter temperatures over the study years, where winter water temperatures were around (north shore) or above (south shore) 5°C (Fig. 12a,b). Similarly, summer water temperatures were consistently above 10°C since 2014 on both shore sides.

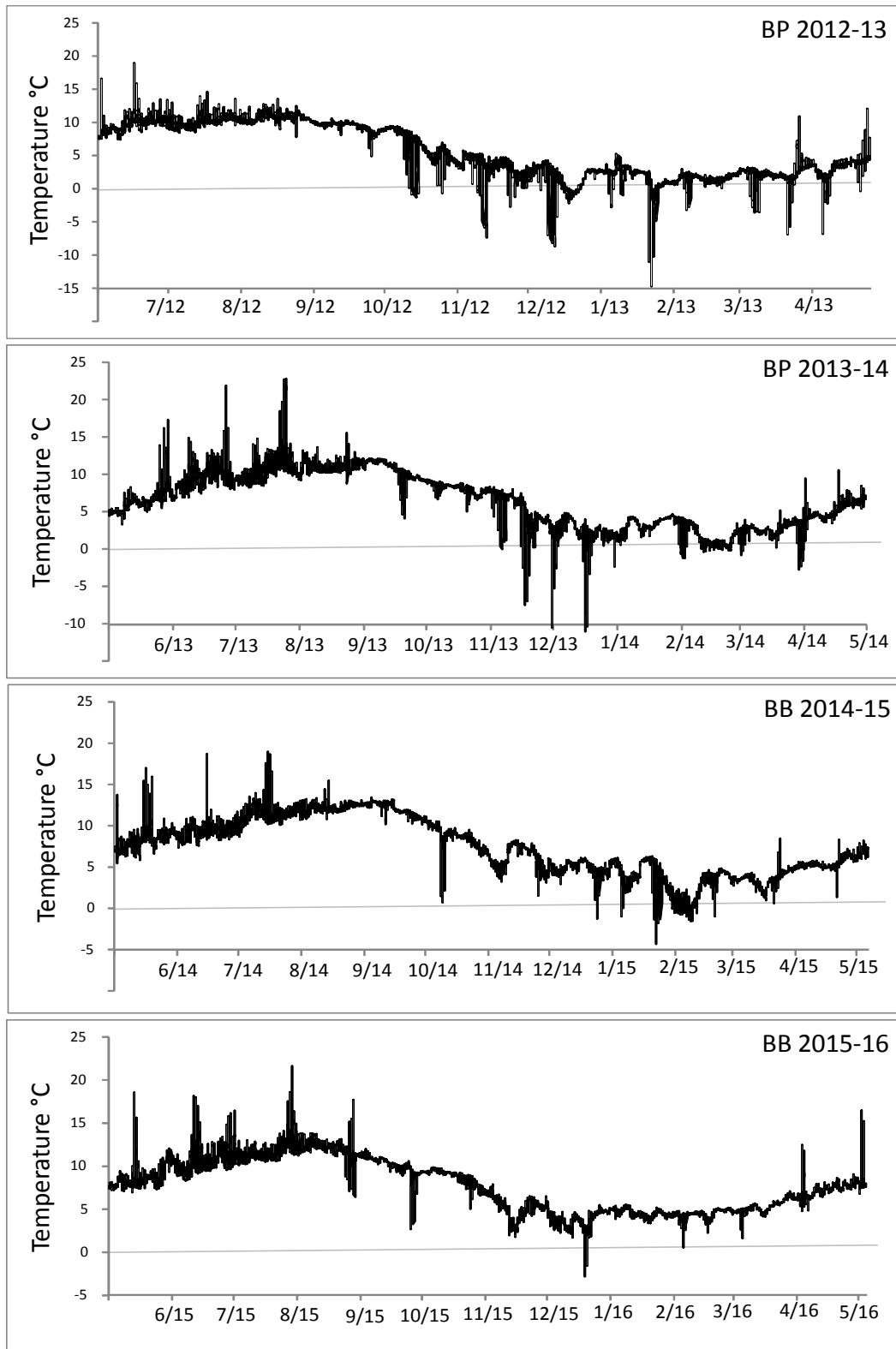
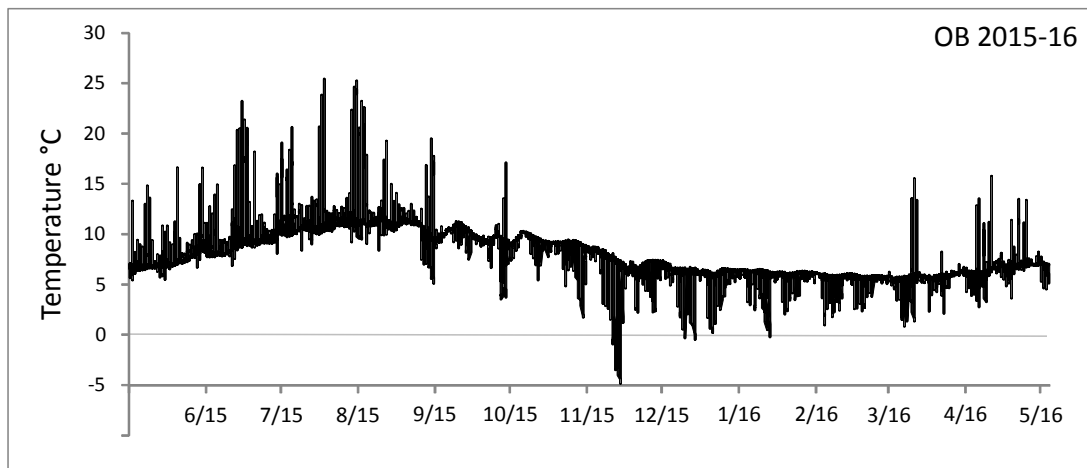
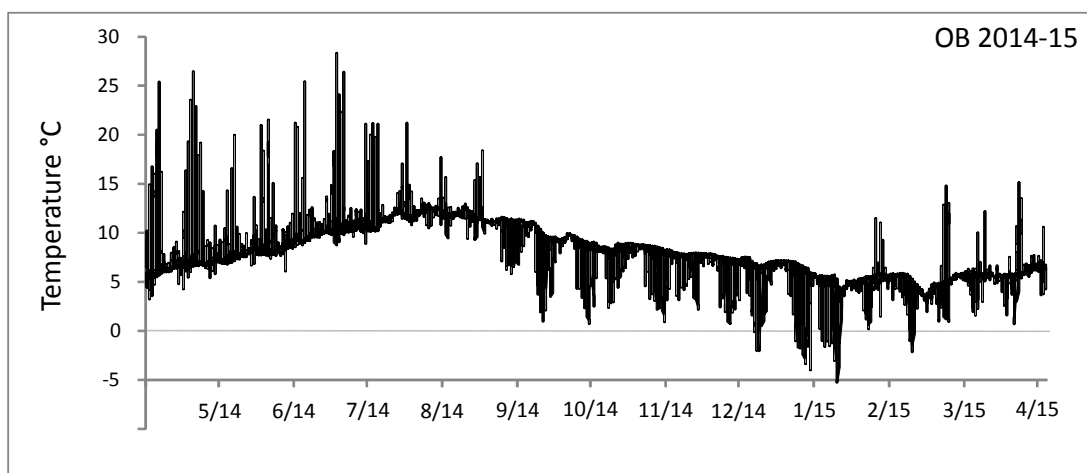
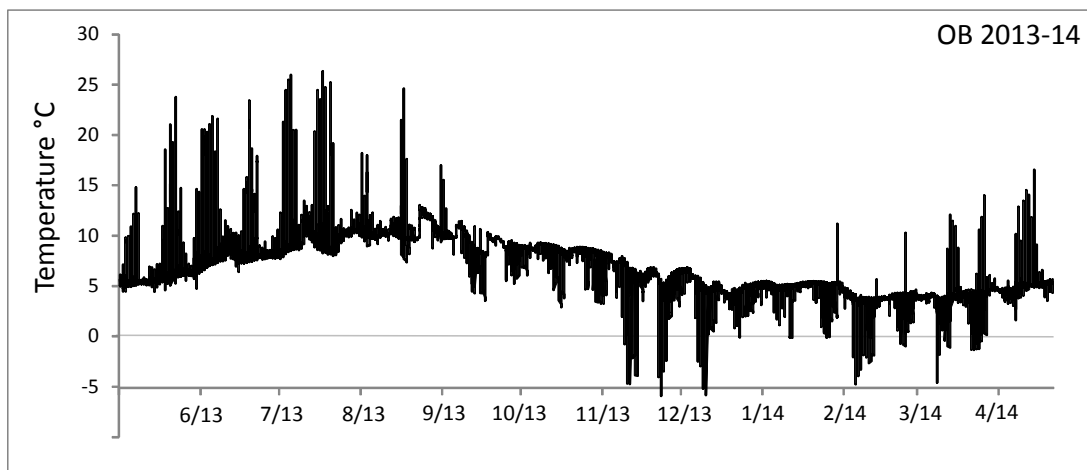


Figure 12. Temperature records (HOB0 loggers at the low intertidal level). Spikes are air temperatures at tidal cycles when the low tidal stratum becomes exposed. (A) Sites on the north shore of Kachemak Bay (see Table 1).



(B) Sites at Outside Beach on the south shore of Kachemak Bay.

We also measured static environmental drivers, those that do not change over short time scales such as seasons to a few years. Those included direct measurements of substrate in the rocky intertidal as well as derived measures of exposure, fetch, distance to freshwater and glaciers, etc. We led an effort to correlate these static drivers to rocky intertidal community structure on a regional scale (including Prince William Sound, Katmai National Park and Preserve, Kenai Fjords National Park). See publication for report on this topic: Konar et al. 2016 (Appendix 3).

Sea otters

Sea otter population assessments

The best estimate of sea otter abundance in Kachemak Bay is $5,927 \pm 672$ animals from an aerial-based survey conducted in 2012 (the abundance estimate is still preliminary until finalized by the USGS). No other surveys of abundance were conducted during the reporting period; however, incidental observations of marine mammals and birds were recorded during the oceanographic surveys in Kachemak Bay and lower Cook Inlet 2012-2016 (Doroff and Holderied 2017). Sea otters were the most abundant marine mammal encountered in the study area.

Sea otter prey assessment

Visual Observations: All current and historical focal animal sampling data on sea otter diet were incorporated into the USGS Gulf Watch Alaska Benthic Monitoring sea otter forage database and are not reported on here (see Coletti et al. 2018). Historical data from before the GWA monitoring period are summarized in Doroff et al. (2012). In the past, we identified based on visual observations in Kachemak Bay that clam, mussel, and crab make up 38%, 14%, and 2% of the diet, respectively, for prey items that could be identified (Doroff et al. 2012).

Scat Analyses: To summarize the categorical data on diet from scat samples, we used the median frequency index value for each prey category and averaged by winter period (Fig. 16).

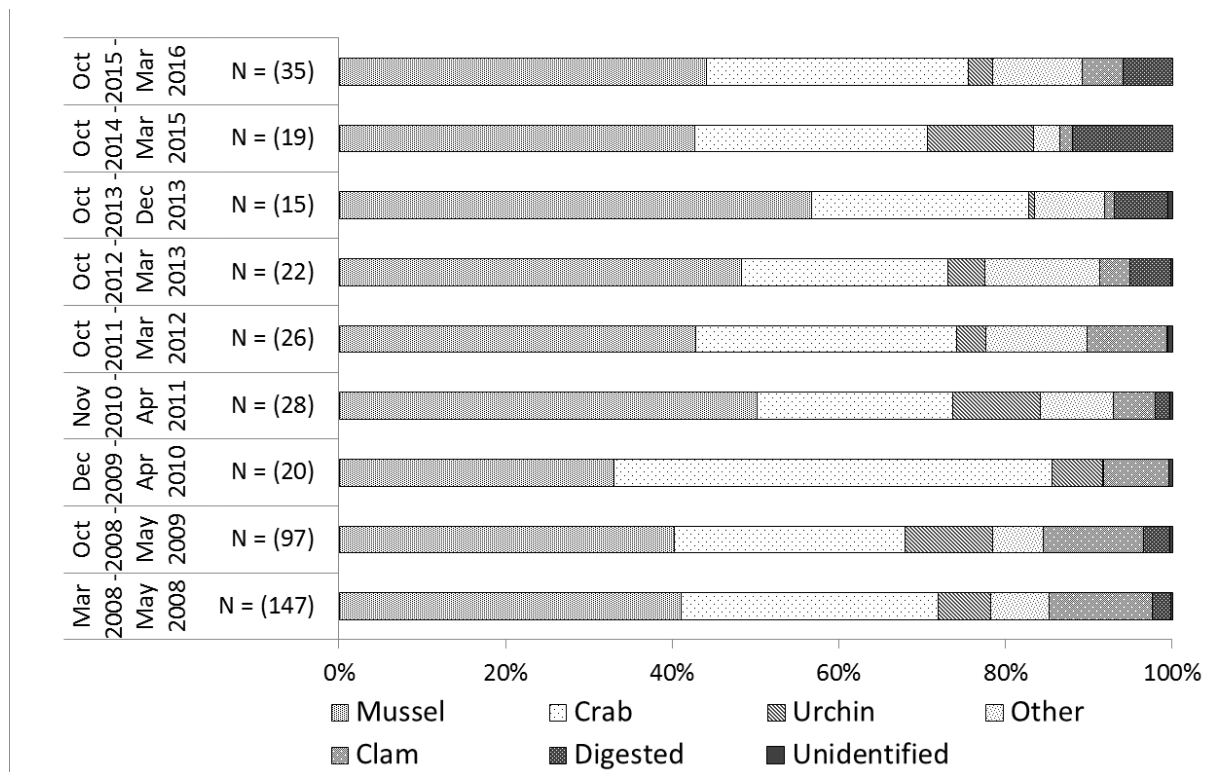


Figure 13. Relative prey composition from sea otter scat collected during 2008-2016 during the winter months in Kachemak Bay, Alaska. Prey composition of individual scat samples was averaged by “winter period” and composition was compared over time. In 2008-2009, scats were collected and processed from multiple sampling sites; however, in 2009-2015 a single site was sampled monthly from late fall through the spring.

Individual scat samples on average contained 3-4 distinct prey types per sample; however, mussels (*Mytilus trossulus*) generally made up most of the recorded prey in any given sample. Mussels are an important prey, particularly for the young-of-the-year otters but they are less nutritious than the larger clams. Crab shell fragments were the second most frequent prey category documented in the sea otter scat and most were *Telmessus cheiragonus*, with occasional identification of *Glebocarcinus oregonensis*, *Pugettia gracilis*, *Oregonia gracilis*, and *Hapalogaster mertensi* in the scats.

The scat sampling site in Kachemak Bay is primarily an adult female area. To document which sex/age classes of sea otter were hauling out at our site, we deployed a Reconyx wildlife game camera in winters 2015 and 2016 (some failures are still being investigated). The camera is motion sensitive and allows us to identify the animals using the floating dock during the daylight and night time hours. Thus far, the camera has confirmed the haulout is mostly an adult female area (Fig. 17) and has documented multiple species using the winter haulout site. For example, we documented a sea otter and river otter interaction on the haulout (Fig. 18). When neither otter species was present, we identified another small mustelid that has used the raft on more than one occasion, very likely a mink given the behavior of the animal.



Figure 14. This is a fairly typical image from the Reconyx wildlife motion sensor camera at the scat collection site. Sea otters tend to haul out more at night (though not exclusively); this image shows three adult-sized otters and two dependent pups on a floating raft.



Figure 15. A: Four North American river otters (*Lontra canadensis*) hauled out at our Kachemak Bay scat sampling site during daylight hours. B: A sea otter and two river otters interact while hauled out on the float. The river otters approached the resting sea otter multiple times without physical contact. The sea otter hissed at the two river otters but gave no further sign of disturbance until we recorded a single frame where all otters had left the haulout.

Our observations on naturally occurring and experimentally dug pits showed that pit dimensions are not a reliable tool to distinguish otter foraging from sea star foraging. Fresh

pits become indistinguishable after 2 weeks. In contrast, shell litter proved useful in quantifying predator-specific predation. For details see Traiger et al. 2016 (Appendix 1).

Sea otter mortality

Sea otter carcasses numbered 41, 62, 90, 201, and 120 for project years 2012, 2013, 2014, 2015, and 2016, respectively, in lower Cook Inlet, Anchor Point region (n=28) and Kachemak Bay (n=486). Strep Syndrome was identified in approximately 18% of the known causes of mortality in 2012-2014. Strep Syndrome in this context is described as a bacterial streptococcal infection and it manifests itself in a variety of ways such as valvular endocarditis, septicemia, or encephalitis (Burek et al. 2005). During 2015, documented mortality of adult male otters spiked (Fig. 13-15), and 83% of the recovered animals necropsied presented with Strep Syndrome conditions; results are pending for 2016.

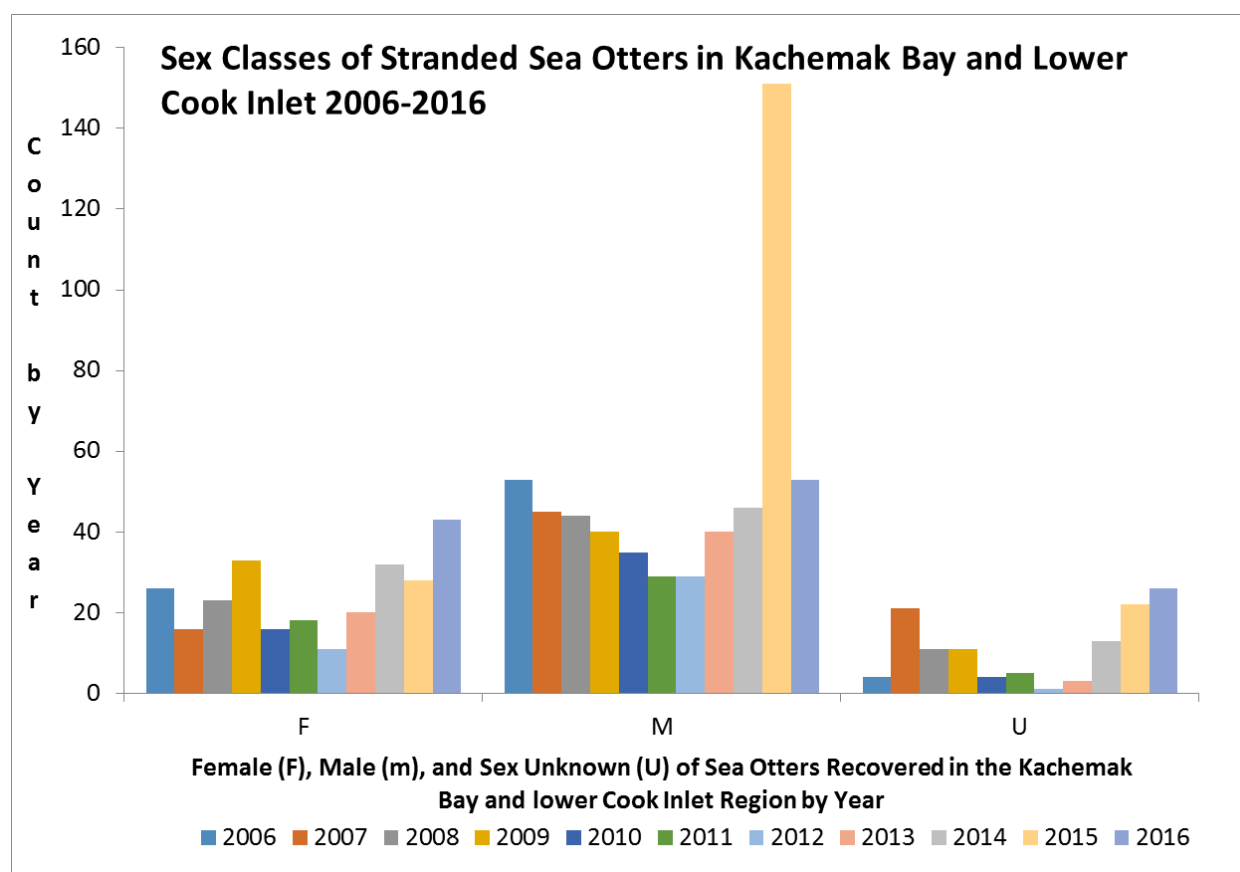


Figure 16. Number of dead sea otters recovered by the Marine Mammal Stranding Network of volunteers in Kachemak Bay and lower Cook Inlet during 2006-2016, summarized by sex and year (data provided by the U.S. Fish and Wildlife Service).

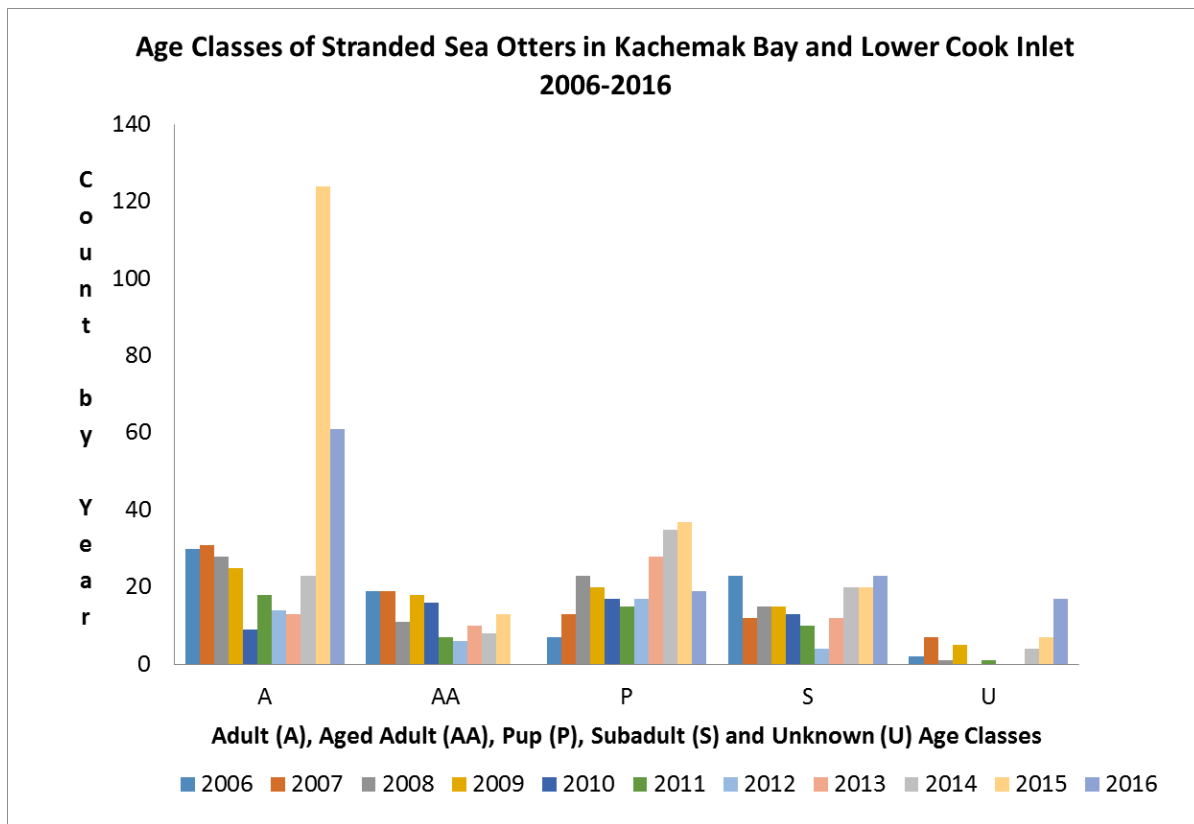


Figure 17. The number of dead sea otters recovered and reported on national marine mammal stranding Level A data forms by year and age class; ages were estimated at the time of necropsy. A = adult (≥ 4 yrs); AA = aged adult (>10 yrs) S = subadult (1-3 yrs); P = pup (0-1 yrs); U = unknown age class.

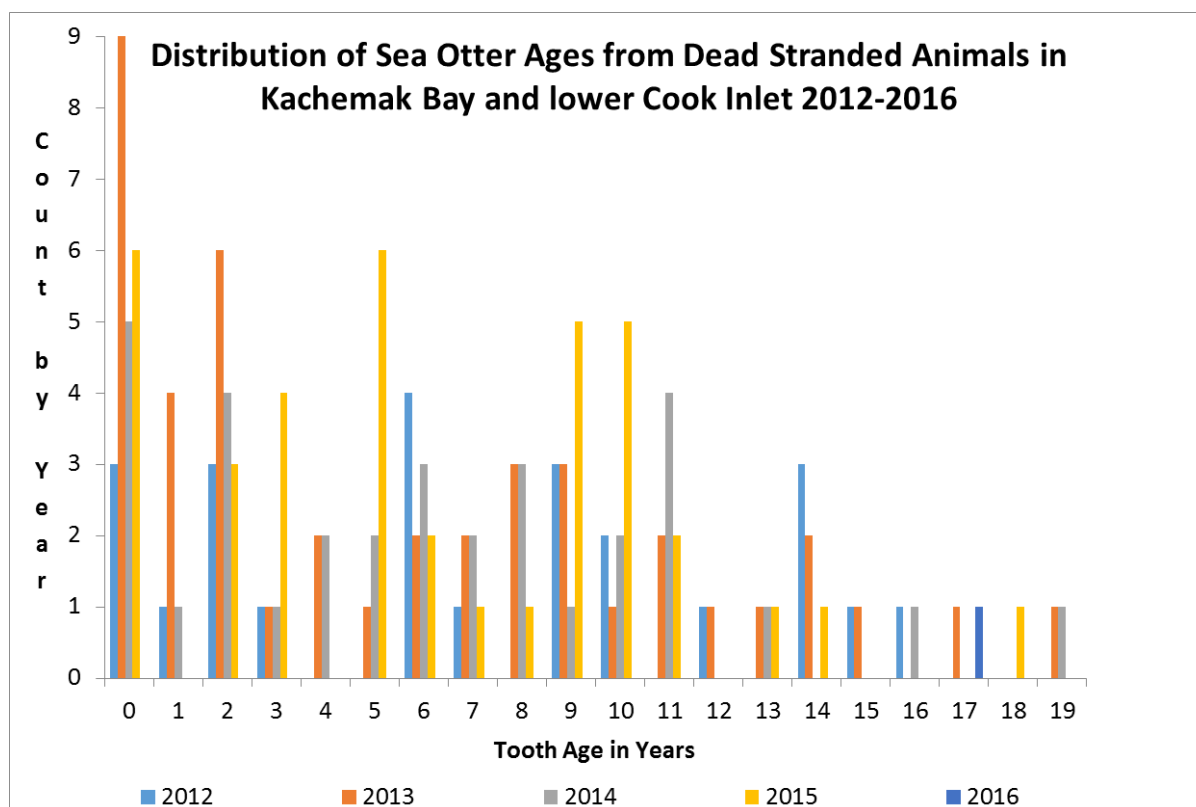


Figure 18. The number of dead sea otters recovered and reported on national marine mammal stranding Level A data forms by year, and age determined by premolar annuli (Matson's Laboratory, LLC) and provided by the U.S. Fish and Wildlife Service. At the time of this report, not all ages were processed for 2016.

Marine debris

The CACS collected marine debris in the Kachemak Bay and lower Cook Inlet region in 2013-2016. The results are summarized in the Table 3. Debris findings, when standardized to person -hours) were not obviously different among years, except for noticeably lesser collections in 2015 (0.9 pounds of trash per person-hour in 2015 compared with 1.5 - 1.9 pounds of trash per person-hour in other years). We currently are not able to link debris loads to any cause.

Table 3. Effort and debris collected by Center for Alaskan Coastal Studies citizen groups in Kachemak Bay.

	2013	2014	2015	2016
# Observers	632	248	289	553
Hours spent	98	49	44	76
Person-hours	1172	399	838	1030
Shoreline walked (miles)	50	28	28	32
Total trip mileage	68	89	63	48
Trash bags collected	104	43	66	233
Estimated weight of trash (pounds)	2246	599	792	1701

Advancing technology

When data obtained from sUAV imagery were compared to data from observers on the ground, observer visual data always resulted in the highest taxon richness. But when observer data were aggregated to the same taxonomic resolution obtained by the sUAV images, overall community composition was mostly similar between the two methods. In seagrass beds, we found that sUAV imagery was useful to determine overall seagrass cover versus bare substrate, and with that assess variability over the large spatial scales that can be covered with the sUAV. Hence, this technology could benefit those research questions or monitoring goals that can be answered at a low taxonomic resolution. See publication on this topic: Konar and Iken *in press* (Appendix 2).

DISCUSSION

The first five-year phase of the GWA in Kachemak Bay has led to a better understanding of the system and an appreciation of the scales of variability of important nearshore habitats. We have made strides to better integrate work in Kachemak Bay with that in the other Gulf Watch nearshore regions and have led multiple efforts on Gulf of Alaska-wide publications and presentations. This first 5-year phase of the planned 20-year GWA Program has successfully expanded historical information we have of these nearshore systems in Kachemak Bay, contributing the much-needed long-term time series that will eventually allow us to better understand temporal variation and drivers of this variation. Much of these long-term data should also be valuable and relevant to management because the habitats that are monitored as part of the program are of subsistence, recreation, and commercial importance. Long-term monitoring is the only way that trends in these important habitats can be discerned and causes of events such as high recruitment and mortality can be found and potentially explained.

All objectives were met, and additional ones were added (analysis of sea star versus sea otter pits, advance technology to monitoring intertidal communities). Some objectives that were addressed through collaborations, such as the marine debris assessments, were difficult to analyze in-depth and should be considered ancillary. We gained valuable learning experiences in the first 5-year phase of this project of what can be accomplished with available resources; we will use these experiences to adapt the design of the next phase of this long-term monitoring program.

Rocky intertidal communities

In the rocky intertidal, we found an overall strong effect of year on community composition. This shows that while sites differ, common trends among sites are observed over time. This suggests some environmental drivers that act on a Kachemak Bay-wide level have an influence on rocky intertidal community composition. This is seen in the shifting of these communities in similar directions across sites. This means that these drivers most likely are dynamic, i.e., change interannually. This confirms the conclusion we also have drawn from our work on investigating the influence of static environmental conditions on community composition (Konar et al. 2016, Appendix 3), where we found

that static drivers (i.e., distance to fresh water inputs, fetch, etc.) left a significant amount of variation in community composition unexplained.

Differences in the response of rocky intertidal communities on an annual basis (Fig. 3) suggests that the effect of any specific drivers varies with the specific site location and the level of intertidal exposure (i.e., strata are differently affected), or that responses are based on different taxa dominating the communities at different strata. It seems that the time series for rocky intertidal community composition in Kachemak Bay we are accumulating through this long-term monitoring program may soon be sufficient to discern the effects of specific environmental drivers, such as temperature. Recent years have experienced a strong warming trend in the Gulf of Alaska based on climate warming, a strong El Niño effect, and the warm water anomaly (Kintisch 2015). This temporal warming across all our sites should provide some years where extreme values of this driver should assist with strong correlation values, if temperature is indeed a driver of these systems. Accordingly, we have found that temperatures in the low intertidal in Kachemak Bay have changed, namely have become warmer, over the monitoring period (Figs. 12a and b).

Sea stars

Within the rocky intertidal, sea stars are important predators and can act as keystone species that affect the entire community structure (Paine 1969). While sea stars in the Kachemak Bay rocky intertidal may not fulfill a true keystone species function, they undoubtedly are important ecological components regulating their prey resources. Thus it is important to monitor their abundance over space and time (Chenelot et al. 2007). This has become more critical with the arrival of the sea star wasting disease in the central Gulf of Alaska (Fig. 5) in 2015. This disease, transmitted by a densovirus and leading to mass mortalities in sea stars along the central Pacific coast (Hewson et al. 2014), seems to be regulated by warming temperatures (Bates et al. 2009). A drastic change in sea star abundance based on mass mortalities has the ability to greatly change rocky intertidal community structure. We observed up to 25% of sea stars affected by the disease in 2015, with most of the affected individuals being *Evasterias troschelii* (Fig. 5). At the same time, we observed a strong increase in the abundance of this species in Kachemak Bay since 2015 (Fig. 4). Hence, it does not seem that the disease has had a detectable effect on sea star abundance, although continued monitoring is needed to assess whether there will be effects in the future – be that from a decrease in sea stars from the wasting disease or the observed increases in sea stars over the past two years. Sea star trends are important for management because many of these sea star species are top predators and can have large impacts of other species of subsistence and recreational interests (mussels, clams, and some chitons (“bidarki” = *Katharina tunicata*).

Intertidal mussel size-frequency distribution

Similar to sea stars, mussels are ecologically important components of rocky intertidal systems in Kachemak Bay. We found over the past 5-year monitoring period that size-frequency patterns of mussels differed at the three main rocky intertidal monitoring sites (Fig. 6). Settlement of new mussels was particularly high in Port Graham in all years, only exceeded by settlement at Outside Beach in 2016. It is possible that differences in settlement are driven by differences in larval supply, which could be driven by

oceanographic processes that force larval dispersal patterns. Port Graham is the outermost location in Kachemak Bay, under the direct influence of inflowing water from the Gulf of Alaska (Muench et al. 1978). There also is local upwelling in this region, which could create local oceanographic patterns of larval retention that enhances settlement in this region of the bay (Morgan et al. 2009). Similarly, tidal flux and/or density stratification patterns due to varying freshwater influence can influence larval abundance on local scales, and may thus be a strong influence on local settlement patterns (Murphy and Iken 2013).

The observed consistent site-specific differences in new mussel larval settlement did not translate into differences in mussel age classes. While local drivers such as predation, other physical removal pressures (storms, ice scour, etc.), or available food supply for mussels influence the abundance of larger mussels at each site, overall conditions in the bay or similar genetic makeup could be reasons for the overall similar maximum age of less than four years (Fig. 7). Similar explanations could account for the regional differences in mussel size-frequency distribution across regions within the Gulf of Alaska (Fig. 8). Prince William Sound was striking with low mussel settlement across study years, possibly indicating limitations in larval supply or retention in that region. This could contribute to the lack of recovery in mussel density and bed size in Prince William Sound after recent declines in these metrics (Bodkin et al. 2017).

Infaunal clam density trends

The GWA allowed us to begin monitoring infaunal clam populations in Kachemak Bay. In the two years we sampled clams, we found variability within and among our sites. Clam abundance and species composition is known to be influenced by substrate composition, environmental conditions (e.g., salinity), food availability, and disturbance pressure from natural (e.g., predation) or physical (e.g., storm events) causes (Schoeman and Richardson 2002). As some of these metrics can change among years, variation in clam abundance or species composition could be explained, even though clams are relatively long-lived (e.g., at least 8 years for *Macoma balthica* [Powers et al. 2002], and *Leukoma staminea* [Paul and Feder 1973] in the Gulf of Alaska) and integrate at least some of the temporal environmental variation. Events that could decimate clam abundances very suddenly would be major predation events or other local disturbances. We have no knowledge of those factors at the monitoring sites but those could be important metrics to study in the future. Certainly more static attributes such as substrate composition will likely play a role in clam distribution and composition. Notably, the least number of clam species was found in Port Graham (Fig. 9) and visual inspection suggests that this could be due to a more sandy substrate. We plan to measure substrate grain size in the following 5-year monitoring period (2017-2021) of this program. Two of the monitored species, the butter clam *Saxidomus gigantea* and the littleneck clam *Leukoma staminea* are both important recreational and subsistence species in Alaska. For both species we saw a decline between 2013 and 2015, which coincides with reports of other bay-wide declines and concerns for these species. Future monitoring years will show if this trend continues and these monitoring data should help to better understand trends and potential causes.

Seagrass shoot density trends

The final habitat that was monitored in Kachemak Bay is seagrass beds. Previous to the GWA, we had some prior seagrass data from Jakolof Bay from the NaGISA project and we were part of a global experiment testing the effects of nutrient addition and grazers on seagrass beds (ZEN = *Zostera* Experimental Network, Duffy et al. 2015, Ruesink et al. in review). The GWA Program has enabled us to expand our sampling to include three more seagrass beds. Seagrass shoot density is an important measure of habitat quality for a diverse assemblage of fish and invertebrate users of this essential coastal habitat type. Higher shoot density fosters higher associated community diversity and also higher protection against wind-induced stresses (Boström and Bonsdorff 2000). In Alaska, seagrass also is known as a substrate for herring spawn (Haeghele and Schweigert 1985), and higher shoot density may play an essential role in the recovery of this injured resource by the *Exxon Valdez* oil spill. We observed some dramatic changes in shoot density over the monitoring time (Fig. 10) and beyond (at Jakolof Bay since 2003, Fig. 11). One reason for variation in shoot density among study years may be related to timing of the surveys: monitoring in Kachemak Bay typically happens early in the growing season (late April, early May). Seasonal emergence of shoots and shoot density in *Zostera* sp. is sensitive to ambient light conditions, which triggers monopodial branching of the rhizome, increasing shoot density (Vermaat and Verhagen 1996). In a high-latitude system such as Kachemak Bay that has a strong seasonal light signal, differences of just a few weeks of survey time (driven every year by the timing of a good low tide series, which is needed for intertidal monitoring) may influence shoot densities found. However, if this were to be a strong driver of shoot density, one would expect that during years of early monitoring (e.g., April in 2014), all sites would have lower shoot densities compared with years of later monitoring times (e.g., May in 2013). We did not see consistently low or high levels of shoot densities across sites for the different monitoring years, indicating that this seasonal variability has likely a small overall effect.

The inconsistent trends in seagrass shoot density over survey years indicate that drivers of this variability are local rather than regional (i.e., not Kachemak Bay wide). These factors could be sedimentation or competition with other space occupants (e.g., kelp). At a high intertidal seagrass site adjacent to a salt marsh such as Jakolof Bay, we assume that the sediment-depositing, land-gaining environment may play a role in the drastic changes in shoot density over time (Fig. 11). At low energy sites at the heads of bays, sediment accretion can limit seagrass development unless major disturbances (like storms) create open space for seagrass growth again (Cabaço et al. 2008). It seems that seagrass sites in Kachemak Bay (example Jakolof Bay) can undergo decreases of up to 95% in shoot density (Fig. 11, between 2003 and 2014), possibly due to sedimentation effects, but that recovery is possible. Only longer-term monitoring can show if recovery is stable over time. The continued monitoring will be of interest to management because of these beds are of such importance as nursery grounds to many commercial and subsistence species.

Sea otters

Given the sea otter population survey data to date, it is difficult to assess where the Kachemak Bay/ lower Cook Inlet sea otter population is relative to equilibrium density. Through 2012, we were estimating an approximate population growth of 13% yr⁻¹, which

is below the maximum for the species given unlimited food resources but well above recorded estimates recolonizing populations in nearby the Kodiak Archipelago. During 2014, the USFWS conducted sea otter population estimates around the Kodiak Archipelago and preliminary survey results indicate an abundance estimate of $13,274 \pm 1,885$ animals. Estimates of sea otter abundance were not significantly different from the Kodiak Archipelago 2004 estimate of $11,005 \pm 2,138$ animals. In 2015 and 2016, USFWS initiated sea otter population surveys for lower Cook Inlet and Kamishak Bay but were unable to complete them due to weather (J. Garlich-Miller, pers comm). We will be working with USFWS and USGS in the next monitoring period to update the sea otter population estimate for Kachemak Bay/ lower Cook Inlet in 2017.

Since an “unusual mortality event” of sea otters in 2006 in Kachemak Bay, the USFWS has been tracking the Strep Syndrome in Kachemak Bay area otters. However, sea otters dying from the syndrome in late 2015 appeared healthier than in past years and there is concern that viral infections may be playing a contributing role in high mortality recorded that year. In 2015 and 2016, there were documented cases of harmful algal blooms in Kachemak Bay. It is unclear how biotoxins in prey may impact sea otters that might already be compromised with Strep Syndrome, and further investigations are needed.

In Kachemak Bay, most of the marine mammal stranding response effort occurs on the northern side of the Bay near Homer along the Homer Spit. The number of sea otter carcasses recovered in 2015 increased dramatically compared with previous years (Fig. 13). It is unlikely that the increased carcass recovery in the program is an artifact of sampling effort. The AMMSN and associated agencies provided a consistent support to the program during the study period. During 2006-2012, USFWS provided a seasonal paid internship to respond to sea otter stranding and mortalities and since 2013, student internships have helped respond to local marine mammal strandings. The north side of Kachemak Bay tends to be a male sea otter area; therefore, it is not surprising that most of the dead animals recovered are male. It is of concern that adult females may be under-represented in this sampling effort. In a study on sea otter survival and movement patterns in Kachemak Bay, Doroff and Badajos (2010) found that reproductive-aged females were sensitive to disease likely due to the energetic demands of pup rearing. The age structure of the 2015 mortality event was biased toward adult animals by classification and age determined by tooth annuli (Fig. 13-15). In general, a mortality age structure reflective of a well-established population (at numeric equilibrium with the habitat) is composed of older adults and young-of-the-year animals that are more vulnerable to disease and environmental stressors (Ballachey et al. 2014).

The GWA uses calculations of energy gained per foraging dive as a metric of population status relative to equilibrium population density for all study sites within the program. In Kachemak Bay, there has been less effort during 2012-2016 on collecting visual foraging observations than in other regions of the program. Methods for determining caloric gain per sea otter dive are biased toward the near shore habitat and in the past, approximately 50% of the foraging behavior was documented in open water areas >1 km from shoreline in Kachemak Bay (Doroff and Badajos 2010). However, this bias is consistent across all

sites sampled for GWA, and we plan to increase visual observations to match other regions in the new monitoring period starting in 2017.

Sea otter scat allows for the identification of small, hard-shell prey that passes through the intestine and provides an indication of the relative proportion of mussel, crab, urchin in overwinter diet among years. For example, in soft and mixed sediment habitats, a significant proportion of the sea otter diet is hard-shell clams. Declines of *Saxidomus gigantea* (butter clam) and *Leukoma staminea* (little neck clams) documented in this and other studies is a concern for sea otters. However, sea otter scat analyses are not particularly sensitive indices of complete diet (see Doroff et al. 2012). The value that the scat data provide is an index of overwinter diet and may capture large changes in shell-forming sea otter prey over time.

Advanced technology

The technology that we tested in Kachemak Bay was possible because the GWA was used to leverage funds that we received from the Bureau of Ocean Energy Management and the Coastal Marine Institute. This allowed us to test the use of sUAVs in intertidal monitoring for a rocky intertidal system and an intertidal seagrass system. We found that the low resolution of the sUAV imagery created problems in reliably identifying many taxa to species. Some of these shortfalls could be remedied by using higher resolution cameras and switching to a sUAV system that is able to carry the larger payload of a more stable mounting systems and higher resolution camera. Also, lower flight altitude of the sUAV would help with image resolution, but depending on region, this can be challenging when a beach contains large boulders that present obstacles to flight altitude. Still, the value of using sUAVs over the more traditional monitoring method of observer surveys remains dependent on the goals of a monitoring program. Questions that can be addressed by a lower taxonomic resolution than observers produce could benefit greatly from the sUAV approach, mostly because of the much larger spatial extent that can be covered during a single low tide period. Our approach of assessing large-scale distribution patterns of seagrass is such an example where the coarse taxonomic resolution of sUAV images was sufficient to yield highly valuable results. Similar examples could be done for the rocky intertidal, for example by focusing on key taxa such as rockweed (*Fucus* sp.). It seems that sUAVs can be a valuable tool in monitoring and are likely to become an important tool in routine, long-term monitoring and ocean observing in the future (Lomax et al. 2005).

CONCLUSIONS

The first five-year phase of GWA has enabled us to expand and continue previous sampling efforts in Kachemak Bay and to better integrate monitoring efforts in Kachemak Bay with those in the greater Gulf of Alaska. The publications and presentations that we have led resulting from this monitoring have demonstrated that because of this program, we now have a better understanding of the nearshore system, both of Kachemak Bay and the broader northern Gulf of Alaska. We now know that static drivers alone do not control rocky intertidal community structure and that shorter-term dynamic drivers probably play a very important role. The continued monitoring over the next five years will poise us to better examine dynamic drivers of rocky intertidal community variability, especially

because we have now experienced some extreme events (i.e., temperature). The warming trend observed in the northern Gulf of Alaska is also thought to be responsible for the spreading of the sea star wasting disease, which might also influence rocky intertidal systems through altered trophic and competitive interactions. We expect that the data collected in the next five years should also enlighten our understanding of the variability in seagrass beds as well as population dynamics of clam populations not only within Kachemak Bay, but through integration with other existing nearshore GWA programs, across the northern Gulf of Alaska (a preliminary presentation of these results were given at the Alaska Marine Science Symposium in January 2017). While the Kachemak Bay sea otter population appears to be at stable levels, new population estimates are needed, specifically given observations of diseases in dead otters and a potential increase in biotoxins in some of their prey, or declines of their prey, due to recent warming events in the Gulf of Alaska. This second five-year phase of the GWA Program (2017-2021) should be particularly important for these questions of variability and environmental drivers. If temperature is indeed a driver of nearshore systems, the recent dramatic warming events observed since 2015 in the northern Gulf of Alaska should create an ideal natural experiment to observe potential responses in these systems and inform management response to a changing ecosystem.

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APPENDIX 1

Citation:

Traiger SB, Konar B, Doroff A, McCaslin L. 2016. Sea otters versus sea stars as major clam predators: evidence from foraging pits and shell litter. *Marine Ecology Progress Series* 60: 73-86.

TITLE: Sea otters versus sea stars as major clam predators: evidence from foraging pits and shell litter

RUNNING PAGE HEAD: Assessing methods of determining clam predation

ABSTRACT:

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

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KEY WORDS: *Enhydra lutris*, *Pycnopodia helianthoides*, clams, foraging pits

INTRODUCTION:

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

Healthy and recovering sea otter populations have often been associated with reductions in the abundance and size of their prey, including clams (Hines & Loughlin 1980, Kvitek et al. 1992, Doroff & DeGange 1994). However, clam populations have also been able to persist and sustain otter populations for many years despite otter-associated mortality. In Prince William Sound, Alaska, sea otters reduced crab populations quickly after recolonizing, but continue to be sustained at an equilibrium density in the region where clam populations exist (Garshelis et al. 1986). Sea otters have been perceived as a threat to commercial and recreational clam fisheries. In California, the recolonization of sea otters prevented the opening of a recreational clam fishery (Wendell et al. 1983). In the Czech Republic, fishers' attitudes toward the recovering Eurasian otters (*Lutra lutra*) were negative, although damage to fish stocks by the otters was not as severe as perceived (Vaclavikova et al. 2011). Understanding and accounting for primary sources of mortality in native bivalve populations will help resource management agencies inform human harvest levels in coastal Alaska.

Sea stars are diverse and abundant in the intertidal and subtidal in the North Pacific and in Kachemak Bay (Chenelot et al. 2007, Iken et al. 2010) and, like sea otters, may be major clam predators. *P. helianthoides* are generalist predators and burrowing clams are a large component of their diet in soft-substrate habitats (Shivji et al. 1983), contributing up to 72% of their diet in the subtidal zone (Mauzey et al. 1968). *P. brevispinus*, *Evasterias troschelii*, and *O. koehlerii* feed on clams in Washington (Mauzey et al. 1968, Smith 1961) and these species also occur in Alaska (Chenelot et al. 2007). *A. amurensis* dig shallow pits for clams and have reduced commercial clam stocks in Tasmania where they are invasive (Ross et al. 2002). As one of the most common and active sea stars in Alaska, *P. helianthoides* is the most likely sea star to prey on clams at levels comparable to those of sea otters. Foraging by sea otters can facilitate *P. helianthoides* predation on clams by allowing easier access to remaining small clams excavated and not consumed by the sea

otters (Kvitek et al. 1992). However, in habitats with high population densities of both sea stars and sea otters, predation pressure on all clam size-classes may be elevated. Further information on prey competition or facilitation between sea otters and sea stars such as *P. helianthoides* is needed to assess their respective impacts on clam resources.

Foraging pits can provide information about clam consumption by benthic foragers without direct foraging observations. For example, the presence and density of foraging pits has been used to determine sea otter foraging rates and locations (Kvitek et al. 1992) and to assess their potential exposure to lingering oil in oil spill impacted areas (Boehm et al. 2007, Bodkin et al. 2012). Sediment disturbance through pit digging has ecological consequences across a range of terrestrial and marine habitats (woodlands; Eldridge & Mensinga 2007, ponds; Adamek & Marsalek 2013, marine soft-sediments; Oliver & Slattery 1985). However, determining the source of foraging pits based on measured dimensions may be difficult. There is a high degree of overlap and a wide range of values in described characteristics of sea otter and sea star pits in the literature (Table 1). Sea otter pits have been described as oblong with excavated sediment piled on one end of the pit (Kvitek et al. 1992); however, their dimensions have not been consistently reported among studies. Similar to sea otters, *P. helianthoides* also excavate pits while foraging for clams (Sloan & Robinson 1983, Mauzey et al. 1968). *P. helianthoides* push sediment aside with their arms and extend half of their legs into the pit (Sloan & Robinson 1983). Their pits have been described as being rounder and shallower than otter pits, with sediment piled in a ring around the pit (Kvitek et al. 1992). This description has been used by others to distinguish between otter pits and *P. helianthoides* pits (Boehm et al. 2007). In British Columbia, *P. helianthoides* were observed digging pits 6 to 14 cm deep (Sloan & Robinson 1983). Variation in observed pit dimensions among studies could be due to differences in sea otter foraging behavior, depth of the prey being targeted, or other factors affecting pit persistence such as the physical processes of wave action, currents, and sedimentation.

A major challenge in using foraging pits as a metric of foraging activity is that pit persistence is uncertain. Experimental pits dug around Kodiak Island were present after six months but were gone after twelve months (Kvitek et al. 1992). However, no detailed measurements or analyses were done on these pits since pit persistence was not the focus of their study. Foraging pits in the northern Knight Islands, Prince William Sound, Alaska may persist for one year based on photographs taken one year apart (Boehm et al. 2007); while experimental pits at mean lower low water (MLLW) in western Prince William Sound persisted for approximately 4 to 6 months (Bodkin et al. 2011). In Elkhorn Slough, California, recently made otter pits had claw marks on the inner walls, which wore away over time (Kvitek et al. 1988), but this characteristic of foraging pits has not been reported elsewhere. If foraging pits actually fill in and are replaced by new pits by the time researchers return to a site, foraging activity could be underestimated. Foraging pit persistence may vary with environmental factors such as water motion or sediment grain size. In mixed grain size gravel beds, smaller particles are sorted through the interstitial spaces between larger particles (Buscombe & Masselink 2006). Foraging pits may fill in more quickly in areas with high amounts of interstitial space in the sediment. High water motion would also likely facilitate sediment movement. In addition, pits may change shape due to *P. helianthoides* foraging activity as there is clear evidence that *P. helianthoides* are

attracted to otter pits (Kvitek et al. 1992). They are chemoreceptive (Brewer & Konar 2005), quickly aggregate at experimentally dug pits, and prey on the smaller clams that sea otters leave behind (Kvitek et al. 1992). While foraging for remaining smaller clams within a sea otter pit, *P. helianthoides* could change the shape of the pit, or how the sediment mounds around the pit. This will make distinguishing between sea otter and *P. helianthoides* pits difficult and may lead to inaccurate designation of predators. Without a better understanding of pit persistence and changes in pit dimensions over time, studies using pit dimensions as a metric of foraging intensity on clams are not able to draw accurate conclusions about their predators. The use of foraging pits for determining otter predation on clams needs to be validated by comparing estimates with other methods, as was done for time-depth recorder data (Tinker et al. 2007).

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

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

METHODS:

Study area

This study was conducted in Kachemak Bay, a large estuary in southcentral Alaska with a tidal range of approximately 9 m. Sea otters were extirpated from this area by 1792 (Lensink 1962) and after the close of the commercial fur trades for sea otter pelts, the region recovered through natural recolonization processes during the late 1960s and 70s (Schneider 1976, Gill et al. 2009). Between 2002 and 2008, the population increased by 26% per year, reaching 3.9 otters/km² (Newsome et al. 2015). Based on this last estimate,

the Kachemak Bay population is below its carrying capacity based on estimated available food sources (Gill et al. 2009, Newsome et al. 2015). Since then, the sea otter population has continued to grow in this region at approximately 13%/yr (USFWS and USGS unpublished data). *Saxidomus gigantea* and *Leukoma staminea* are the most popular clams for recreational fishing in Kachemak Bay (ADFG 2009). Surveys of clam populations in Kachemak Bay in 2007 and 2008 found that *S. gigantea* was abundant (up to 58/m²) and *Macoma balthica*, *Mya truncata*, and *L. staminea* were also observed (Stewart et al. 2014). *Pycnopodia helianthoides* are common in Kachemak Bay and can reach densities of 0.1 to 0.28/m² (Brewer & Konar 2005, Traiger & Konar in prep).

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

Distinguishing unknown pit sources using quantitative dimensions

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

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

used to detect differences in pit dimensions among sites (random, five levels: KB 0-m, KB 10-m, MS 10-m, PB, and PG).

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

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

Experimental pit dimensions were measured immediately after digging the pits. Partly because of infill while digging and larger rocks in the substrate, actual dimensions varied from the target dimensions. Actual dimensions were typically within 10 cm of the target but ranged from 12 cm below and 35 cm above the target dimension. Even with the infill, average starting dimensions for the two experimental pit types were significantly different (PERMANOVA, $p = 0.0007$, Table 2).

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

The rates at which experimental pits fill in or change dimensions may be influenced by water motion. To assess relative water motion at each site where experimental pits were dug, three replicate clod cards were deployed at each site and at each depth contour (Denny 1985). Clod card cubes were made of Plaster of Paris using ice cube trays (plaster to water ratio of 1:1 based on manufactures instructions), glued to plastic sheets, and attached to bricks. After the cards were assembled, they were cured in seawater for two days, then dried for one week and weighed twice to ensure they were fully dried before they were deployed in the field for approximately two weeks. Handling controls were taken to the sites (either intertidal or subtidal) and then returned to the lab and placed in still sea water for two weeks. Average weight loss of controls for each site was subtracted from the weight loss of the field-deployed clod cards. Weight loss of clod cards was compared among sites using ANOVA with Tukey pairwise comparisons to assess relative water motion (Thompson & Glenn 1994) using the R program (R Development Core Team 2008).

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

Predator Importance Based on Shell litter

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

To determine whether sea star density is an indication of sea star predation, all sea stars were counted and identified along the transects at the same time that shell litter was collected. Only *P. helianthoides* were used in our analysis because the other two stars that were found, *Evasterias troschelii* and *Orthasterias koehleri*, occurred at very low densities. We tested for Spearman correlations between shell litter (total shell litter and star-preyed shells) and *P. helianthoides* abundance. We also compared density of *P. helianthoides* across sites using ANOVA in R (R Development Core Team 2008). Since surveys of shell litter and *P. helianthoides* abundance at the 0-m sites were performed during low tide, these sites were excluded from the correlation analysis. *P. helianthoides* can move into the intertidal zone during high tide to feed but typically retreat to the subtidal zone as the tide drops (personal observation); hence, surveys of their abundance at low tide probably do not reflect their true use of the habitat.

RESULTS:

Distinguishing unknown pit sources using quantitative dimensions

One-hundred nine foraging pits were measured across all four 10-m sites and one of the 0-m sites from May to August 2014. Although sea otters were seen in the area, no pits were observed at the KB 0-m site during the study. There were no significant clusters within the data set of measured pits based on the cluster analysis and SIMPROF test ($p = 0.174$), and no clusters were apparent from the PCO plot either (Figure 2A) so pit source could not be determined. Most pits were elongate with the major axis on average $18\% \pm 13\%$ s.d. longer than the minor axis. Major axes ranged from 0 to 56% longer than minor axes. Fourteen percent of pits were perfectly round. Although most pits surveyed (53%) had no sediment pile, 26% had up to 25% of the pit edge with piled sediment, which is indicative of sea otters. This contrasts with only 2% of pits having sediment piled on 76-100% of the pit edge, which is indicative of sea stars. Pit depths averaged $11.8 \text{ cm} \pm 4.7$ s.d. and ranged from 3 to 27 cm. Surface area averaged $958 \text{ cm}^2 \pm 674$ s.d. and ranged from 71 to 3,533 cm^2 .

There were some differences in pit dimensions among sites (ANOSIM, $R = 0.095$, $p = 0.006$), so separate CLUSTER analyses and SIMPROF tests were run for each site (excluding MS 0-m due to low sample size). There were no significant clusters within KB 10-m, MS 10-m, or PG (SIMPROF, $p = 0.727$, 0.710 , and 0.430 , respectively). There were three significant clusters within the pits measured at PB (Figure 2B). There was a wide range of values for each dimension in cluster a, so we were unable to determine the source of pits in this cluster (Figure 2C). The pits in cluster b were deep compared to pits in cluster a ($13.5 \text{ cm} \pm 2.1$ s.d. vs. $7.9 \text{ cm} \pm 3.0$ s.d.), both pits had 26 – 50% of the rim covered in sediment mound, surface area was large relative to cluster a ($834 \text{ cm}^2 \pm 180$ s.d. vs. $468 \text{ cm}^2 \pm 369$ s.d.) and both pits were perfectly round (% Major axis > Minor axis = 0) while pits in cluster a had major axes 11% longer than minor axes on average (7% s.d.; Figure 2C). Due to the round shape of the pits and the presence of sediment on more than $\frac{1}{4}$ of the pit perimeter, we

assigned this cluster as sea star source. Cluster c had one pit, which was large (surface area 1236 cm²), had a major axis 22% larger than the minor axis, was 10 cm deep, and had sediment mounded on 50 – 75% of the pit perimeter, which was more than any other pit at PB. We were unable to assign a source to this pit because the characteristics of sediment mound and pit shape give conflicting indications of pit source based on literature descriptions of pits (Table 1). The sediment mound value indicates a sea star source; however, the pit shape indicates sea otter source, and size of the pit is very close to the lower limit of pit size observed by Kvitek et al. (1992).

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

Persistence of characteristics distinguishing sea otter and sea star foraging pits

After two weeks, the two experimental pit types (otter vs star) did not have significantly different dimensions from each other (Table 2, Figure 3). There were significant differences in the degree of change in pit dimensions among sites (Table 3) with most of these differences being between intertidal and subtidal sites. At 0-m, all of the experimental pits at KB were filled in after two weeks. At MS 0-m, 67% of experimental sea star pits were filled in, while all six of the experimental sea otter pits were still present. Across all sites, 90% of the experimental pits dug at 10-m were still visible after two weeks. The pit characteristics that changed the most were pit depth (average -44% change) and sediment pile. After two weeks, no sediment pile remained at 72% of sea otter pits and 62% of sea star pits.

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

Predator Importance Based on Shell litter

One hundred twenty-five shells were collected over the study period. Fifty-six percent of the shells were otter-cracked, 42% were star-preyed, and 2% contained bore-holes. Across all sites, there was a significantly lower density of bore-holed shells than otter-cracked or star-preyed shells (ANOVA, $p < 0.001$ and $p = 0.011$, respectively) (Figure 4). Density of otter-cracked and star-preyed shells was only different at PG (ANOVA, $p = 0.002$) (Figure 4), with 70% of the shells being otter-cracked at this site. This indicates that sea otters and

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

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

DISCUSSION:

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

Our hypothesis that recent (two weeks old or less) foraging pits can be distinguished based on measurable characteristics was not supported. We did not observe any patterns in the multivariate data cloud of pit dimensions that indicated that different types of predators were making them. We also found that the multivariate data did not align with any of the existing literature descriptions (Table 1). For example, the amount of piled sediment increased toward the lower right end of the nMDS, which could indicate that pits in this portion of the graph are sea star pits (Kvitek et al. 1992); however, pit shape (% major axis > minor axis) and surface area do not show clear decreasing values in that direction (compare vector directions on Figure 2). As such, we do not recommend using foraging pits to determine levels of clam predation by sea otters and sea stars separately. There is not enough quantitative information in the literature to clearly distinguish the types of pits made by each predator, and the lack of clustering in the pit dimensions indicates that either both predators make pits of very similar size and shape, or that one predator is responsible for all the pits observed. Foraging pits are more useful for determining the role of

individual predators in study systems where only one pit digging predator occurs (Dor et al. 2014, Eldridge & Mensinga 2007, Hines et al. 1997), or there are large differences in the sizes of pits produced by different predators (Nelson et al. 1994).

Our hypothesis that after two weeks, sea otter and sea star pits can still be distinguished was not supported. After two weeks, experimental sea otter and sea star pits were no longer significantly different from each other, largely because the differences in roundness and amount of piled sediment that distinguished pits at the beginning of the experiment were not present after two weeks. These results suggest that the metrics typically found in the literature to differentiate foraging pits are likely not accurate for pits older than two weeks. Since sediment piles are quickly eroded, previous studies using sediment piles to distinguish pits may be underestimating the contribution of sea stars to foraging pits. As a result, the role of sea stars in shaping soft-sediment communities could be underappreciated in areas with sea otters. More than half of the recent shells that were collected were a result of sea star predation, indicating that they are currently important predators of clams at these sites in Kachemak Bay. The high degree of change in pits we observed over two weeks is likely an important reason why we could not distinguish foraging pits. Very frequent resurveys would be necessary to accurately distinguish the source of foraging pits and to accurately quantify foraging pit dimensions, regardless of their source. In other study systems, surveys of foraging pits have involved frequent resampling (4 days; Hines et al. 1997, 24 hours; O'Shea et al. 2012). In contrast, surveys of foraging pits attributed to sea otters have been repeated every two weeks (Kvitek et al. 1988) or have not been repeated, using a snapshot approach (Bodkin et al. 2012, Boehm et al. 2007, Kvitek et al. 1992). A snapshot approach, combined with an inaccurate estimate of pit persistence, could result in underestimation of foraging. Appropriate sampling frequency will depend on infill rates, which may be influenced by sediment grain size, water motion, and potential for continued use of the pit.

The changes we observed in pit dimensions overtime may have been influenced by a lack of sea star activity in the pits (given that sea star activity can prevent infill), water motion, and sediment grain size. Sea stars were never observed using pits that had been previously marked with a landscaping flag or in our experimental pits, which were marked slightly differently, with a nail with flagging at the edge of the pit. While it is possible that the landscaping flag placed at the center of the pits deterred further use of the pits by sea stars or sea otters, we believe that the rate of pit reuse is low in our system, due to the lack of activity in our experimental pits. We also do not believe that *Pycnopodia helianthoides* would be deterred by landscaping flags because we have observed them overturning bricks and large rocks in order to dig for clams underneath. We do not know of any evidence of sea otters reusing pits. The high rate of pit in-fill in this study differs from previous studies that found sea otter foraging pits persisting for four months to a year (Kvitek et al. 1992, Boehm et al. 2007, Bodkin et al. 2011). Pit persistence has also been studied in Australia where most stingray foraging pits filled in within seven days, but some pits became larger from continued use by the stingrays (O'Shea et al. 2012). Although *P. helianthoides* have been shown to be attracted to foraging pits (Kvitek et al. 1992), it seems that they were not attracted to our experimental pits since most experimental pits became smaller or filled in over time.

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

The difference in pit persistence across depth contours has important implications for interpreting foraging pit data. It should not be assumed that foraging pits are indicators of foraging over the same time span at intertidal and subtidal sites because of these differences in their persistence. In contrast to western Prince William Sound where intertidal foraging pits persisted several months (Bodkin et al. 2011), foraging pits at our intertidal sites may only represent foraging activities within the last two weeks or less. Similarly, foraging pits and furrows formed by walrus in Bristol Bay are not observed in areas with dynamic sediment movement, even though walrus are known to forage in those areas (Bornhold et al. 2005). While we observed fewer pits at our intertidal sites (zero at Kasitsna Bay and three at McDonald Spit), we may be missing some foraging activity due to high infill rates. Kachemak Bay has a 9 m tidal range, so at high tide, the intertidal is very accessible to sea otters. Indeed we expected to see higher numbers of foraging pits in the intertidal since other studies using foraging pits and radio tags recorded frequent foraging in the intertidal (Bodkin et al. 2012, Gilkinson et al. 2011). The number of foraging pits may also have been low at our intertidal sites if clam abundance was low due to previous sea otter or sea star predation, recreational clam fishing, or other factors. We also found low numbers of shells at our intertidal sites (zero at Kasitsna Bay and four at McDonald Spit), which may also be indicative of low prey abundance.

Our hypothesis that shell litter can be used to assign relative clam predation by sea otters and sea stars was supported. We observed very few shells with indications of other predators, and were able to classify predation source for all shells collected. We did not observe any shells with contradicting predation signs (i.e., a shell with both bore-holes and otter-cracks). Like any method of determining predation rates, using shell litter has potential biases. Sea otters eat clams on the surface, so otter-preyed shells may be distributed farther from their origin than star-preyed shells, resulting in underestimation of sea otter predation. In California, sea otters were observed to move away from shore to eat on the surface after collecting clams in shallower water (Kvitek et al. 1988). Small clam prey of sea otters may also be underestimated because sea otters have been observed to consume whole clams 3 to 5 cm long (Calkins 1978). However, these potential biases are

outweighed by the higher confidence in identifying the source of clam mortality and benefits of additional information gained compared to using foraging pits. Surveys of shell litter provide the added benefit of being able to identify small individuals, which can be difficult in observational studies (Dean et al. 2002, Wolt et al. 2012). Unlike counts of foraging pits, shell litter can also be directly linked to the number of predated clams. Shell litter can be used to determine recent foraging activity of sea otters on clams, as in this study, as well as historical predation of clams at a site (Kvitek et al. 1992, Stewart et al. 2014). While shell litter is useful for distinguishing between sea otter and sea star clam predation, it does not account for all predation on clams. Clams are important diet items for wintering sea ducks, which consume small clams (≤ 40 mm) whole, so their fecal pellets need to be sampled to assess their predation on clams (Lewis et al. 2007). Crabs prey on clams by chipping away the edge of the clam valves (Boulding 1984; Kvitek pers com); however, at the sites we sampled, only one *Saxidomus gigantea* was found chipped in this way. Larger crab species, such as Tanner crab (*Chionoecetes bairdi*) generally would be found in deeper water than our sampling sites.

Multiple methods of determining sea otter foraging should be used to account for method biases. For example, Smith et al. (2015) found that estimates of diet specialization differed between stable isotope and observation methods, with stable isotopes providing less biased estimates of specialization. Shell litter, when combined with other methods could help provide a more complete view of sea otter foraging on clams. In contrast to shell litter, direct foraging observations are time consuming, and clam species may be impossible to identify from great distances, although statistical methods can be used to account for these biases (Tinker et al. 2012). Observations also allow for a more complete prey dataset, which include soft-bodied organisms (Dean et al. 2002). Scat collections are often done to determine sea otter prey but these data are limited to sea otter haul out sites and only prey with hard parts are observed (Green et al. 1991, Faurot et al. 1986, Doroff et al. 2012). Pairing shell litter with direct observations and scat collections will ensure that soft bodied and small size class organisms are incorporated (Green et al. 1991).

To better predict changes in clam populations, we need to understand the relative contributions of sea otters and sea stars to their mortality. In Kachemak Bay, according to the shell litter, sea stars are as important as sea otters for clam predation and as such, clam mortality due to sea stars should be considered in clam management strategies. In addition to preying on equal number of clams, sea stars also prey on a wider range of species and sizes of clams, including *Diplodonta* sp., *Hiatella arctica*, *L. staminea*, and *Mactromeris polynyma*. Size-specific predation pressure evident from the shell litter could be built into population models for clams. While the Kachemak Bay sea otter population has been rising since recolonization (Gill et al. 2009), its impact on clam populations is unknown. As the sea otter population recovers in Kachemak Bay, public perception is mixed and there is concern that the population recovery is a threat to local clam fisheries. Sea otters also prey on Tanner crabs (*C. bairdi*), fat innkeepers (*Urechis unicinctus*), sea stars such as mottled stars (*Evasterias troschelii*), green urchins (*Strongylocentrotus droebachiensis*), octopus (*Octopus* sp.), mussels (*Mytilus* spp.), and fish (Calkins 1978, Dean et al. 2002, Garshelis et al. 1986, Gill et al. 2009, Green and Brueggeman 1991, Doroff et al. 2012), which are also present in Kachemak Bay. Although clams are a high-energy food source (Ofstedal et al.

2007), sea otters may target prey that do not require excavation while they are still abundant.

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

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FIGURES AND TABLES:

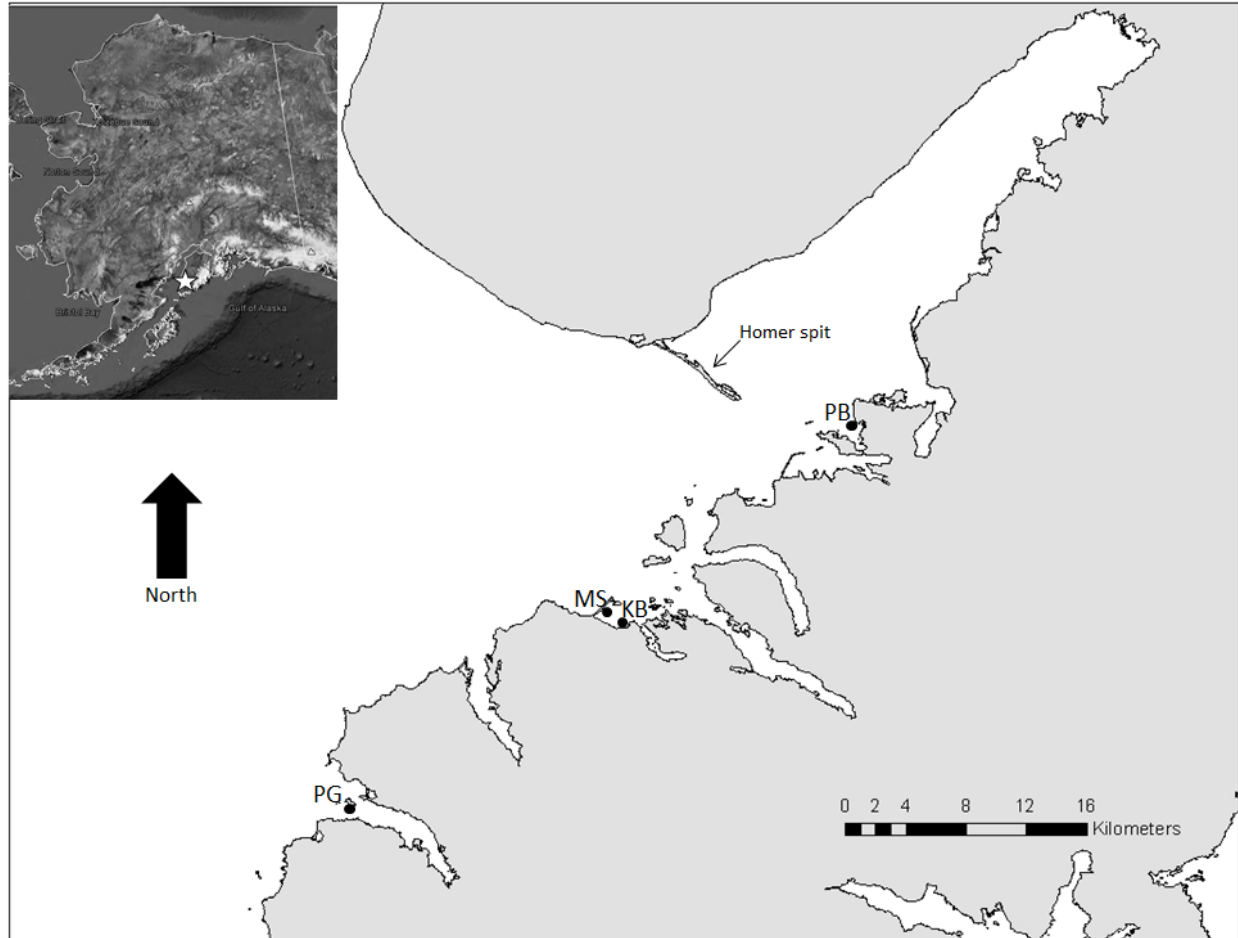


Figure 1. Map showing the locations of the four study sites within Kachemak Bay. The white star on the inset map shows the location of Kachemak Bay within Alaska. Site abbreviations are as follows: Port Graham (PG), Peterson Bay (PB), MS (McDonald Spit), and Kasitsna Bay (KB).

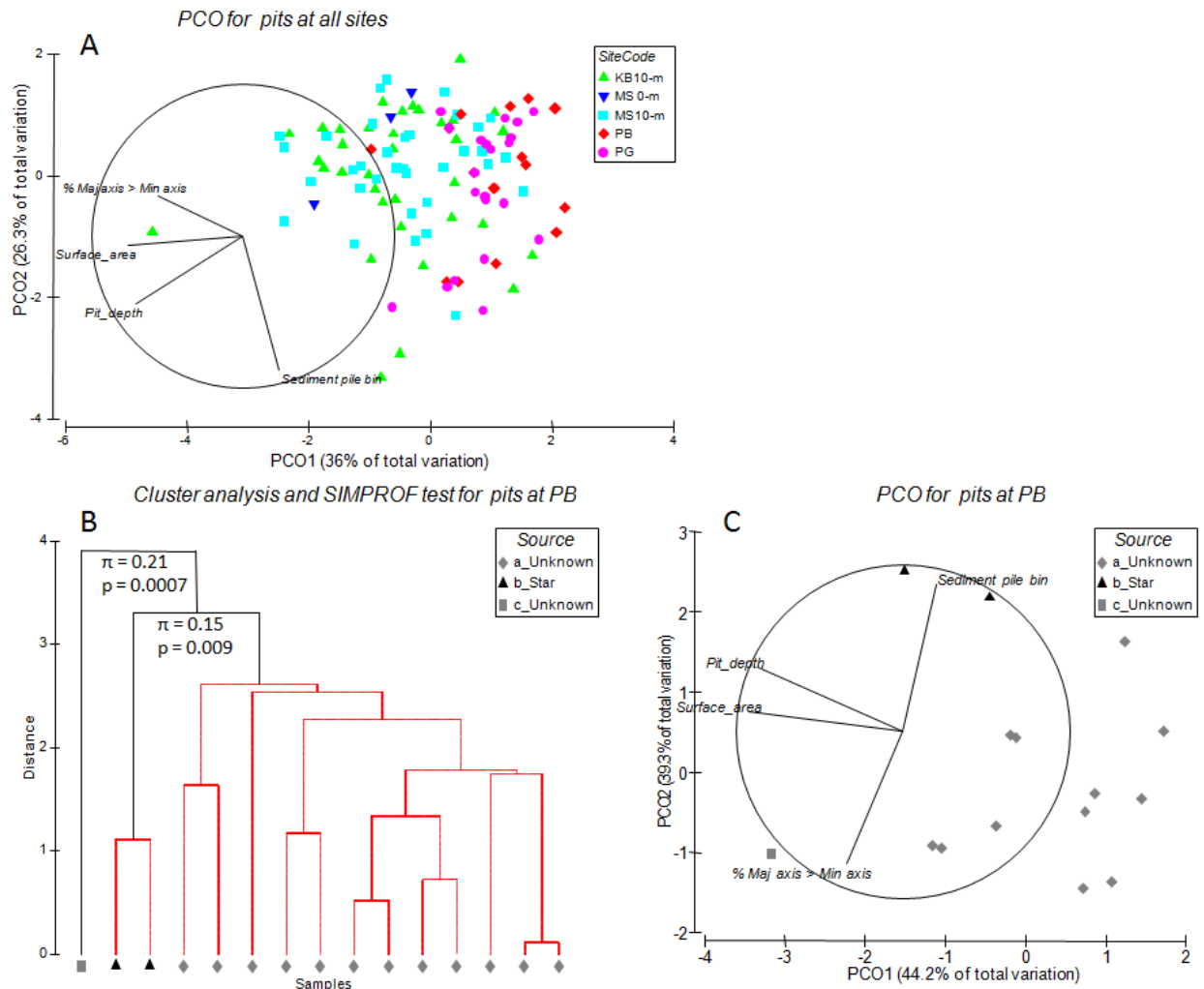


Figure 2. A) Principal coordinate analysis (PCO) plot based on Euclidian distance of dimensions of surveyed foraging pits color coded by site. Each point represents one pit. Solid lines represent vectors of pit dimension variables. Vectors show directions of correlations with the PCO axes. B) Dendrogram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

Dimensions of Experimental Pits at Initial Set-up and After Two Weeks

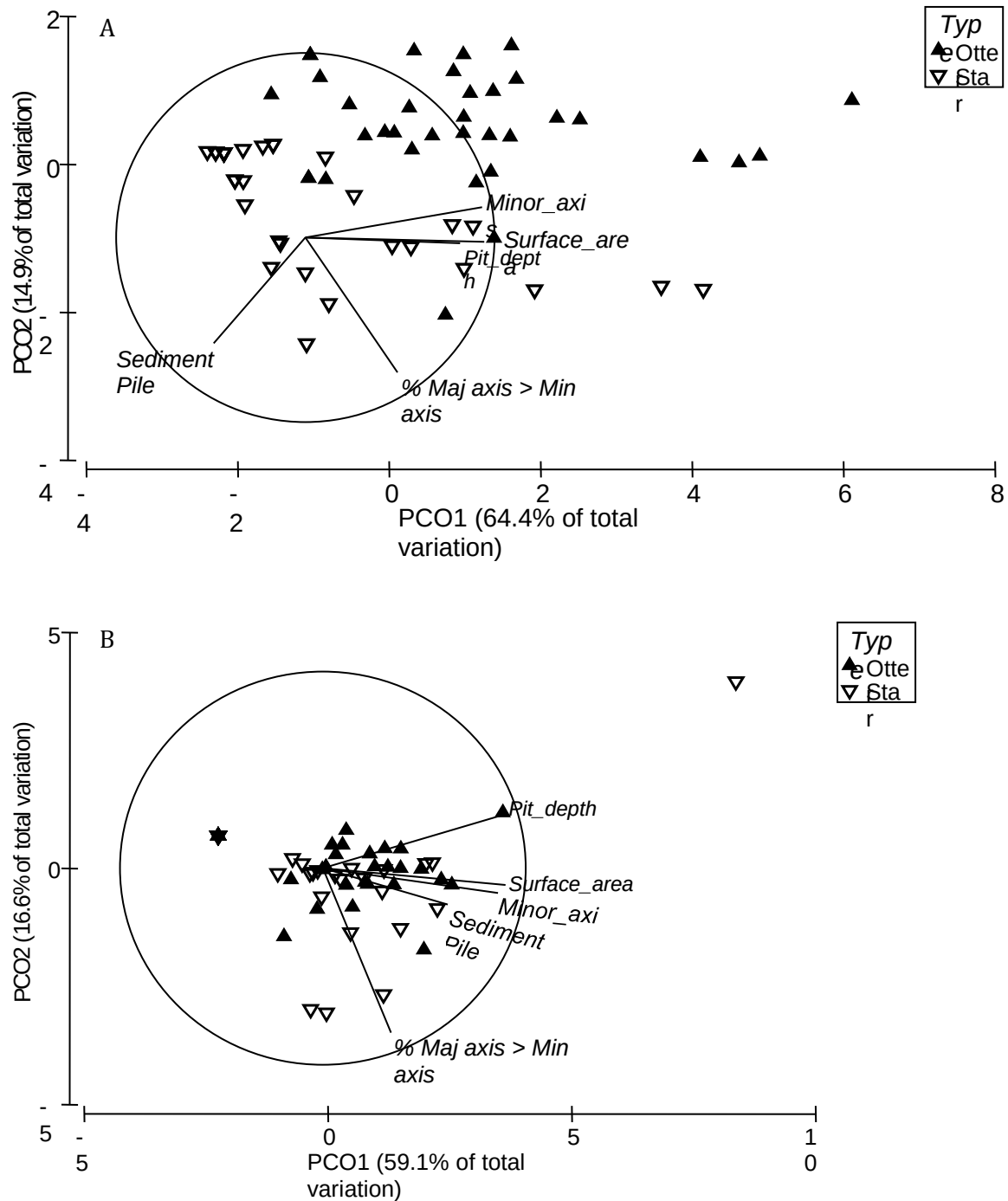


Figure 3. A) PCO plot showing clear separation in starting dimensions between experimental otter and sea star pits just after they were dug (Initial Set-up). B) PCO plot showing that after two weeks, the experimental otter and sea star pits are indistinguishable. In both plots, each point represents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

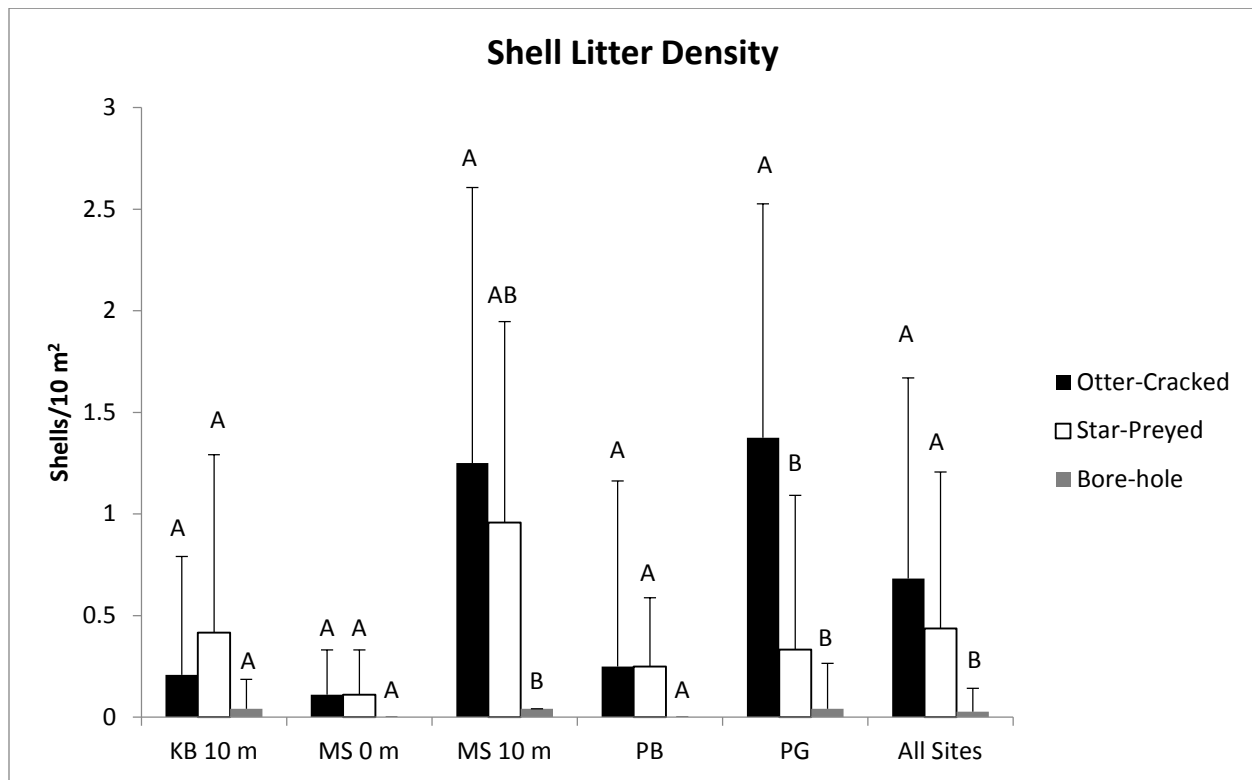


Figure 4. Densities of star-preyed and otter-cracked shells collected along same 2 x 10 m transects where foraging pits were surveyed. Separate ANOVAs were performed to compare density of otter-cracked, star-preyed, and bore-holed shells across all sites, and within each site. Letters above bars indicate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

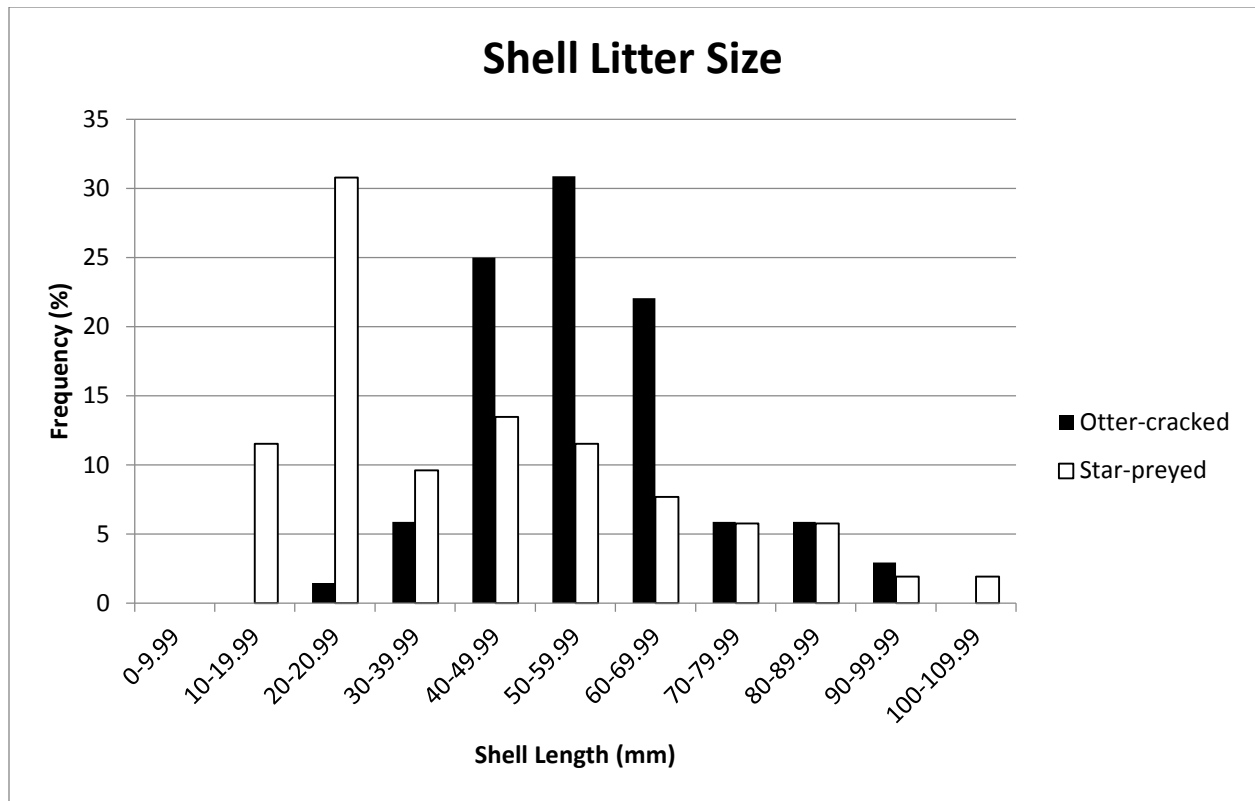


Figure 5. Range of sizes of clams preyed on by sea otters and sea stars as shown by shell litter. All shells collected with bore-holes ($n = 3$) were in the 20 – 20.99 mm size category (data not shown).

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

Dimension/Characteristic	Sea otter source	Sea star source	Literature Basis
Sediment piled on pit rim	On one side of the pit (1) Observed pits 1300 cm ² – 2000 cm ²	Evenly around perimeter (1) Smaller than otter pits	Kvitek et al. 1992 (1)Kvitek et al. 1992 (2) Calkins 1978 (3) Kvitek et al. 1988
Area/Size	(2) 15 to 45 cm across (3) 14000 cm ² on average		
Pit depth	(1) Up to 50 cm (2) 10 – 15 cm	(3) 6 – 14 cm (4) 5 – 23 cm	(1) Calkins 1978 (2) Boehm et al. 2007 (3) Sloan & Robinson 1983 (4) Mauzey et al. 1968
Shape	Elongate	Circular	Kvitek et al. 1992

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

A

Source	d.f.	Sum of square	Pseudo-F	p value
Type	1	48.57	1.68	0.216
Sampling Event	1	88.96	3.31	0.073
Site	5	54.17	0.40	0.930
Type x Sampling Event	1	22.74	4.84	0.022
Type x Site	5	45.39	1.92	0.134
Sampling Event x Site	5	136.95	8.23	<0.001
Type x Sampling Event x Site	5	23.64	1.42	0.141
Residual	112	372.55		
Total	135			

B

Type x Sampling Event	t	p values
Otter, Star at Set-up	4.09	<0.001
Otter, Star After two weeks	0.77	0.532

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

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

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

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

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

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

APPENDIX 2

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The use of unmanned aerial vehicle imagery in intertidal monitoring

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ABSTRACT

Intertidal monitoring projects are often limited in their practicality because traditional methods such as visual surveys or removal of biota are often limited in the spatial extent for which data can be collected. Here, we used imagery from a small unmanned aerial vehicle (sUAV) to test their potential use in rocky intertidal and intertidal seagrass surveys in the northern Gulf of Alaska. Images captured by the sUAV in the high, mid and low intertidal strata on a rocky beach and within a seagrass bed were compared to data derived concurrently from observer visual surveys and to images taken by observers on the ground. Observer visual data always resulted in the highest taxon richness, but when observer data were aggregated to the lower taxonomic resolution obtained by the sUAV images, overall community composition was mostly similar between the two methods. Ground camera images and sUAV images yielded mostly comparable community composition despite the typically higher taxonomic resolution obtained by the ground camera. We conclude that monitoring goals or research questions that can be answered on a relatively coarse taxonomic level can benefit from an sUAV-based approach because it allows much larger spatial coverage within the time constraints of a low tide interval than is possible by observers on the ground. We demonstrated this large-scale applicability by using sUAV images to develop maps that show the distribution patterns and patchiness of seagrass.

1. Introduction

Monitoring and assessing biological communities in intertidal habitats is a common practice and much needed in our changing climate as these communities will be amongst the first to exhibit impacts (Helmuth et al., 2006). Traditional intertidal monitoring is restricted to low tide events, when researchers manually quantify organisms using percent cover, abundance, biomass, or similar measurements (Konar et al., 2009; Leujak and Ormond, 2007; Menge et al., 2015). This is typically done by a small team of surveyors who assess species composition from quadrats or lines along intertidal strata. The commonly used quadrat sampling is a tested, accurate, and efficient sampling method for quantifying benthic biological communities (Heltshe and Forrester, 1985; Obermeyer, 1998), and is a mainstay in monitoring programs (Delaney et al., 2008; Konar et al., 2009) and impact studies (Cox and Foster, 2013; Minchinton and Fels, 2013). For example, in the Gulf of Alaska, quadrat sampling was broadly used in assessing damage and intertidal recovery after the Exxon Valdez oil spill (Boehm et al., 1996; Skalski et al., 2001; Stekolnik and Deysher, 2000) and is still being used by the current Gulf Watch Alaska intertidal monitoring (Konar et al., 2016). The advantages of traditional survey methods are that experts can identify the species in the field at high taxonomic resolution and/or can collect vouchers of unknown organ-

isms for later identification. A limitation of quadrat sampling in intertidal systems is the limited spatial extent that can typically be surveyed per low tide interval (on the order of 10 s to 100 s of meters) (Godet et al., 2009). This spatial limitation can cause problems in representatively capturing species occurrence and distribution, intertidal community structure, and variability in community composition.

In addition to traditional sampling, photographic surveys are also an effective and cost efficient method for assessing benthic communities (Aronson et al., 1994; Bohnsack, 1979; Witman et al., 2004). Photographic methods provide advantages over traditional *in situ* surveys because photographs reduce the time required in the field to collect quadrat information, and images offer a permanent historical record (Reimers et al., 2014; although see Foster et al., 1991). While this sampling can accelerate the time it takes to sample a single quadrat (Bohnsack, 1979), the amount of beach that can feasibly be sampled is still limited because surveyors still need to walk along the beach stratum and photograph each sample during the limited low tide period. In a comparison of benthic survey methods, photographic images were less taxonomically detailed than ground surveys because images only reveal the taxa that are on the surface and are most abundant, and photographic analyses also were more time consuming (Godet et al., 2009).

Recently, other means of acquiring photographs across broader

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APPENDIX 2

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areas have been tested. For example, kite aerial photography produced maps that covered 200 m of intertidal shoreline (Bryson et al., 2013). These photographs were used to construct high-resolution, three-dimensional, multi-spectral terrain models of intertidal rocky shores. Similarly, low-altitude aerial photography from a balloon-mounted digital camera platform was used to acquire an intertidal landscape mosaic of eelgrass (*Zostera marina*) and blue mussels (*Mytilus edulis*) (Barrell and Grant, 2015). In addition, multispectral LiDAR surveys have been used to evaluate the structural complexity of coastal habitats (kelp habitat, eelgrass meadow, beach, salt-marsh, farm and urban coastal environments) and to classify the spatio-temporal distribution of these habitats across a large spatial area (Collin et al., 2012). Photographic and video surveys from airplanes have become common for characterizing intertidal communities, as exemplified by NOAA's ShoreZone mapping program along most of Alaska's shoreline and much of the US west coast (www.shorezone.org). While the use of various types of aerial photography has allowed for the expansion of the spatial extent of intertidal surveys, the resulting imagery typically is not of high enough resolution to identify intertidal organisms at the taxonomic resolution needed for biological monitoring.

Ideally, an intertidal survey method should be completed quickly and cover a large spatial area, but also have high enough taxonomic resolution so that accurate and detailed biological descriptions of large intertidal areas can be made. We suggest that small Unmanned Aerial Vehicles (sUAV) equipped with a high-resolution camera may be used to spatially expand biological intertidal sampling. We tested this methodology for an ongoing rocky intertidal and intertidal seagrass monitoring program in the Gulf of Alaska. In Alaska, sUAVs have been successfully operated in marine mammal monitoring, resource mapping, and sea ice and glacier mapping (Koski et al., 2009; Walker, 2012). However, altitudes flown for those purposes are much higher than needed to get adequate images for the taxonomic resolution required for most biological intertidal monitoring programs. Here, we flew a small sUAV at low altitude to test if the images created with its camera would allow for the analysis of percent cover of individual intertidal taxa or taxon groups. We also tested using sUAV images in an intertidal seagrass bed to assess percent cover of seagrasses versus other taxa. In addition, we used imagery over the seagrass bed to produce a large-scale (on the order of 100s of meters) map of the bed to assess variability in seagrass cover, which is difficult to achieve for a representative area using ground surveys. Seagrass bed size and patchiness are important monitoring metrics as seagrass beds tend to shrink in size under high sedimentation conditions such as from coastal erosion (Cabaço et al., 2008). Therefore, our over-arching objective was to determine if sUAVs can be used to spatially expand current traditional rocky intertidal and intertidal seagrass monitoring. We tested the hypotheses that observer data yield higher taxonomic resolution than images taken by a camera mounted to an sUAV, but that there is no difference in community structure if both methods are used at a unified, coarser taxonomic level. In addition, we hypothesized that community composition determined from images taken on the ground by observers will not be different from that determined from images taken by the sUAV. Lastly, we hypothesized that sUAV images can be used to create large-scale distribution maps of total seagrass cover as the dominant taxon in that system.

2. Methods

This study took place in April to May 2015 in Kachemak Bay, Alaska, in the northern Gulf of Alaska at 59.725°N and 151.141°W, where ongoing intertidal monitoring efforts through the Gulf Watch Alaska program (www.gulfwatchalaska.org) include the biological assessment of rocky intertidal and intertidal seagrass systems. We paired the annual ground observer monitoring at two permanent intertidal sites, one rocky intertidal at Outside Beach (59.4642°N, –151.7085°W) and one intertidal seagrass bed at the Homer Spit

(59.6485°N, –151.4365°W), with images obtained by ground observers and images obtained from an sUAV.

For ground surveys in the rocky intertidal site, a field team placed a 50-m transect tape at the mean higher high water (MHHW), the mean tidal level (MTL), and the mean lower low water (MLLW) levels (see Konar et al., 2009). One 50-m transect was placed in the center of the seagrass site. At the rocky intertidal site, the observer surveys included the visual estimation of percent cover of macroalgae, sessile invertebrates (such as mussels and barnacles), and bare substrate in ten randomly-placed 1-m² quadrats along the transect at each of the tidal strata. In addition, a photograph was taken of each quadrat and used for later comparisons with the sUAV images. Each rocky intertidal stratum was examined separately as strata significantly differ in community composition and are not comparable in this region (Konar et al., 2009). At the seagrass site, percent cover of seagrass and other groups such as mussels, macroalgae, diatom mats, and open substrate was calculated along the 50-m transect in the approximate center of the bed from five randomly-placed 0.25-m² quadrats. A picture of each of these quadrats was taken to compare with five randomly selected sUAV image frames along this transect (see below).

The sUAV was a quadcopter Aeryon Scout™, which carried a GoPro Hero 3, 12-megapixel camera (visible spectrum sensor) modified with a rectilinear lens to eliminate the fish-eye effect. At the rocky intertidal site, the sUAV was flown over the three 50-m transects laid out by the ground observer team at the MHHW, the MTL, and the MLLW levels. At the seagrass site, the sUAV was deployed from a single starting point on the beach and flown in various directions across the seagrass bed, including over the 50-m transect in the center of the seagrass bed. These transects and quadrats were used to orient the sUAV, scale the size of sUAV images to ground-taken images, and to ensure that the sUAV surveyed the same spatial area as the ground crew. To assess the distribution and patchiness in seagrass cover over a larger spatial extent, we also flew the sUAV along extended haphazard flight paths over the seagrass bed. In both intertidal systems, the sUAV was flown at an altitude of approx. 5 m above ground level (AGL) at very low speeds of approximately 2 km/h to maximize the resolution of the imagery. Images were taken every 5 s.

Percent cover of benthic biota for each of the three rocky intertidal transects and for the seagrass transect was determined from the ten quadrat images taken by the ground observer team as well as ten randomly selected images taken by the sUAV. For the sUAV images, an area of the image was selected that scaled to the same size as the quadrats surveyed on the ground. It was impossible to capture the exact same ground survey quadrats; however, the ten randomly chosen quadrats on the ground are considered representative of the community and its variability along the 50-m transect, so that ten sUAV images of the same size along the same transect should be representative of the same overall community and variability. In all cases, data from ground quadrats or images were then averaged across the transect. Each image from the ground camera and the sUAV was manually inspected for percent cover of taxa or categories (see details below) by the authors based on their familiarity with the taxa occurring in these systems (see Konar and Iken, 2009; Konar et al., 2009, 2016). Thus, percent cover data were obtained by the same investigators using the same quantification methods for ground surveys as for image analyses. No automated image analysis system was used. Data for both the rocky and seagrass systems were collected at the finest taxonomic resolution possible by each of the three methods (sUAV image, ground image, and observer visual). For ground observer data, this resolution was typically at the species or genus level. For both the ground camera and the sUAV images, resolution varied from species to genus to class level or was done by operational groupings (such as “other red algae” or “rock/shell”) (see Table 1 for taxonomic resolution details by tidal stratum for rocky intertidal). The maximum number of taxa or groups identified for each of the methods was considered “fine” resolution. We then aggregated the taxonomic resolution from the observer ground surveys

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Table 1

ANOSIM results of comparisons between observer and sUAV data, and sUAV and camera data. ANOSIM R values range from 0 to 1, with values above 0.45 representing biologically relevant differences in community composition. Taxonomic resolution used for each comparison is listed as Tax. Res. The taxonomic categories for each data set are listed.

Stratum	Comparison	Tax. Res.	ANOSIM R	Taxonomic categories
MHHW	sUAV-observer	fine	0.768	sUAV (4): other macroalgae, Fucus, rock/shell, barnacles observer (10): Fucus, <i>Glolopeltis furcata</i> , <i>Odonthalia floccosa</i> , <i>Mazzaella</i> sp., <i>Pterosiphonia bipinnata</i> , <i>Cryptosiphonia woodsii</i> , <i>Endocladia muricata</i> , rock/shell, barnacles, mussels
MHHW	sUAV-observer	coarse	0.436	both (4): other macroalgae, Fucus, rock/shell, barnacles
MHHW	sUAV-camera	fine	0.833	sUAV (4): other macroalgae, Fucus, rock/shell, barnacles camera (5): other macroalgae, Fucus, rock/shell, barnacles, mussels
MTL	sUAV-observer	fine	0.736	sUAV (9): Fucus, <i>Palmaria</i> spp., <i>Cladophora</i> /Acrosiphonia, <i>Ulva</i> /Monostroma, encrusting corallines, other red algae, other green algae, barnacles, rock/shell observer (25): Fucus, <i>Saccharina sessilis</i> , <i>Alaria</i> sp., <i>Scytosiphon lomentaria</i> , <i>Acrosiphonia</i> sp., <i>Cladophora</i> sp., <i>Monostroma grevillei</i> , <i>Ulva intestinalis</i> , <i>Ulva lactuca</i> , <i>Ulva linza</i> , <i>Neorhodomela</i> sp., <i>Halosaccion glandiforme</i> , <i>Mazzaella</i> sp., <i>Palmaria callophyllodes</i> , <i>Palmaria hecatensis</i> , <i>Pterosiphonia/Polysiphonia</i> , <i>Cryptosiphonia woodsii</i> , <i>Odonthalia floccosa</i> , <i>Microcladia borealis</i> , <i>Tokidadendron</i> sp., <i>Porphyra/Pyropia</i> -complex, <i>Corallina vancouveriensis</i> , encrusting corallines, barnacles, rock/shell
MTL	sUAV-observer	coarse	0.200	both (10): Fucus, kelp, <i>Cladophora</i> /Acrosiphonia, <i>Ulva</i> /Monostroma, <i>Palmaria</i> spp., encrusting corallines, other red algae, other green algae, barnacles, rock/shell
MTL	sUAV-camera	fine	0.208	sUAV (9): Fucus, <i>Cladophora</i> /Acrosiphonia, <i>Ulva</i> /Monostroma, <i>Palmaria</i> spp., encrusting corallines, other red algae, other green algae, barnacles, rock/shell camera (10): Fucus, <i>Saccharina sessilis</i> , <i>Cladophora</i> /Acrosiphonia, <i>Ulva</i> /Monostroma, encrusting corallines, <i>Pterosiphonia/Polysiphonia</i> , <i>Halosaccion glandiforme</i> , <i>Palmaria</i> spp., barnacles, rock/shell
MLLW	sUAV-observer	fine	0.736	sUAV (10): <i>Cladophora</i> /Acrosiphonia, <i>Ulva</i> /Monostroma, <i>Palmaria</i> spp., encrusting corallines, kelp, <i>Pterosiphonia/Polysiphonia</i> , other red algae, other green algae, barnacles, rock/shell observer (24): Fucus, <i>Saccharina sessilis</i> , <i>Alaria</i> sp., <i>Scytosiphon lomentaria</i> , <i>Acrosiphonia</i> sp., <i>Monostroma grevillei</i> , <i>Ulva intestinalis</i> , <i>Ulva lactuca</i> , <i>Halosaccion glandiforme</i> , <i>Mazzaella</i> sp., <i>Palmaria callophyllodes</i> , <i>Palmaria hecatensis</i> , <i>Pterosiphonia/Polysiphonia</i> , <i>Cryptosiphonia woodsii</i> , <i>Ahnfeltia</i> sp., <i>Odonthalia floccosa</i> , <i>Microcladia borealis</i> , <i>Tokidadendron</i> sp., <i>Porphyra/Pyropia</i> -complex, <i>Corallina vancouveriensis</i> , encrusting corallines, diatoms, barnacles, rock/shell
MLLW	sUAV-observer	coarse	0.354	both (10): Fucus, kelp, <i>Cladophora</i> /Acrosiphonia, <i>Ulva</i> /Monostroma, <i>Palmaria</i> spp., encrusting corallines, <i>Pterosiphonia/Polysiphonia</i> , other macroalgae, barnacles, rock/shell
MLLW	sUAV-camera	fine	0.100	sUAV (10): <i>Cladophora</i> /Acrosiphonia, <i>Ulva</i> /Monostroma, <i>Palmaria</i> spp., encrusting corallines, kelp, <i>Pterosiphonia/Polysiphonia</i> , other red algae, other green algae, barnacles, rock/shell camera (13): Fucus, <i>Saccharina</i> sp., <i>Alaria</i> sp., <i>Saccharina sessilis</i> , <i>Halosaccion glandiforme</i> , <i>Cladophora</i> /Acrosiphonia, <i>Ulva</i> /Monostroma, <i>Palmaria</i> spp., encrusting corallines, <i>Pterosiphonia/Polysiphonia</i> , other green algae, barnacles, rock/shell

and from sUAV images, or from ground cameras and sUAV images, to the same lowest common resolution level. We refer to this aggregated level as “coarse”. In most cases, the “fine” resolution from sUAV images was the lowest resolution among all methods and was the level at which data were aggregated for the coarse level. Hence, the fine and the coarse taxonomic resolutions were mostly identical for sUAV images. These aggregated data sets were used to test our hypothesis that community composition at the coarse taxonomic level is comparable between the observer ground surveys and sUAV images. For the comparison of sUAV images and ground camera images, we only used the coarse taxonomic resolution.

For both intertidal systems, we compared the mean percent cover for each individual coarse taxon group between ground observer data and sUAV images using t-tests at a significance level of $\alpha = 0.05$ (SYSTAT v10). The averaged community compositions in rocky intertidal (separately for each of the three 50-m transects) and seagrass systems (along one 50-m transect) were compared between ground observer data and sUAV images at both the fine and coarse taxonomic resolutions and between ground camera images and sUAV images only at the fine taxonomic resolution. In the rocky intertidal, this was done for each tidal stratum separately. We used nonmetric Multidimensional Scaling (nMDS) to visualize the data and Analysis of Similarity (ANOSIM) to determine differences between the sampling methods (Primer-e V7). An ANOSIM yields global R values that range from 0 to 1, with smaller values indicating little differences in community structure and R values above 0.45 being considered to represent biologically relevant differences in community composition (Clarke et al., 2014). In cases where we detected differences between ground observer data and sUAV images at the coarse taxonomic level, we used a Similarity Percentage Analysis (SIMPER) to determine the taxon categories that contributed most to the differences in community composition. Similarly, we used SIMPER to determine the categories

that contributed most to community differences between the ground camera images and the sUAV at the fine taxonomic resolution in those comparisons where differences were detected.

For the large-scale analysis of patchiness in the seagrass bed we first selected non-overlapping images of a total of four flights flown at a relatively even flight height (~ 5 m AGL), assessed from the altimeter information recorded by the sUAV camera. For each image (n = 662 for all flights combined), we manually estimated the percent cover of seagrass. We converted the GPS coordinates of each image into eastings and northings to represent actual distances (in meters) and to avoid spatial distortion. We spatially plotted the seagrass percent cover using a linear interpolation function using Matlab to create a “heat map” to visualize regions of high and low seagrass cover. In this map, warm colors (red) represent high percent cover of seagrass, whereas cool colors (blue) represent low percent cover of seagrass. The interpolation in this application typically creates slightly lower seagrass cover values than when plotting seagrass cover based on values from each individual image.

3. Results

In the rocky intertidal, ground observer percent cover surveys at the fine taxonomic resolution yielded 10, 25 and 24 different taxa/categories at the MHHW, MTL, and MLLW, respectively (Table 1). This was much higher than what was obtained from the sUAV images at the fine resolution, with 4, 9 and 10 taxa/categories at the same tidal strata. The ground camera images yielded similar or slightly higher taxon/category numbers than the sUAV images, with 5, 10, and 13 categories at the MHHW, MTL, and MLLW, respectively. Mostly, the much higher taxonomic resolution from the observer data resulted from macroalgae that typically could be identified to species level by observers while they had to be grouped into larger categories for ground camera and

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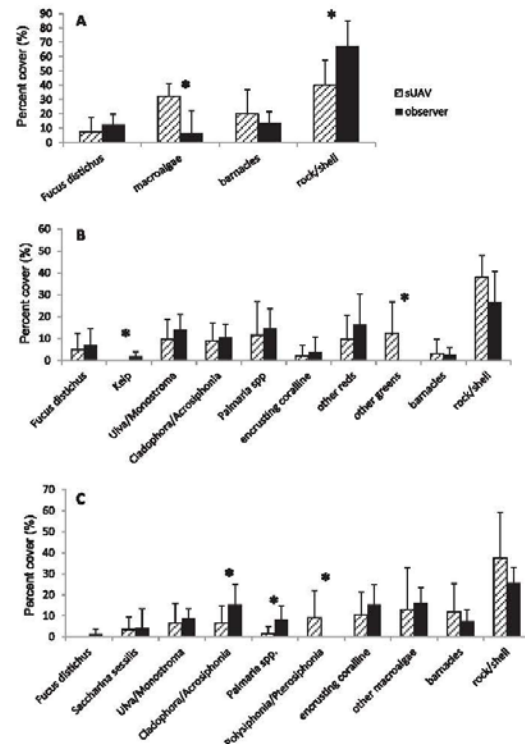


Fig. 1. Percent cover of coarse taxonomic categories from the rocky intertidal as assessed by observer visual surveys versus images taken by the sUAV. A) MHHW, B) MTL, C) MLLW. Asterisks above bars indicate statistical differences for the respective category between sUAV images and observer surveys (at $p \leq 0.05$; results from t-test).

sUAV images (Table 1). Data from the ground observers and sUAV images were then unified at the coarser taxonomic level available for the sUAV images into 4 categories at the MHHW, 10 categories at the MTL, and 10 at the MLLW (Fig. 1). A higher number of categories existed for sUAV after aggregation at the MTL (10 versus 9) because ground observations captured a kelp category that did not occur in the sUAV images; hence, kelp was added to the aggregated coarse resolution and set at zero for the sUAV images (Table 1). At the MHHW, significant differences between observer and sUAV data existed for the macroalgae and rock/shell categories (Table 1, Fig. 1). At the MTL, the only significant differences in categories between the two methods were for kelp and other green algae; however, kelp occurred overall only at a very low percentage in that tidal stratum. At the MLLW, significant differences between the two methods were seen for *Palmaria* spp., *Polysiphonia/Pterosiphonia*, and *Cladophora/Acrosiphonia* categories. Of these, the *Cladophora/Acrosiphonia* category was the only one of the significant groups that had higher percentages in the sUAV images than the ground observer data (Fig. 1).

Similarities in the overall community composition between the ground observer and sUAV images depended mostly on the taxonomic resolution used, but also varied slightly by the rocky intertidal stratum considered (Fig. 2). As expected, observers always produced the highest taxon number in each tidal stratum, and community structure based on fine taxonomic resolution (i.e., the highest resolution yielded by either method) was always different between observer data and sUAV data (Fig. 2 fine, Table 1). When taxonomic resolution of the ground observer data was aggregated at the same level as for the sUAV images,

community composition as determined from the two methods was no longer different, although statistical results at the MHHW were right around the threshold at which biologically meaningful differences may still occur (ANOSIM $R=0.438$) (Table 1, Fig. 2 coarse). The coarse categories “macroalgae” and “barnacles” combined contributed most (58%) to the differences in community structure at the MHHW (SIMPER analysis) and were both higher in the sUAV images than the ground observer data. When comparing the two image systems (sUAV and ground camera), we found a strong community difference at the MHHW but not at the other two strata (Fig. 3, Table 1). In the comparison between sUAV images and ground camera data, macroalgae and barnacles again contributed most to the community differences (56%, SIMPER), and both categories were again higher in the sUAV images. Both image systems yielded highly similar community compositions at fine resolution at both the MTL and MLLW (Fig. 3, Table 1).

Observer ground surveys in the seagrass bed yielded 9 categories: seagrass, 5 macroalgal taxa (*Saccharina* sp., *Ulva* sp., *Pterosiphonia/Polysiphonia*, *Halosaccion firmum*, unidentified foliose red alga), diatoms, rock/shell, and mud. In contrast, seagrass sUAV images did not provide sufficient resolution for diatoms or macroalgae except kelps, resulting in only 5 categories: seagrass, kelp, macroalgae, rock/shell, and mud. Even when categories for ground observer data were unified at the coarser resolution obtained from the sUAV images (i.e., pooling all macroalgal species except kelp into a common “macroalgae” category), sUAV images and observer data still differed significantly between the two methods (Fig. 4). Observer data resulted in significantly higher ($p=0.002$, t-test) macroalgae, and sUAV images had a significantly higher ($p=0.023$, t-test) rock/shell percentage (Fig. 4). However, seagrass cover as the dominant habitat feature in this system was not different between the two methods. Differences in overall community composition based on the sUAV images and the ground observer data also were obvious at both the fine (ANOSIM $R=0.892$) and the coarse (ANOSIM $R=0.832$) taxonomic resolution levels (Fig. 5). At the coarse level, community structure differences were primarily due to rock/shell and macroalgal cover (56% of dissimilarity, SIMPER). Overall community composition based on images from sUAVs versus ground camera also were different (ANOSIM $R=0.540$), mostly due to the contributions of rock/shell, kelp, and diatoms (54% of dissimilarity, SIMPER), but also the higher taxonomic resolution for macroalgae with ground camera images.

Based on the result that seagrass percent cover taken by the observer and from sUAV images were not significantly different (see Fig. 4), we used the sUAV images from a larger spatial extent to assess variability in seagrass cover. The heat map based on percent cover of seagrass from sUAV images clearly identified the high-density center of the seagrass cover with sharply decreasing concentrations towards the edges of the bed (Fig. 6A). Plotting the percent cover for each image individually instead of using interpolation can be a useful tool to document the, at times, strong small-scale variation in seagrass cover (Fig. 6B). Especially in the center of the bed, small-scale variability was obvious where neighboring images can have seagrass cover from 10 to 80% (see circle in Fig. 6B).

4. Discussion

The data support our hypothesis that observer percent cover surveys on the ground consistently achieve a higher resolution of taxonomic categories compared with sUAV images. Most of these differences resulted from the much higher taxonomic resolution of macroalgae obtained by the observers in both the rocky intertidal system (see Table 1) as well as the seagrass system. Naturally, observers on the ground have more means to determine taxonomic features of macroalgal species identification such as texture, branching patterns, holdfast structure, natural color, etc. In addition, an observer can move organisms to get a better view of partially hidden organisms, which is not possible from an image. These advantages may be especially

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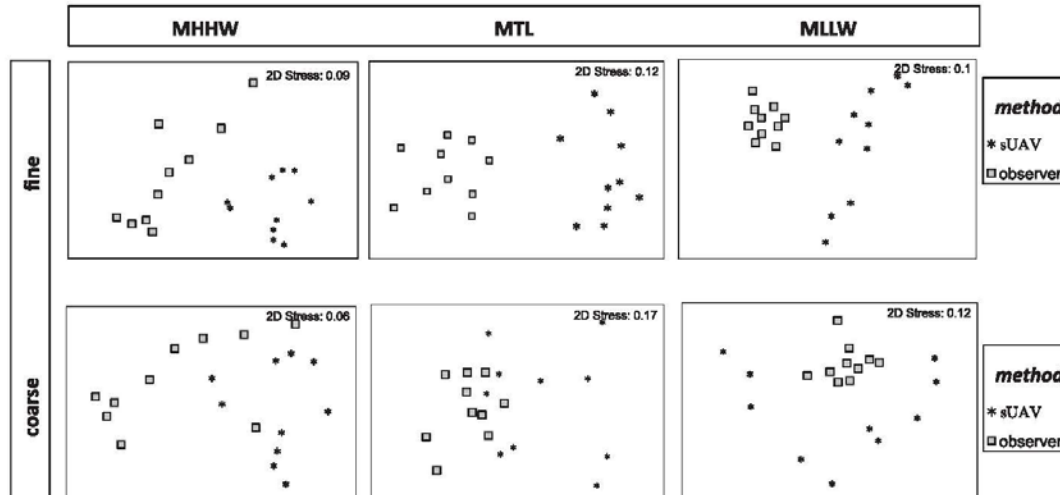


Fig. 2. nMDS ordinations of images taken by the sUAV and observer visual surveys for the MHHW, MTL, and MLLW tide levels. nMDS are shown for the fine (upper panel) and coarse (lower panel) taxonomic resolutions at each rocky intertidal stratum. All data were square-root transformed and nMDS are based on Bray Curtis similarity matrices. For ANOSIM results see Table 1.

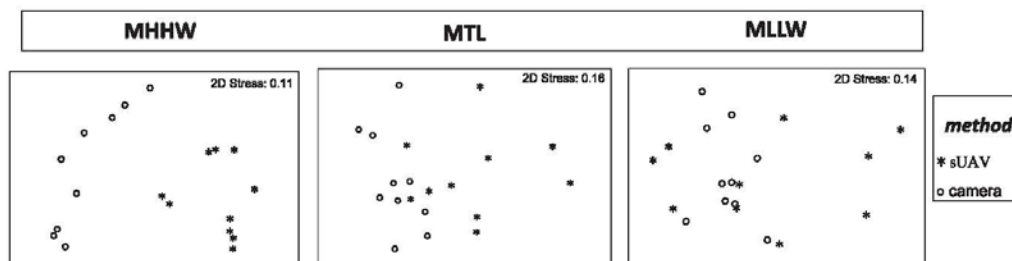


Fig. 3. nMDS ordinations of community structure from images taken by the sUAV versus images from the ground camera for MHHW, MTL, and MLLW tide levels. nMDS are shown for the fine taxonomic resolution at each rocky intertidal stratum. All data were square-root transformed and nMDS are based on Bray Curtis similarity matrices. For ANOSIM results see Table 1.

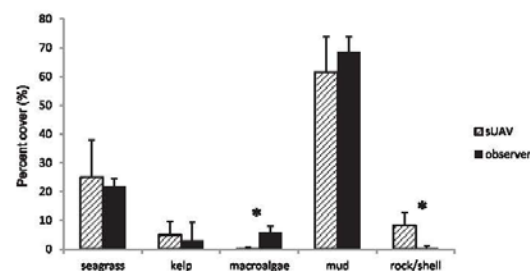


Fig. 4. Percent cover of coarse categories from the seagrass bed as assessed by observer surveys and images taken by the sUAV. Asterisks above bars indicate statistical differences for the respective category between sUAV images and observer surveys (at $p \leq 0.05$; results from t-test).

important for taxa that occur at a very low percent cover (Godet et al., 2009). A study comparing various methods of estimating benthic cover in rocky intertidal systems found that photographic images can reliably identify taxa that occur at $> 30\%$ in a plot (Meese and Tomich, 1992). Likely, the chance that taxonomic features are discernable on an image is higher if a larger area is covered by a taxon. Many of the algal species in our study in both the rocky intertidal as well as the seagrass system

covered much less than 30%; in fact, many taxa only covered 1–5%, making it more likely that these taxa are overlooked or not distinguishable on an image. The number of macroalgal species in rocky intertidal systems has been proposed to be a useful monitoring tool of water quality and system ecological health (Wells et al., 2007). That study, however, also recognized that reliability of species identification depends heavily on observer expertise and needs to be carefully evaluated. Thus, assessment of community structure on a coarser taxonomic level may in fact be more reliable for monitoring purposes where taxonomic expertise cannot be guaranteed.

Much of the low taxonomic resolution from sUAV images is likely due to the specific camera and mounting systems used instead of insufficient pixel resolution. The HERO has a rolling shutter system where the exposure occurs by scanning the scene in rows across the image instead of instantaneously with a global shutter. While the rolling shutter can increase sensitivity and light exposure, it also leads to blurring of the image at high motion (of the scene or the camera). This is a likely cause for the lack of focus in the images that led to the low resolution of identifiable taxa. In addition, the mounting system of the camera to the sUAV likely did not sufficiently isolate the camera from the sUAV platform vibration, which exacerbates image blurriness. In addition, the glare in many of the images often made it difficult to distinguish small features. Improvements on these technical aspects of the sUAV system could remedy many of the issues with image quality,

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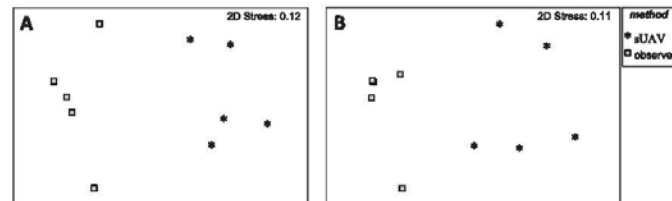


Fig. 5. nMDS ordinations from seagrass beds of fine (A) and coarse (B) taxonomic resolution community composition from images taken by the sUAV versus observer visual surveys. All data were square-root transformed and nMDS are based on Bray Curtis similarity matrices. For ANOSIM results see text.

although the abovementioned benefits of species identification by a ground observer would still apply. However, the long-term record created by images can be extremely useful if there is a need to revisit community composition even years later.

In most cases, percent cover of individual categories and overall community composition were very similar once the observer data were aggregated at the taxonomic resolution level of the sUAV images in the rocky intertidal, supporting our hypothesis in most cases. We still detected notable differences in community structure at the coarse taxonomic resolution at the MHHW. On an individual species level at the MHHW, sUAV images yielded higher macroalgal cover while observer data yielded higher rock/shell cover (Fig. 1A), while on a community-wide level, macroalgae and barnacles contributed most to the community differences. It is possible that the white barnacles are not easily distinguished from light-colored rock on an sUAV image in the high intertidal and that the small size of many high intertidal macroalgal species (e.g. *Gloiopeltis furcata* and *Endocladia muricata*) renders them cryptic in an image. In addition, or alternatively, it is possible that spatial variability in the MHHW is so high that the randomly chosen observer plots and randomly chosen sUAV images, which did not survey the exact same quadrat locations, happened to capture different aspects of this community. The relatively high scattering of replicate samples for both sUAV and observer data in the nMDS plots suggests that spatial variability is high in the MHHW in this system (Fig. 2). While we aimed to assess community composition at the transect level, where individual quadrats serve as representative subsamples of this community, we cannot exclude that pronounced small-scale variability in the high intertidal zone was not sufficiently captured by the randomly chosen images and ground plots. This is supported by the fact that ground images (which were taken at the

same location as the ground observer quadrats) also provided significantly different community composition in the MHHW compared with sUAV images. While most of the spatial variability in rocky intertidal systems is associated with the vertical extent of the system, i.e., the tidal strata, a significant amount of variation can also be associated with the horizontal extent along a transect (e.g., Araújo et al., 2005; Konar et al., 2009).

Similar to the MHHW, we found significant differences in the percent coverage of some individual species at the MTL and MLLW (Fig. 1B and C), although the transect-level community compositions were similar (Fig. 2 and Table 1). Community analysis is a multi-species, permutational approach using rank-based data to calculate similarities of samples and, thus, the species that contribute to the multivariate differences in community structure are not always the same as those where abundances differ in single species comparisons (Clarke, 1993; Clarke et al., 2014). Therefore, if the goal of the monitoring is to assess changes in overall community structure or monitoring non-biological beach attributes, then the coarse taxonomic level achievable with an sUAV can be a useful tool. For example, sUAVs were successfully used for monitoring disturbance in the rocky intertidal in northern Spain by comparing images of boulder position over time (Pérez-Alberti and Trenhaile, 2015). In addition, sUAV imagery can produce 3D high resolution (mm scale) orthogonal images that can document changes (i.e., disturbance) in intertidal substrates over time, and spectral analysis could be used to automate classification and comparison of surface features (likely on coarse scales) over time. If the goal of the monitoring is to assess overall species richness or the abundance of specific species, the sUAV resolution may not be sufficient. However, if ground camera resolution is sufficient and can be matched by a higher quality sensor and mount on the sUAV, then it

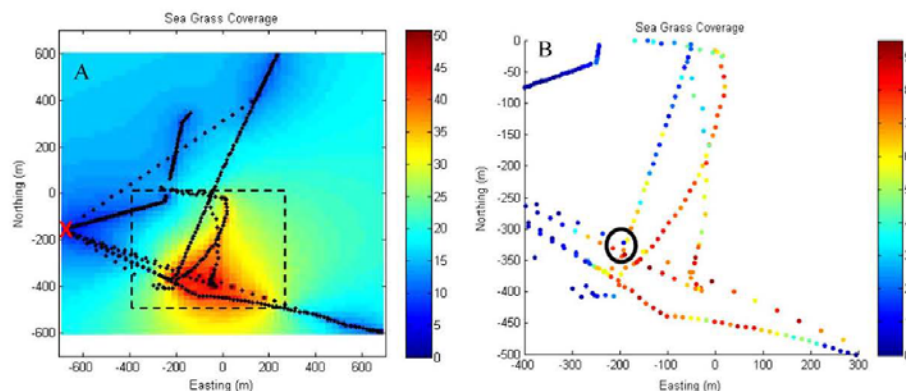


Fig. 6. Percent cover of seagrass derived from sUAV images during flights across the seagrass bed. A. Heat map of seagrass cover according to the scale on the right as % seagrass cover derived from a linear interpolation function; black dots indicate locations of pictures taken during the flight paths; dashed outline indicates the part of the plot displayed in detail in panel B. The "X" at the left side of the plot indicates the beach location where the sUAV was started and returned. B. Seagrass cover according to color scale given to the right for each individual image during flight paths, focusing on the center of the seagrass bed. The circle indicates a region of high patchiness in seagrass cover among neighboring images. Note that the color scales for the two plots are not the same as one is based on interpolation (A) and one on actual image values (B).

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may prove useful for this purpose. It has been suggested that presence of opportunistic species is an important metric in rocky intertidal monitoring (Juanes et al., 2008; Wells et al., 2007), and it would be important to select such opportunistic species for a specific region in which to conduct monitoring. Should such species be recognizable on sUAV images, sUAV surveys could become a highly valuable tool. In previous work in the northern Gulf of Alaska, we determined that the genus or order levels of macroalgal identification, or groupings on a functional level, are sufficient to distinguish community patterns among various regions (Konar and Iken, 2009). While the sUAV did not consistently provide sufficient resolution on the genus or order level for all species, our results here are promising to test if an improved sUAV imaging approach could be useful to detect larger spatial scale (regional) differences in community structure on the coarse resolution.

We hypothesized that ground camera and sUAV images would provide comparable community-level data, and in the rocky intertidal this was the case at the MTL and MLLW but not at the MHHW. Both imaging techniques had the disadvantage over observer data of not reliably capturing some of the more detailed taxonomic features and not being able to move an organism to clear a partially hidden organism underneath. However, the quality and resolution of ground images, typically taken from < 2 m height, is much higher than the quality of sUAV images taken from a greater height and a moving platform. The better quality of the camera images may have contributed to the greater detection of barnacles and small red algae, the two categories that contributed most to the differences in community structure. However, the slightly higher taxon resolution achieved with the ground camera than the sUAV (see Table 1) did not affect results on the community level at the two lower tidal strata. Therefore, sUAV imagery could be an alternative to the more time consuming method of walking along the tidal strata at low tide to capture ground images. Again, an sUAV system with a higher resolution camera, a global shutter system, and a vibration-free mount could make the sUAV and ground camera imagery more comparable, thus minimizing these differences. Cost-benefit analyses would need to be done for specific projects to see whether sUAV imagery is also more cost effective.

In the seagrass system, the main difference between sUAV images and observer data was the higher taxonomic resolution of macroalgae in the observer data. While overall macroalgal species richness in seagrass beds is much lower than in the rocky intertidal in Alaska, epiphytic macroalgae on seagrasses are often delicate and cryptic species that are difficult to distinguish on an image. Many of the same reasons as for rocky intertidal apply to the seagrass system where the limited quality of sUAV imagery prohibited identification of these delicate algal species. The ground camera imagery also proved a more reliable tool in detecting these epiphytic macroalgal species than the sUAV camera, suggesting a higher quality sensor and mount on an sUAV could bring these two imaging options into line. As seagrass system functioning depends heavily on seagrass-epiphyte interactions, the detection of epiphytes may be important to monitoring. For example, epiphytes are vital to nutrient recycling in the system when they take up a majority of nutrients released from seagrass leaves that would otherwise be diluted and lost from the benthic system (McRoy and Goering, 1974; Penhale and Thayer, 1980). Epiphytic algae also contribute significantly to the above-ground productivity of seagrass systems (e.g., Heijs, 1985), which then feeds into the associated food web (Kitting et al., 1984). Epiphytic algae also contribute significantly to overall diversity in seagrass beds, which is tied to the resilience of seagrasses against perturbations (Blake and Duffy, 2010; Duffy, 2006; Duffy et al., 2015). Therefore, the lack of detection of epiphytic algae using sUAV images could be a significant hindrance of using sUAV imagery for seagrass monitoring if the goals of the monitoring are associated with those functions unless a higher resolution sUAV system can be found.

Seagrass cover itself was not significantly different between sUAV images and observer data (Fig. 4), which could be a very promising

venue for monitoring programs using sUAVs where the goal is to assess seagrass cover over large spatial scales. Seagrasses are foundation organisms that harbor a rich diversity of associated species, many of which are of commercial interest (e.g., Johnson et al., 2003). In Alaska, seagrasses also serve as spawning substrate for herring (Haegele and Schweigert, 1985), thus having important nursery function for this important forage fish that has experienced significant declines and little recovery after the Exxon Valdez oil spill in Prince William Sound, Alaska in 1989 and other stressors (Carls et al., 2002). Therefore, reliably assessing seagrass cover itself is ecologically valuable. We successfully used sUAV images to create distribution maps of seagrass cover over a much larger scale than is feasible by observers on the ground (Fig. 6). The maps demonstrate that the size of a seagrass bed can be reliably determined as the relatively sharp transition from seagrass cover to unvegetated regions was clearly recognizable. In addition, it was possible to gain an understanding of the small-scale variability and patchiness of seagrass cover even in the densest region of the bed.

5. Conclusion

The use of sUAVs in intertidal monitoring was assessed for a rocky intertidal system and an intertidal seagrass system in the northern Gulf of Alaska. The low resolution of the sUAV imagery created problems in reliably identifying many taxa to species. Some of these shortfalls could be remedied by using higher resolution cameras with a global shutter system and an improved mounting system to reduce camera vibrations. This may require switching to an sUAV system that is able to carry this potentially larger payload. Also, lower flight path of the sUAV would help with image resolution, but depending on region, this can be challenging when a beach contains large boulders that present obstacles to flight altitude. Still, the value of using sUAVs over the more traditional monitoring method of observer surveys remains dependent on the goals of a monitoring program. Questions that can be addressed by a lower taxonomic resolution than observers produce could benefit greatly from the sUAV approach, mostly because of the much larger spatial extent that can be covered during a single low tide period. Our approach of assessing large-scale distribution patterns of seagrass is one such example where the coarse taxonomic resolution of sUAV images was sufficient to yield highly valuable results. Similar examples could be found for the rocky intertidal, for example by focusing on key taxa such as rockweed (*Fucus* sp.). Potentially, spectral image analysis could automate the process of identifying and comparing changes in these dominate intertidal community players over time. Finally, high resolution 3D orthogonal imagery could be useful for documenting physical disturbance events within intertidal communities over time.

Whether or not the sUAV approach is more cost effective and logistically easier remains to be determined for each application, and depends on the specific logistical situation. sUAV use requires permits in more urban areas that can be logistically difficult to obtain and may also require a licensed pilot to fly the sUAV. Still, it seems that such limitations will become easier to overcome in the future with the increased use and application of sUAV systems in monitoring science. Considerable time is needed for the sUAV image analysis when done individually by researchers. Time may be optimized by using automated imaging systems that can either 1) accurately calculate area of recognizable taxa/categories, 2) be trained to identify a library of images of common taxa, or 3) use spectral properties of the organisms in the image to automatically identify organism groups (Pech et al., 2004). Therefore, while we obtained mixed results for the applicability of sUAVs in the rocky intertidal and seagrass bed in our study, we also have shown that sUAVs can be a valuable tool in monitoring and are likely to become an important tool in monitoring and ocean observing in the future (Lomax et al., 2005). More testing of their use in various systems and the optimization of camera resolution to flight height will lay the groundwork for more routine applications.

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APPENDIX 3

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Influence of static habitat attributes on local and regional rocky intertidal community structure

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Abstract

Rocky intertidal communities are structured by local environmental drivers, which can be dynamic, fluctuating on various temporal scales, or static and not greatly varying across years. We examined the role of six static drivers (distance to freshwater, tidewater glacial presence, wave exposure, fetch, beach slope, and substrate composition) on intertidal community structure across the northern Gulf of Alaska. We hypothesized that community structure is less similar at the local scale compared with the regional scale, coinciding with static drivers being less similar on smaller than larger scales. We also hypothesized that static attributes mainly drive local biological community structure. For this, we surveyed five to six sites in each of six regions in the mid and low intertidal strata. Across regions, static attributes were not consistently different and only small clusters of sites had similar attributes. Additionally, intertidal communities were less similar on the site compared with the region level. These results suggest that these biological communities are not strongly influenced by the local static attributes measured in this study. An alternative explanation is that static attributes among our regions are not different enough to influence the biological communities. This lack of evidence for a strong static driver may be a result of our site selection, which targeted rocky sheltered communities. This suggests that this habitat may be ideal to examine the influence of dynamic drivers. We recommend that future analyses of dynamic attributes may best be performed after analyses have demonstrated that sites do not differ in static attributes.

Introduction

Rocky intertidal communities naturally experience and are resilient to a large range of physical conditions, which is not surprising considering they cycle between submersion in water and exposure to air on a regular basis. Some physical conditions are driven by dynamic forces and fluctuate on various temporal scales (e.g., temperature, salinity, nutrients, etc.), whereas others are static (*sensu* Meager et al. 2011) and do not greatly fluctuate from year to year (substrate, beach slope, exposure to wave action, etc.). Although static attributes typically change minimally over time scales of at least years to decades, they can vary greatly among spatial scales of regions, local sites, and even within a site (i.e., the various intertidal strata) and can influence biological community structure. We have previously documented that intertidal communities in the northern Gulf of Alaska vary with tidal stratum, but high variability in zonation patterns among sites within each region reduced the generality of this pattern (Konar et al. 2009). In that study, significant interactions were found in the algal and invertebrate community between regions and sites (nested within region) and depth. Currently, the specific role of static habitat attributes in driving community structure throughout the northern Gulf of Alaska is unclear. Because the relative importance of environmental drivers is difficult to define due to the high number of potential factors and the interactions among them (Little and Kitching 1996), we start here with an attempt to better understand the role of static attributes. Understanding how and on which spatial scales (regional, local, intertidal stratum) static attributes structure intertidal communities will help narrow future studies to the most important community drivers.

Possible static attributes that may influence rocky intertidal community structure in high latitude systems include distance to freshwater, tidewater glacial presence, exposure to ocean swell, fetch (distance to next land mass), beach slope, and substrate composition. Freshwater entering the nearshore from rivers can lower local ocean salinity, increase sedimentation, and play a role in structuring rocky intertidal communities (Held and Harley 2009, Law et al. 2013). Given equally sized rivers with similar discharge and tributaries, the closer a community is to a river the more the community will be impacted. Lower salinity can affect the physiology and behavior of invertebrates (Garza and Robles 2010, Montory et al. 2014). These impacts can increase during flood events (Nishijima et al. 2013). In addition to salinity, increased sedimentation from rivers can be deleterious to marine organisms. Specifically for algae, sediments can prevent the settlement of algal propagules and can smother newly settled individuals (Schiel et al. 2006, Deiman et al. 2012). Algal grazer efficiency and general diversity can also decrease, and overall community composition can change in areas with increased sedimentation (Spurkland and Iken 2012, Pulfrich and Branch 2014).

Similar to river discharge, glacial discharge lowers salinity and increases sedimentation but it can also lower water temperature (Beszczyńska-Möller et al. 1997, Spurkland and Iken 2012). Changes in water temperature can influence various processes, including feeding,

metabolic and population growth rates, and changes to species-specific interactions (Sanford 1999, Kordas et al. 2011). For example, a slight decrease in water temperature dramatically reduced the effects of a keystone predator, the sea star *Pisaster ochraceus*, on its principal mussel prey in Oregon, suggesting far-reaching impacts on the structure of these rocky communities initiated by environmental drivers (Sanford 1999).

Intertidal communities are also structured by exposure to waves (Dayton 1971, Ricciardi and Bourget 1999, Pulfrich and Branch 2014, Bloch and Klingeil 2015). For example, species turnover rates (Bloch and Klingeil 2015) and algal palatability (Long et al. 2013) have been correlated with measures of wave exposure. Similarly, high species richness has been found at sites with high wave variability (deJuan and Hewitt 2013). Beach slope and composition of the substrate also can have large ramifications on the structure of intertidal communities by influencing recruitment, disturbance, thermal stress, and survival (Ricciardi and Bourget 1999, Gedan et al. 2011, Bloch and Klingeil 2015). For example, substrate size can impact community structure by mediating the thermal stress experienced by species with larger rocks remaining cooler than smaller rocks (Gedan et al. 2011).

Although many static drivers may influence which species survive at different locations (stratum and sites) in the intertidal, the available species pool from the general geographic region also will determine which species are able to settle. The assembly of species within a site is determined by a process involving the dispersal of species from a regional pool and then filtered by local dynamic and static environmental drivers (Mittelback and Schemski 2015). Typically, communities are less similar at the local scale (between sites) compared with the regional scale because local processes will differ among sites within a region (Edwards 2004, Konar et al. 2015). It has been suggested that there are different regulating processes operating at different spatial scales. In some cases, regional processes can be important in structuring communities at the local scale (Rivadeneira et al. 2002). For example, El Niño resulted in the near-complete loss of giant kelp over hundreds to thousands of kilometers (regional scale) but the level of recovery of kelp varied at multiple smaller spatial scales, including local (Edwards 2004). Understanding the role that static drivers play in filtering species at various spatial scales will enable us to better define the role of temporally variable dynamic drivers in structuring intertidal communities, which are of concern because these are the drivers being influenced by climate change.

This paper seeks to determine how and on which spatial scales rocky intertidal communities may be structured by static habitat attributes. Specifically, we examine how mid and low intertidal communities at 31 sites within six regions across the northern Gulf of Alaska vary depending on their distance to freshwater, tidewater glacial presence, wave exposure, fetch, beach slope, and substrate composition. As such, we assess mid and low intertidal community structure across sites and regions in the northern Gulf of Alaska and describe the static habitat attributes at these same locations. These data are used to address the hypotheses that 1) intertidal community structure is less similar at the local scale compared with the regional scale, coinciding with static drivers being more variable on smaller scales (sites within regions) than larger scales (across regions), and 2) static attributes drive local biological community structure.

Materials and methods

Study area

Six regions around the Gulf of Alaska (GOA) were surveyed (Fig. 1). In 2012, Western Prince William Sound (WPWS), Eastern Prince William Sound (EPWS), Kenai Fjords National Park (KEFJ), Katmai National Park and Preserve (KATM), and Kachemak Bay (KBAY) were sampled. In 2013, the same regions were sampled except that Northern Prince William Sound (NPWS) was sampled instead of EPWS. Prince William Sound, centered at approximately 60° N, 147° W, is a sub-arctic embayment having characteristics of a small inland sea with abundant freshwater inputs. Within the Sound, NPWS contains glaciated fjords with deep open water basins to >870 m depth. In EPWS, the tidal glacial influences are less pronounced, leaving a coast generally characterized by sedimentary formations and nutrient-rich watersheds. In WPWS, an archipelago forms a network of islands and passes stretching from the northern sound down to the open Gulf and production is driven by a portion of the Alaska Coastal Current. KEFJ (60° N, 150° W) is located along the southeastern side of the Kenai Peninsula in southcentral Alaska. It is glacially fed by the Harding Icefield, one of the largest ice caps in the US, and is characterized by steep glacial fjords and lagoons sheltered by moraines. KATM (59° N, 155° W) is located on the Alaska Peninsula. Storms, wind mixing, and terrestrial inputs result in high productivity in KATM. KBAY is located north of the Gulf of Alaska at 60° N and 151° W. The bay is a large estuary that can be divided into an inner and outer bay. The outer bay is largely free of glacial influence, whereas several points of glacial discharge from the Harding Icefield enter the inner bay.

Sampling procedure

Sites were initially chosen based on their slope (not vertical), substrate, and extent (at least 100 m continuous rocky habitat). All sites were also relatively protected from high wave exposure and were associated with freshwater sources, although to varying degrees. Five sites were sampled in the summer in each region except in KBAY where a sixth site was added in both years. Sites were sampled in the mid and low intertidal strata (approximately at +1.5 and +0.5 m, respectively, relative to MLLW). In addition, an exception occurred in 2012 in KBAY, when one site was only sampled in the low intertidal stratum.

Static habitat attributes used in this analysis included distance to the nearest freshwater source, tidewater glacial presence by region, exposure to wave action, fetch, beach slope, and substrate type (i.e., percent of bedrock, boulder, cobble, gravel, mud/sand; categories according to the Wentworth scale). For the analysis, data layers were rasterized for glaciers, shoreline, and freshwater sources and were all based on an equal number and size of pixels (50 m x 50 m pixel size) to standardize distance measures. Freshwater sources (stream outflow and tidewater glacier locations) were obtained from the National Hydrography Dataset (NHD), a comprehensive set of digital spatial data that includes marine and coastal information created in the early 2000s for Alaska. Using ArcGIS Spatial

Analyst Cost Distance tool (ESRI, Redlands, CA), distances from sites to the nearest freshwater source within each region were calculated only across water bodies, excluding land masses. This includes only those sources of flowing water that appear on USGS maps and excludes small freshwater discharges on beaches and static bodies of water. We recognize that although the distance to a freshwater source and tidewater glacial presence are static elements, the discharge rates of these two sources are variable over seasonal and annual scales. These discharge rates should therefore be included in future analyses of the influence of dynamic attributes. However, the presence and distance of these sources were still deemed important in the static habitat attribute setting.

Exposure was determined from the ShoreZone Alaska web site (<http://alaskafisheries.noaa.gov/mapping/szflex/index.html?T=SZ@L=B>), where locations are classified based on the Biological Wave Exposure classifications of protected, semi-protected, or semi-exposed. Fetch is another commonly used proxy for the wave exposure of a shore (Burrows et al. 2008, Mieszkowska et al. 2013, Tam and Scrosati 2014) and provides a continuous scale of potential wave energy. In this study, fetch was calculated by creating vertices every 10° for 360° centered on each study site (i.e., spoke pattern) to a length of 200 km. Vertices were clipped once a land mass was encountered. A sum of the remaining vertices' distances was used to estimate the total potential fetch at each site. Two land resolutions, or buffers, were created to evaluate the effect of small rocks or islets on any particular site: 200 m and 5000 m. All land masses that fell within the buffers were erased for the respective distance fetch measurements. This allowed calculation of fetch distance after removing potentially non-effective barriers to wave energy. Slope (in degrees) was measured at each site in all regions for every 1 m rise in elevation at five equally-distanced points along each transect (at mid and low stratum). Slopes for the low and mid strata were then calculated at each site as a mean of the five slope measurements for the 0 – 1 m and 1 – 2 m rises, respectively. Substrate type was visually estimated as percent substrate cover within each quadrat and the mean calculated for each stratum at each site. Substrate categories used the Wentworth scale and included percent of bedrock, boulder, cobble, gravel, mud/sand.

Biological sampling generally followed Gulf Watch Alaska protocols (http://www.evostc.state.ak.us/Store/Proposal_Documents/2196.pdf) in the mid and low intertidal strata (approximately at +1.5 and +0.5 m, respectively, relative to MLLW). In addition, an exception was in 2012 in KBAY, when one site was only sampled in the low intertidal stratum. At each site, the intertidal community was visually quantified at randomly placed quadrats along a 50-m transect in both strata for percent cover of sessile invertebrates and algae, which were identified to the lowest feasible taxonomic level (as low as species but sometimes phyla). This sampling was completed in one of two ways, depending on the type of long-term monitoring that is conducted in each region. At all sites except for those in KBAY, cover was determined within twelve 0.25 m² quadrats in each stratum, which were systematically positioned along the transects based on a random start point uniquely selected each year. Within quadrats, the presence of algae and sessile invertebrates was determined at 25 systematically placed points, and the percent cover was calculated based on the proportion of points occupied by each taxa. In KBAY, percent cover of the overstory kelp layer (i.e., primarily species of *Alaria*, *Hedophyllum*, *Laminaria*,

and *Saccharina*), if present, and the top layer of sessile invertebrates and algae were visually estimated from ten randomly placed 1 m² quadrats. Data from the kelp layer and the underlying layer were combined and their abundances re-standardized to 100 %. Because all taxa occurring within multiple layers were recorded at the non-KBAY sites, only the overstory kelp layer and the first, uppermost layer underneath kelp were included in this analysis.

To ensure comparability between the two methods (KBAY and all other regions), both methods were completed and then compared in both intertidal strata at the KBAY sites in 2015. For this, the same five random quadrats along each transect for each stratum at every site were assessed using both methods. These data were then square root transformed and a Bray Curtis similarity matrix was constructed. A three-factor PERMANOVA (factors were tidal height, quadrat nested in height, and the sampling method) demonstrated that the two methods did not yield significantly different results within quadrats at either of the tidal strata (Table 1). This enabled us to compare communities sampled with both methods across regions in subsequent analyses.

DATA ANALYSES

All statistical analyses were done in PRIMER v 7. Data for static habitat attributes were checked for correlations among each other (at 90 % or greater) using bivariate draftsman plots and Spearman rank correlations. The highest correlation was between bedrock and boulder ($\rho = -0.84$). Because of the lack of meaningful correlations, all attribute data were retained in the analysis, square root transformed, and then normalized to a common measurement scale. To normalize data, PRIMER subtracts the mean and divides by the standard deviation over all samples, which makes the variance along all axes similar. A resemblance matrix of similarities among all sample site pairs based on habitat attributes was then created on the transformed and normalized data using Euclidean distances. To determine if there were differences in regions based on the static habitat attributes, a mean of the mid and low strata slopes and substrate type were calculated for each site. A resemblance matrix based on Euclidean distances of the transformed and normalized habitat attribute data was then created among all sample site pairs (Clarke et al. 2014). A SIMPROF analysis was used to determine grouping of sites based on static attributes. This analysis objectively identifies group members from a classical hierarchical agglomerative clustering method. The clustering results of the SIMPROF were overlaid on the nMDS of the sites as described by their static attributes. To test for differences among regions, a one-factor PERMANOVA was used. In addition, the highest ranked static habitat attributes (from the BEST BIO-ENV routine; Clarke et al. 2014) were overlaid as vectors on the static attribute cluster nMDS plots to assess which drivers separated the clusters at each stratum. Lastly, a CLUSTER analysis was conducted separately for each stratum on the static habitat attributes of each site and the resulting static groupings were superimposed on the nMDS plots that were based on the biological communities to compare community groupings by static habitat characteristics.

All biological percent cover data were square root transformed, and a resemblance matrix created based on Bray-Curtis similarities (Clarke et al. 2014). Quantitative differences in biological community structures were examined between the two years, among the six

regions, and among the different sites within each region separately for each stratum. A three-factor mixed-model nested PERMANOVA was used, with year and region as fixed factors, and site nested within region as a random factor. A second PERMANOVA was completed with the KBAY data removed to determine if results were similar. The relative differences in biological communities between regions and sites were evaluated graphically with nMDS for each stratum separately. A SIMPER analysis was conducted on each stratum to determine the primary taxa contributing to community structure in each region.

In addition, the overall relationships between the static habitat attributes and the biological communities for each stratum were evaluated using the BEST BIO-ENV routine and a subset of variables identified that maximized the rank correlations between these data. This was done by comparing the Bray-Curtis and Euclidean distance resemblance matrices of the biological and environmental data, respectively, to determine if any environmental drivers correlated with the biological communities.

Results

All static attributes varied to some extent among regions (Appendix 1). When the mid and low strata attributes were averaged to describe each site, some sites clustered within their regions; however, there was much overlap of sites among regions (PERMANOVA Pseudo-F = 5.482, $P(\text{perm}) = 0.001$; Fig. 2). Based on a SIMPROF analyses, two of the KBAY sites clustered together and three KBAY sites clustered with one KATM and one KEFJ site. There was much overlap among the PWS sites with only one WPWS site clustering alone. In general, the mid and the low intertidal strata were characterized by different static attributes (Fig. 3). The mid stratum was most characterized by fetch (200 m buffer), slope at +0.5, tidal glacial presence, and proportional boulder and gravel substrate ($\rho = 0.630$; BEST-BIOENV routine). Tidal glacial presence, beach slope, and proportional rock substrate were most responsible for separating sites in KBAY from those in other regions (Fig. 3a). In the low intertidal, distance to freshwater, exposure, and percent of mud/sand substrate were the most influential drivers of the site characteristics ($\rho = 0.499$; BEST-BIOENV routine). Tidal glacial presence and proportional rock substrate most separated the KBAY sites from sites in the other regions; however, there was much overlap among KBAY, KATM, and KEFJ in their static attributes (Fig. 3b). In both the mid and low intertidal, regions were significant for the static attributes (Table 2, PERMANOVA).

For the mid intertidal stratum, biological communities were significantly different at the site level (Table 3 top, PERMANOVA). While region was also significant, it was less influential (lower Pseudo-F value) than site. Year was not significant. In the mid stratum, bare substrate and *Fucus distichus* were important contributors to all regions. Differences were apparent for NPWS and KBAY, which had *Cladophora/Chaetomorpha/Rhizoclonium* complex and *Palmaria* spp, respectively (Online Resource 1; additional data are given in Online Resource 2). In the mid stratum, individual taxa and categories did not have a higher correlation coefficient than that of the entire community (*Odonthalia/Neorhodomela* complex, *Ulva/Monostroma* complex, *Alaria* spp, *Mytilus trossulus*, barnacles, and bare rock

were tested with the highest $\rho = 0.150$ for bare rock; BEST-BIOENV routine). For the low intertidal stratum, significant differences also were associated with site nested within region (Table 3 bottom, PERMANOVA). Here, both region and year were also significant, but again less influential (lower Pseudo-F values) than site. In the low stratum, no one taxon was an important contributor to all regions. The *Odonthalia/Neorhodomela* complex was unique to KEFJ and *Acrosiphonia* spp. was unique to KBAY (Online Resource 3; additional data are given in Online Resource 2). In the low stratum, the individual taxa and categories that were tested did not have a higher correlation coefficient than that of the entire community (*Odonthalia/Neorhodomela* complex, *Ulva/Monostroma* complex, *Alaria* spp, *Mytilus trossulus*, barnacles, and bare rock were tested with the highest $\rho = 0.401$ for bare rock; BEST-BIOENV routine). Given the differences in sampling between KBAY and the other regions, we repeated the analyses without KBAY, even though our method comparison did not show significant differences between the two methods (Table 1). Overall PERMANOVA results for both mid and low intertidal strata remained the same when KBAY was excluded, with significant site effects (highest Pseudo-F values) (Table 4).

The biological communities at most sites did not cluster by their regions in the nMDS plots for either intertidal stratum (Fig. 4). The exception to this was seen with the KBAY sites, which formed a fairly distinct regional group in both strata (Fig. 4). Some of the KATM sites also formed a small cluster but only for the low tidal stratum (Fig. 4b). All sites within the PWS regions and the KEFJ sites strongly overlapped (Fig. 4). By comparison, the only clearly defined groupings of sites when categorized by static attribute clusters were static groups 1 and 3 in the mid intertidal (Fig. 5a). These two static groups combined coincided with the KBAY sites (compare Figs. 4a and 5a). These two static groups were similar in their glacial presence, percent rock, and beach slope. In general, sites from multiple regions shared static attribute groupings (i.e., static attribute groups were spread across regions), especially for the low intertidal stratum. This suggests that except for KBAY mid intertidal, the regions did not consistently differ in the static attributes that were measured in this study.

Discussion

Intertidal communities are assembled by processes operating over various spatial scales. Typically, the species that recruit and survive at the local scale are a subset of the species available from a regional pool that are selected by dynamic and static environmental drivers acting at local scales (deJuan and Hewitt 2011, Mittelback and Schemski 2015). For example, intertidal species composition often differs depending on substrate grain size (Gedan et al. 2011) and wave energy (Bloch and Klingeil 2015), both of which are typically relatively homogeneous over small/local scales, but can be highly variable among large regional scales. These local drivers result in a subset of species at the local scale when compared to the regional scale, where all substrate types and wave exposure levels are represented and all available species exist within the region. This implies regional differences in species composition would presumably be driven by differences in the proportion of habitats with particular substrate types and wave exposures, which will likely be much less variable than local scale differences among sites.

An extreme example of local scale variability is differences in community composition between intertidal elevations. That is, the characteristic zonation pattern of intertidal communities is similar across many regions (e.g., Knox 2001, except see Harley and Helmuth 2003) but the strata differ greatly at the site level. Many of the differences between the community structures of intertidal strata can be explained by species tolerance to desiccation, which can be mitigated by wave exposure, with mean air exposure time over the daily tidal cycle and relative wave exposure as the most important static environmental drivers (Dayton 1971). Here, we used intertidal stratum as a covariate to account for this expected difference in community composition between intertidal elevations and concentrated on among site and regional level differences for each stratum. Our study demonstrated that the different regions across the northern Gulf of Alaska were largely overlapping in their intertidal community structure, similar to previous results involving other regions within the Gulf of Alaska (Konar et al. 2009). This contrasts with a study in the Gulf of Maine that found distinct community types in different regions despite the regions sharing many of the same species (Bryson et al. 2014). In Maine, the different community structures probably emerged because of regional differences in coastal oceanography modulating species recruitment.

Our first hypothesis that intertidal community structure is less similar at the local scale compared with the regional scale was supported. This corresponds to the findings of other studies that concluded that environmental processes dominate at larger scales and ecological (dynamic) processes play a more important role at local scales (Konar et al. 2015, Menge et al. 2015). It is possible that within the northern Gulf of Alaska, environmental processes (including static drivers) influence all sites similarly but it is the ecological processes that structure communities at the site level and these local processes might be very different among sites within the Gulf of Alaska. The one region where sites did cluster together was in the KBAY mid intertidal stratum. This suggests some degree of connectivity among the KBAY sites that is distinct from the other regions. The static drivers that most influenced the separation of the KBAY sites from the others were glacial presence, percent rock, and beach slope. Although KBAY has no tidewater glaciers, PWS and KEFJ have many of them. Slope was generally less steep at KBAY compared with the other regions, which may result in different interactions with wave exposure. On shores with a gentle slope, waves typically break when their height is approximately half the water's depth (Thornton and Guza 1983) whereas on steep slopes, waves generally break when their height is approximately equal to the local water depth (Galvin 1972). This difference in wave exposure, with presumably higher wave impacts in KEFJ compared with KBAY, may be influencing community structure. Similar to wave action, slope also influences desiccation rates, which will influence mortality, particularly of young individuals (Connell 1972). Lastly, KBAY had less bedrock than the other regions, which may also be contributing to community differences as rock complexity has been regarded as a habitat driver in other studies (Kohn and Leviten 1976, Block and Klingbeil 2015). For example, high habitat complexity has been associated with higher community diversity (Eriksson et al. 2006), and we found highest species richness in KBAY in an earlier comparison across Gulf of Alaska regions (Konar et al. 2009).

In our study, we examined the role of static habitat attributes in structuring communities at both local and regional scales. Our second hypothesis that the static attributes measured in this study would separate local from regional biological community structure was largely unsupported, except for the KBAY mid intertidal communities. Study sites within all regions were relatively sheltered and were in proximity to freshwater sources, which may have contributed to the local and regional similarity we found. If true, static drivers may be a stronger factor for intertidal communities at more diverse types of sites. However, comparing sites with similar static attributes may provide an excellent opportunity to examine dynamic drivers that will vary at different temporal scales at the site and region levels without confounding effects of static habitat attributes. We recommend that future analyses of dynamic attributes may best be performed after analyses have demonstrated that the influence of static attributes does not differ among sites.

Although the static attributes measured here did not play a large role in structuring the intertidal communities, the specific attributes that most influenced structure in the mid and low strata were different. Although no one driver was found to influence both the mid and the low intertidal strata, types of drivers were similar for both. For example, substrate type is often a driver of community structure (Sousa 1979) and it was a driver for both intertidal strata included here, although different substrate measures were found to be important in each stratum. In the mid intertidal, percent boulder and gravel substrate were important whereas in the low intertidal, it was percent of mud/sand. This difference in substrate importance could be related to various functions that substrate plays for rocky intertidal organisms. For example, larger substrate sizes are more thermally stable, which is more of a concern for organisms in the mid than the low intertidal (Gedan et al. 2011). Similarly, larger substrate sizes are less movable by hydrodynamic forces that are typically strong in mid intertidal regimes, creating a disturbance for intertidal organisms (Gaylord 1999). Likewise, we found wave exposure to be important but it manifested its importance differently depending on tidal stratum. In the mid stratum, fetch (at a 200 m buffer) was important whereas in the low stratum, exposure category was influential. Historically, wave exposure has been believed to be the most important local driver of intertidal community structure (Lewis 1964, Dayton 1971), although this has not been consistently found (Zacharias and Roff 2001). Two additional drivers were found to be important but not in both strata. In the mid stratum, slope was an important driver whereas in the low, it was distance to freshwater. Slope may be important in the mid because it mediates the length of air exposure in that stratum, which is less important to the low intertidal communities that naturally experience shorter exposure times. Similarly, distance to freshwater may be an important driver in the low stratum because this stratum is submerged longer than the mid and communities may be more impacted by freshwater and presumably the variation in salinity (a dynamic driver) during this extra time of submergence.

Community structure can vary temporally because dynamic drivers fluctuate seasonally and annually (Caffey 1985, Burrows et al. 2012). Dynamic drivers can impact static attributes and biological drivers (Jonsson et al. 2006). For example, waves can change the amount of sand deposition onto rocky intertidal organisms, altering their community structure (Littler et al. 1983). If a habitat has more cobbles than bedrock, these cobbles can

be moved in a way that organisms are damaged during times of large waves (Shanks and Wright 1986). Similarly, waves can reduce grazing activity, which can change algal community structure on intertidal benches (Jonsson et al. 2006). While we tried to isolate a set of static drivers, the reality is likely more complicated because some static drivers are directly influenced by dynamic processes. For example, wave exposure and fetch can be numerically measured but the manifestation of these attributes (i.e., through wind and waves) will vary from year to year based on weather and hence may have different impacts on community structure from year to year (Mazzucco et al. 2015). A longer term study may be able to tease apart the interactions of static and dynamic drivers, but that was beyond the focus of this study. The distinct separation of mid intertidal communities in KBAY from other regions may also be related to alternative drivers not examined in our study including those that may not be static. Within a variety of other potential drivers, top-down predation and differences in grazer density may be contributing to the separation of the KBAY sites. Sea stars, predatory snails, sea otters, and sea ducks, all can have top-down effects and structure communities (Paine 1980, Estes and Duggins 1995, Marsh 1986). In addition, grazers such as limpets, chitons and sea urchins can have large impacts on algal community structure (Konar and Estes 2003, Salomon et al. 2007, Burgos-Rubio et al. 2015). Similar to biological processes, there may be physical processes that differ among our regions. Although all regions are influenced by glaciers and streams, some physical attributes such as turbidity, dissolved oxygen, and nutrients may be differing. In addition, the level of habitat complexity that was measured at our sites was limited and could be further expanded. Currently, these biological and physical drivers have not been examined or compared among our sites or regions.

Understanding and managing nearshore community resilience requires knowledge about how static and dynamic drivers work together to influence community structure. A better understanding of static drivers will assist in analyzing the role of dynamic drivers that are a concern with changes in climate and ocean chemistry (acidification and freshening). In the future, greater frequency of environmental extremes is likely, including greater fluctuations in large-scale events such as the Pacific Decadal Oscillation or the recent warm Blob in the North Pacific (Peterson et al. 2015). In high latitudes, dynamic drivers such as temperature change, increased glacial melt, river discharge due to permafrost melting, sea-level rise, and increases in the frequency of storms will affect rocky shores and coastal environments in general. It is thought that over the next 25 years, rocky shore communities will change subtly and will be subject to increasing degradation (Thompson et al. 2002). Because the static habitat attributes did not vary greatly among the sites studied here, these regions are ideal to examine community variability in the context of short-term (i.e., variations in salinity, temperature and nutrients), long-term (climate change and the Pacific Decadal Oscillation), and episodic (oil spill and eutrophication) dynamic drivers.

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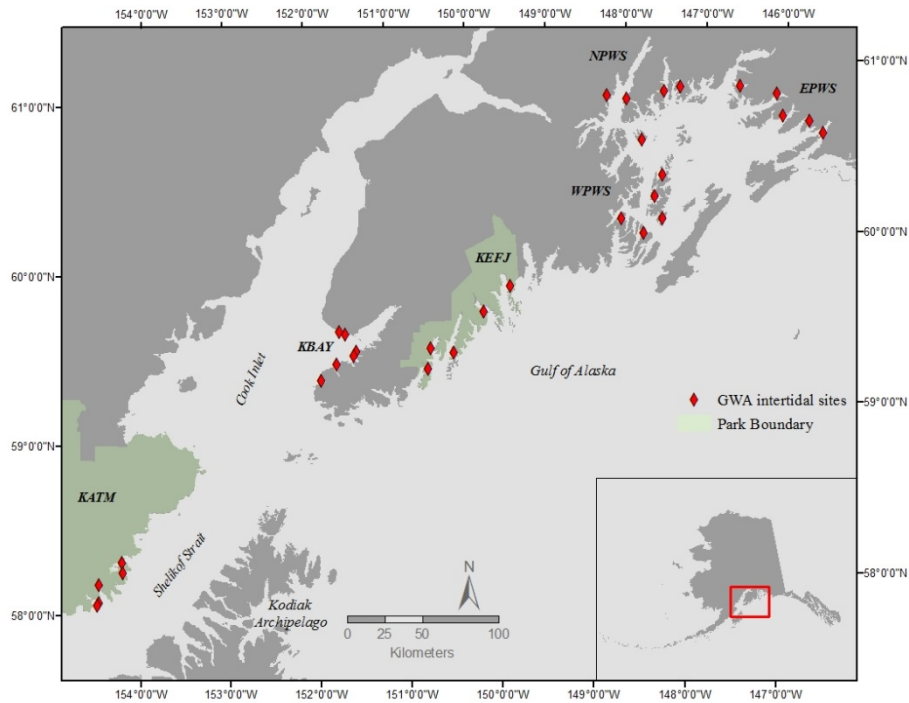


Figure 1. Map showing study sites within the northern Gulf of Alaska: Northern Prince William Sound (NPWS), Western Prince William Sound (WPWS), Eastern Prince William Sound (EPWS), Kenai Fjords (KEFJ), Kachemak Bay (KBAY), and Katmai (KATM).

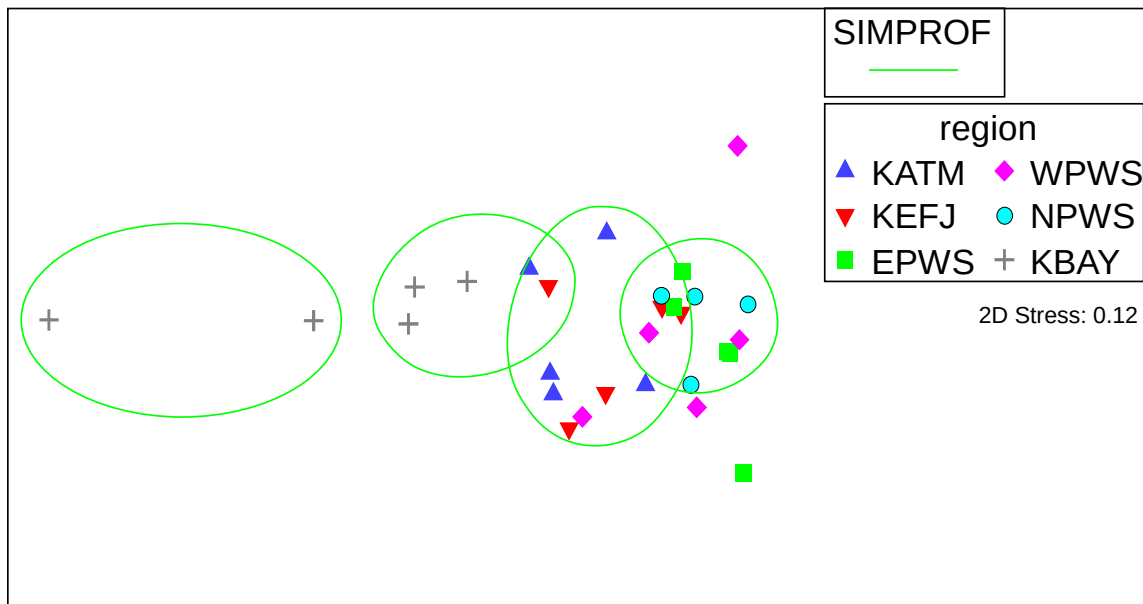


Figure 2: nMDS plots showing differences in static attribute data for each site color-coded by regional association. Data were square root transformed and normalized. A SIMPFROF test was used to obtain groupings.

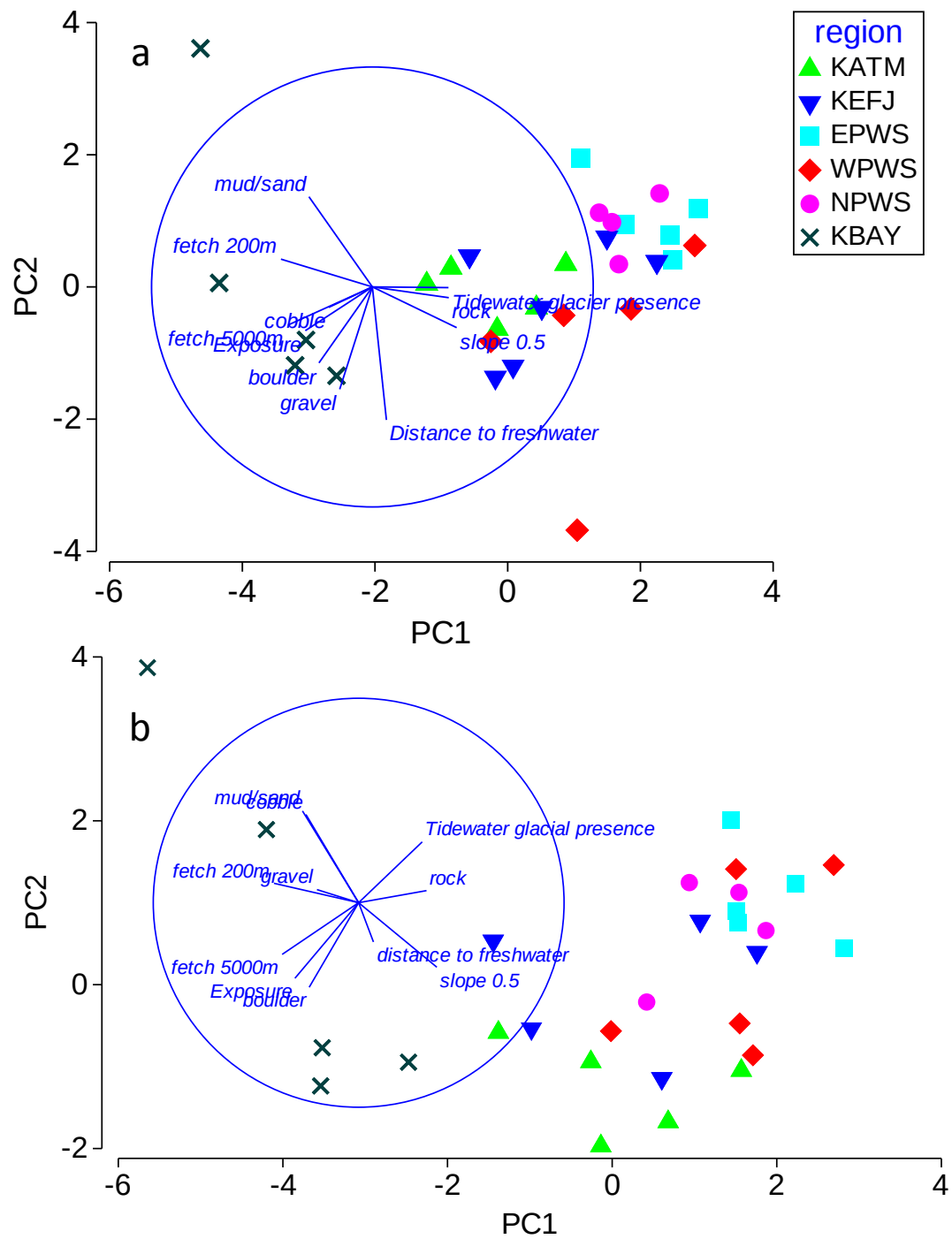


Figure 3: PCA for each site and year color-coded by region for the mid (a), and low tidal stratum (b) with environmental drivers as vectors.

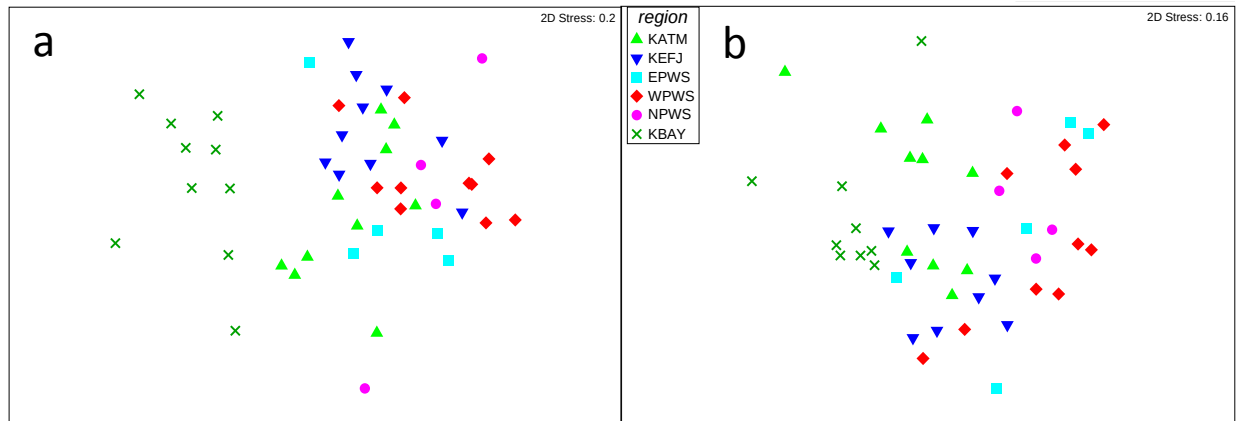


Figure 4: nMDS plots showing differences in biological data for each site and year color-coded by regional association for the mid (a), and low tidal stratum (b). Data were square root transformed.

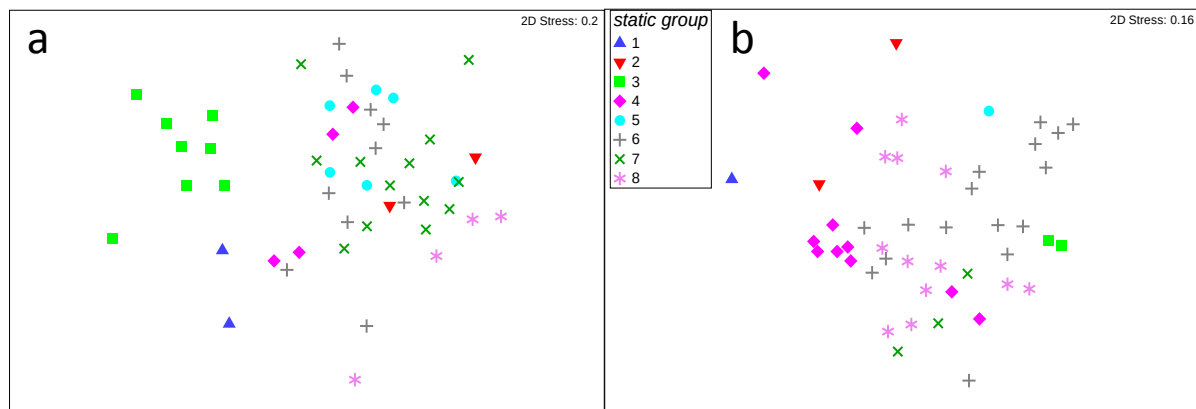


Figure 5: nMDS plots showing differences in biological data for each site and year color-coded by static attribute group for the mid (a), and low tidal stratum (b). Static groups were assigned to a site based on a cluster analysis on the environmental data each site. Data were square root transformed.

Table 1: PERMANOVA results testing differences in the biological data by tidal height, method, and quadrat nested in tidal height. Differences in the biological communities are based on Bray-Curtis similarities of square root transformed percent cover data. Bold values are significant.

Source	df	SS	MS	Pseudo-F	<i>P</i> (perm)
stratum	1	8126.7	8126.7	4.2796	0.013
method	1	1681.9	1681.9	2.3996	0.068
quadrat(stratum)	18	37947	2108.2	1.4152	0.059
stratum x method	1	1148	1148	1.668	0.15
qu(st)xme	13	9065.7	697.36	0.46814	0.998
Res	25	37241	1489.7		
Total	59	99197			

Table 2: PERMANOVA results testing differences in the environmental data by region and site (nested in region). Differences in the environmental data are based on Euclidean distance of square root transformed and normalized data. Top: mid strata, Bottom: low strata. Bold values are significant.

Source	df	SS	MS	Pseudo-F	<i>P</i> (perm)
re	5	159.03	31.806	4.9106	0.001
si(re)	23	148.97	6.477	No test	
Total	28	308			

Source	df	SS	MS	Pseudo-F	<i>P</i> (perm)
re	5	146.81	29.362	4.4299	0.001
si(re)	21	139.19	6.6281	No test	
Total	26	286			

Table 3: PERMANOVA results testing differences in the intertidal biological data by year, region, and site (nested in region). Differences in the biological communities are based on Bray-Curtis similarities of square root transformed percent cover data. Top: mid strata, Bottom: low strata. Bold values are significant. Bold values are significant.

Source	df	SS	MS	Pseudo-F	<i>P</i> (perm)
ye	1	6608.1	6608.1	2.2331	0.054
re	5	2.23E+05	44588	4.2963	0.001
si(re)	23	2.52E+05	10969	9.8405	0.001
yexre	3	14455	4818.3	1.6221	0.066
yexsi(re)	16	47683	2980.2	2.6735	0.001
Res	541	6.03E+05	1114.7		
Total	589	1.16E+06			

Source	df	SS	MS	Pseudo-F	<i>P</i> (perm)
ye	1	10152	10152	3.0778	0.011
re	5	2.27E+05	45421	2.5946	0.001
si(re)	23	4.38E+05	19025	17.81	0.001
yexre	3	18947	6315.5	1.8994	0.019
yexsi(re)	14	47027	3359.1	3.1445	0.001
Res	504	5.38E+05	1068.2		
Total	550	1.30E+06			

Table 4: PERMANOVA results testing differences in the intertidal biological data by year, region, and site (nested in region) excluding the KBAY sites. Differences in the biological communities are based on Bray-Curtis similarities of square root transformed percent cover data. Top: mid strata, Bottom: low strata. Bold values are significant.

Source	df	SS	MS	Pseudo-F	<i>P</i> (perm)
ye	1	10158	10158	3.828	0.007
re	4	93240	23310	2.483	0.002
si(re)	19	1.93E+05	10138	8.571	0.001
yexre	2	9461	4730	1.782	0.089
yexsi(re)	12	31910	2659	2.248	0.001
Res	452	5.35E+05	1182		
Total	490	8.84E+05			

Source	df	SS	MS	Pseudo-F	<i>P</i> (perm)
ye	1	13547	13547	4.791	0.008
re	4	1.44E+05	35953	2.011	0.022
si(re)	19	3.75E+05	19733	17.375	0.001
yexre	2	13115	6557	2.318	0.018
yexsi(re)	11	31178	2834	2.496	0.001
Res	426	4.84E+05	1136		
Total	463	1.08E+06			