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

Gulf Watch Alaska: Nearshore Benthic Systems in the Gulf of Alaska

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

Heather Coletti

National Park Service
Inventory and Monitoring Program, Southwest Alaska Network
4175 Geist Road
Fairbanks, Alaska 99709

Daniel Esler
Brenda Ballachey
Jim Bodkin
George Esslinger
Kim Kloecker
Dan Monson
Brian Robinson
Benjamin Weitzman

U.S. Geological Survey
Alaska Science Center
4210 University Drive
Anchorage, Alaska 99508

Tom Dean

Coastal Resource Associates
1948 Kellogg Avenue
Carlsbad, California 92008

Mandy Lindeberg

National Oceanic and Atmospheric Administration
National Marine Fisheries Service, Alaska Fisheries Science Center
Ted Stevens Marine Research Institute - Auke Bay Laboratories
17109 Point Lena Loop Road
Juneau, Alaska 99801

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Study History: The nearshore monitoring work described in this report builds on a long history of nearshore ecosystem monitoring and research, some of which dates back prior to the 1989 *Exxon Valdez* oil spill. With these longer-term data streams, we are able to document changes to nearshore marine environments and infer underlying causes earlier and with more confidence than if data had been collected only during the past 5 years as part of the Gulf Watch Alaska program. Importantly, these data streams are not continued in isolation, but are part of a carefully-designed and coordinated nearshore monitoring program, described in detail by Dean et al. (2014) and Coletti et al. (2016), and briefly in the Introduction and Methods sections below.

Precursors to the nearshore marine monitoring described in this report were first developed during the early 2000's, when the *Exxon Valdez* Oil Spill Trustee Council supported the design of a restoration and ecosystem monitoring plan (Restoration Projects 030687, 040687, and 050750; Dean and Bodkin 2006). The *Exxon Valdez* Oil Spill Trustee Council provided funding to the U.S. Geological Survey in 2007 to conduct a pilot year of nearshore data collection in western Prince William Sound (Restoration Project 070750; Bodkin et al. 2009). In 2010, the *Exxon Valdez* Oil Spill Trustee Council funded Restoration Project 10100750, for U.S. Geological Survey to implement the nearshore monitoring plan in western Prince William Sound over a three-year period, 2010-2012 (Ballachey et al. 2015).

The same nearshore monitoring plan (Dean and Bodkin 2006) was adopted in 2005 by the National Park Service Southwest Alaska Network for their Inventory and Monitoring program, and implemented in Katmai National Park and Preserve in 2006 and Kenai Fjords National Park in 2007. National Park Service Southwest Alaska Network and U.S. Geological Survey worked collaboratively to implement the nearshore monitoring program in these regions, and data collection has occurred annually in both parks since (with the exception of 2011, in which Katmai National Park and Preserve was not sampled).

In 2012, the *Exxon Valdez* Oil Spill Trustee Council funded implementation of the 20-year Gulf Watch Alaska marine monitoring program (Project 12120114), the subject of this report. Because of their shared history, focus, and design, ongoing nearshore monitoring efforts in western Prince William Sound, Katmai National Park and Preserve, and Kenai Fjords National Park could be seamlessly assembled under the Nearshore Component of the Gulf Watch Alaska program. This has allowed a broad, regional consideration of variation within nearshore ecosystems of the spill-affected area of the northern Gulf of Alaska.

The nearshore monitoring described in this report also is linked to similar GWA monitoring of rocky intertidal and seagrass habitats in Kachemak Bay (Project 12120114-L; Konar et al. 2017), which was originally initiated in 2003 through the Census of Marine Life program. Considerable coordination has occurred to jointly address monitoring objectives, when possible, across the two projects under the Nearshore Component of Gulf Watch Alaska.

Finally, it is critical to recognize the volume of *Exxon Valdez* Oil Spill Trustee Council-funded research addressing nearshore ecosystems since the time of the spill, which has contributed to the design of the nearshore ecosystem monitoring and provided critical background for identifying changes and understanding underlying mechanisms. These research efforts are too numerous to list individually, but are summarized in recent reports (e.g., Ballachey et al. 2014, Esler and Ballachey 2014, Esler et al. 2015, Michel et al. 2016).

Abstract: Nearshore ecosystem monitoring in western Prince William Sound, Kenai Fjords National Park, and Katmai National Park and Preserve has been conducted as part of the Gulf Watch Alaska program over the past five years (2012-2016), building on years and sometimes decades of preceding research and monitoring. During the Gulf Watch Alaska period, we have successfully collected data on a suite of nearshore metrics, including: intertidal water and air temperature; eelgrass cover; abundance of intertidal macroalgae and invertebrates on sheltered rocky shores; size and density of infaunal and epifaunal bivalves on mixed-sediment beaches; size and density of Pacific blue mussels in mussel beds; abundance and distribution of marine birds and mammals; abundance, nest site density, and composition of prey provisioned to chicks for black oystercatchers; sea otter abundance and distribution, age class at death, and diet and foraging rate; and concentrations of contaminants in mussels. These metrics were explicitly selected because of their value as trophically-connected features of nearshore ecosystems that offer insights into causes of changes through bottom-up and top-down forces within the nearshore food web. Change to any trophic level within the food web will likely manifest itself throughout the nearshore ecosystem. For example, we documented increasing densities of sea otters in Katmai National Park and Preserve. Concurrently, we observed decreases in clam biomass and decreases in energy recovery rates of sea otters. Together, these metrics strongly suggest that the sea otter population in Katmai has reached a food-dictated carrying capacity. We observed variation in many metrics, at differing spatial and temporal scales, which led to valuable insights about the various forces that result in observed changes in nearshore marine communities during the first five years of this project.

Key words: Benthic invertebrates, black oystercatchers, Gulf of Alaska, intertidal, Katmai National Park and Preserve, Kenai Fjords National Park, macroalgae, marine birds, monitoring, nearshore marine ecosystem, Prince William Sound, sea otters

Project Data: Following is a summary of the data collected during the initial five years (2012-2016) of the nearshore component of the Gulf Watch Alaska Program. Many data streams originated prior to the start of the Gulf Watch program as part of other *Exxon Valdez* Oil Spill Trustee Council projects and the National Park Service Southwest Alaska Network Inventory and Monitoring program (see Study History, above). In many cases we have included those data in our releases in order to keep the longer time series together. The data have been made publicly available in order to preserve the opportunity for other researchers and the public to access these data in the future. These data and metadata have been peer reviewed through the U.S. Geological Survey Fundamental Science Practices policies (U.S. Geological Survey Manual, 502.7 and 502.8).

(a) *Data descriptions:* All site location information including geographic coordinates, site names, site codes, and date of establishment are included in the site location data release. 2006-2016 doi:10.5066/F78S4N3R.

- **Physical Conditions**

  There have been two data releases for intertidal temperature data. The files include date and time and temperature reading in degrees C. 2014-2016 doi:10.5066/F77S7KXH; 2006-2014 doi:10.5066/F7WH2N3T.

- **Rocky Intertidal Communities**

  Five data sets of the rocky intertidal community data have been packaged together: limpet counts, limpet sizes, Nucella (snail) and Katharina (chiton) counts, random point counts (used to calculate percent cover of sessile invertebrates and algae), and sea star counts. All files include date and site information. 2006-2016 doi:10.5066/F7513WCB.

- **Eelgrass Beds**

  Three data sets associated with eelgrass bed monitoring have been packaged together: camera, sonar ground-truth, and percent cover. Additionally, there are sonar hydroacoustic raw files with this data release. 2008-2016 doi:10.5066/F7RV0KV9.

- **Unconsolidated Sediment Bivalve Communities**

  Two data sets associated with bivalve community monitoring have been packaged together: species counts and sizes. Files include date, site information, bivalve species and measurement in millimeters. 2007-2015 doi:10.5066/F71834N0.

- **Mussel Beds**

  There have been two data releases for mussel bed monitoring data. In both, five data sets associated with mussel bed monitoring have been packaged together: mussels >20mm counts, mussels >20mm sizes, mussel core counts, mussel core sizes, and site layout information (used for bed size calculations). 2016 doi.org/10.5066/F7WS8RD4; 2008-2015 doi:10.5066/F7FN1498.

- **Marine Bird and Mammal Surveys**

  Data files for these at-sea surveys include species sightings, counts, behaviors, and coordinates as well as the coordinates of the vessel track line. The data release includes five data files per year per sampling region. 2012-2016 doi:10.5066/F7416V6H.

- **Black Oystercatchers**

  Three data sets associated with black oystercatcher monitoring have been packaged together: survey transect summaries, individual nest details, and chick diet prey identification and sizes. 2006-2016 doi:10.5066/F7WH2N5Q.

- **Sea Otters**

  Aerial Surveys of Abundance. Data from four surveys have been released. In this package there are three files –transect waypoints, transect strip counts, and transect intensive search unit counts. Data are from Kenai Fjords National Park 2002, 2007, 2010, 2016 surveys and include raw data and metadata, doi:10.5066/F7CJ8BN7. Additional survey data from Katmai National Park and Preserve and western Prince William Sound will also be published.

  Carcass Collections. The data file for sea otter carcass surveys includes date and location found, parts collected, and age at death. 2011-2015 doi:10.5066/F7H993CZ. Tooth age results from 2016 carcasses have not been received from the lab and will be included in a subsequent data release.

  Foraging Observations. The data file for sea otter foraging observations includes date, location, dive and surface times, species, count, and size of prey retrieved. 2012-2016 doi:10.5066/F7N29V4R.

- **Contaminants**

  All data and files from the analysis laboratory have been released and can be located at: http://portal.aoos.org/gulf-of-alaska.php#metadata/53c052b6-8874-46d1-b40a-acc615a3879a/project/files. Mussel samples from 2007, 2012, and 2013 were collected and analyzed for a suite of polycyclic aromatic hydrocarbons, organochlorine pesticides, polychlorinated biphenyls, butyltins, polybrominated diphenyl ethers, polybrominated biphenyls, trace metals and mercury. Laboratory quality assurance and quality control procedures and results are included in the released files.

(b) *Data format:* All data sets are accompanied by Federal Geographic Data Committee compliant metadata. Unless otherwise noted, all data sets are served as comma separated files (*.csv) that are readable with a text editor or spreadsheet program.

(c) *Data location:* Gulf Watch Alaska's *Exxon Valdez* Oil Spill Trustee Council and U.S. Geological Survey data archive link(s) and custodian(s) are below. Links to individual data sets are included in the data descriptions (above).

http://portal.aoos.org/gulf-of-alaska.php#metadata/53c052b6-8874-46d1-b40a-acc615a3879a/project/files
https://alaska.usgs.gov/portal/project.php?project_id=99 or
https://alaska.usgs.gov/products/data_all.php

Alaska Ocean Observing System Point of Contact: Carol Janzen, janzen@aoos.org, 907-644-6703
Alaska Ocean Observing System, 1007 W. 3rd Ave. #100, Anchorage, AK 99501

U.S. Geological Survey Point of Contact: Kimberly Kloecker, kkloecker@usgs.gov, 907-786-7196
U.S. Geological Survey, 4210 University Dr., Anchorage, AK 99508

(d) *Data access limitations:* These data are archived by the Gulf Watch Alaska's *Exxon Valdez* Oil Spill Trustee Council and U.S. Geological Survey. 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 these datasets. It is strongly recommended that careful attention be paid to the contents of the metadata files associated with these data to evaluate data set limitations or intended use.

Citation:

Coletti, H., D. Esler, B. Ballachey, J. Bodkin, G. Esslinger, K. Kloecker, D. Monson, B. Robinson, B. Weitzman, T. Dean, and M. Lindeberg. 2018. Gulf Watch Alaska: Nearshore benthic systems in the Gulf of Alaska. Long-Term Monitoring Program (Gulf Watch Alaska) Final Report (*Exxon Valdez* Oil Spill Trustee Council Project 16120114-R), *Exxon Valdez* Oil Spill Trustee Council, Anchorage, Alaska.

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EXECUTIVE SUMMARY

We conducted nearshore marine ecosystem monitoring from 2012 to 2016, as part of the Nearshore Component of Gulf Watch Alaska, a marine monitoring program funded by the *Exxon Valdez* Oil Spill Trustee Council. Our work was conducted in three regions within the spill-affected area of the northern Gulf of Alaska: western Prince William Sound, Kenai Fjords National Park, and Katmai National Park and Preserve.

The nearshore ecosystem, while strongly influenced by both oceanic and terrestrial biomes, is a distinct entity, with specialized flora and fauna adapted for existence along the coastal fringes of the Gulf of Alaska. Nearshore ecosystems are subject to numerous physical, oceanographic, and biological sources of variation and are particularly sensitive to anthropogenic perturbations. The Gulf of Alaska nearshore ecosystem was severely affected by the *Exxon Valdez* oil spill, and many nearshore species showed evidence of acute and chronic injury as a result of the spill. The nearshore ecosystem marine monitoring work described in this document was designed to detect changes in abundance and distribution of numerous nearshore species, and to lend insight into underlying drivers of change, including the relative influences of oil spill injury versus other natural or anthropogenic effects.

The nearshore monitoring protocol focuses on sampling of multiple components of nearshore ecosystems in the Gulf of Alaska that are both numerically and functionally important to the system's health. These are termed "vital signs" by the National Park Service Inventory &Monitoring program and include kelps (and other marine algae), seagrasses, marine intertidal invertebrates, marine birds, black oystercatchers, sea otters, and marine water quality. Our nearshore monitoring has been carefully designed, with coordinated sampling of all metrics, to provide insights into drivers of variation observed at different spatial and temporal scales.

Our first 5 years of the Gulf Watch Alaska sampling, coupled with the extensive data streams preceding Gulf Watch Alaska for some metrics, have resulted in observations of many interesting patterns, which differ widely among vital signs. For example, some metrics (e.g., large mussel density) show somewhat synchronous temporal patterns across the northern Gulf of Alaska. Others (e.g., sea otter density) vary independently within the different regions. Finally, other metrics (e.g., eelgrass percent cover) appear to vary on a site-by-site basis. The spatial and temporal scales over which metrics vary are beginning to provide insights on the potential drivers of those observed patterns. This understanding will continue to improve as we increase the timeline of the data streams with continued annual sampling.

One important result has been the recognition of differing population trajectories and equilibrium densities of sea otters at our different sampling regions. When coupled with sea otter foraging data that indicate proximity to a food-dictated carrying capacity, this information provides important insights on the factors that influence sea otter populations at each region. For example, sea otter density in Kenai Fjords National Park is quite low in comparison to other populations in Alaska. This is likely due to the sea otters' reliance on

mussels as a predominant prey item and the lack of available sea otter habitat in Kenai Fjords. The sea otter population is likely food-limited and at carrying capacity in Kenai Fjords.

In collaboration with Nearshore Component colleagues working in Kachemak Bay, we evaluated the role of selected static physical factors (distance to fresh water, fetch, distance to glacial inputs, slope, substrate type and exposure) in dictating rocky intertidal community structure across our study regions (project 16120114-L). Somewhat surprisingly, these static drivers were not strongly related to intertidal community structure across regions. This may have resulted from our initial selection of similar, sheltered rocky sites within the Gulf of Alaska. For the purpose of the monitoring program, we restricted sampling of intertidal invertebrates and algae to sheltered-rocky shores and to gravel and mixed sand-gravel beaches. However, the observed similarity in static physical drivers across the sites strengthens our ability to isolate and investigate the role of dynamic sources of variation across the region.

We also have analyzed mussel data collected as part of our nearshore monitoring efforts. All mussel metrics varied considerably on a site-by-site basis, which highlights the importance of local conditions for mussel recruitment and abundance. However, after accounting for site differences, we also found patterns in several measures of abundance that indicated synchronous variation across the entire northern Gulf of Alaska, suggesting an influence of broad-scale drivers.

Furthermore, we have seen a number of interesting patterns in other metrics. For example, our water temperature data confirm that the warm water anomalies that are well-established in offshore measurements also are expressed in intertidal regions across the northern Gulf of Alaska. Nearshore biological effects of abnormally warm water remain under investigation. As another example, in response to the well-publicized common murre die-offs during winter 2015-2016, we examined our marine bird survey data, and determined that we also observed anomalous distributions and numbers of murres preceding the winter die-off. As a final example, we have discovered, in collaboration with Restoration Project 16120114-L, that sea star abundance and species dominance varies markedly among regions, suggesting local drivers of these patterns.

In addition to core monitoring work, we also have engaged in several collaborative efforts to understand nearshore processes, leveraging the field presence facilitated by GWA. These collaborations included stable isotope analyses of nearshore communities, collection of mussels for growth and energetics analyses, evaluation of the prevalence of sea star wasting disease, and collection of clams as part of an evaluation of gene expression and other biomarkers as tools for monitoring health of nearshore ecosystems.

Our overarching objective for the nearshore component was to identify important processes regulating or causing changes within the Gulf of Alaska nearshore ecosystem. The examples above illustrate the nearshore component's progress during the first five years of Gulf Watch Alaska in terms of detecting patterns and understanding process. Concurrently, we also have provided information to management agencies that has allowed for planning and response preparedness to rapidly changing environments.

In the next 5 years (2017-2021), we will continue to add to our data streams, which will continue to advance our understanding of the underlying mechanisms that lead to observed variation in the nearshore system.

INTRODUCTION

The nearshore ecosystem, while influenced by both oceanic and terrestrial biomes, is a distinct entity, with specialized flora and fauna adapted for existence along the coastal fringes of the Gulf of Alaska (GOA; Fig. 1). Nearshore environments of the northern GOA are described in detail by Dean et al. (2014) and Coletti et al. (2016; Appendix A). In brief, nearshore marine ecosystems are characterized by trophic webs that originate with primary productivity largely generated by macroalgae and sea grasses, with smaller inputs from phytoplankton (e.g., Duggins et al. 1989, von Biela et al. 2013). Primary production is consumed by a suite of filter and suspension feeding benthic invertebrates including clams, mussels, and barnacles. Other benthic invertebrates are grazers, feeding primarily on diatoms or small encrusting algae (e.g., limpets, littorine snails, and some crabs) or larger seaweeds and eelgrass (e.g., sea urchins, helmet crabs, and some larger herbivorous snails). Predators in this food web include sea stars, whelks, fish, birds, and sea otters, many of which specialize in foraging on intermediary benthic invertebrates.

Nearshore ecosystems are subject to many sources of variation (Peterson 2005). Physical and oceanographic drivers include substrate composition, shoreline slope, temperature (both water and air), desiccation (for the intertidal zone), light, exposure to waves, the degree of glacial (proximity to glacial source) and freshwater input (i.e., salinity), currents, and ice scour. Biological factors such as competition and predation also can be important drivers. Of particular importance is predation by certain “keystone” predators that consume potentially dominant species and exert influence on community structure that is disproportionate to their abundance. In the GOA, and elsewhere, keystone predators include sea otters (Estes and Palmisano 1974, Lowry and Bodkin 2005) and certain sea stars (Paine 1974). Changes in abundance of these keystone species can produce strong direct and indirect effects that cascade through the ecosystem.

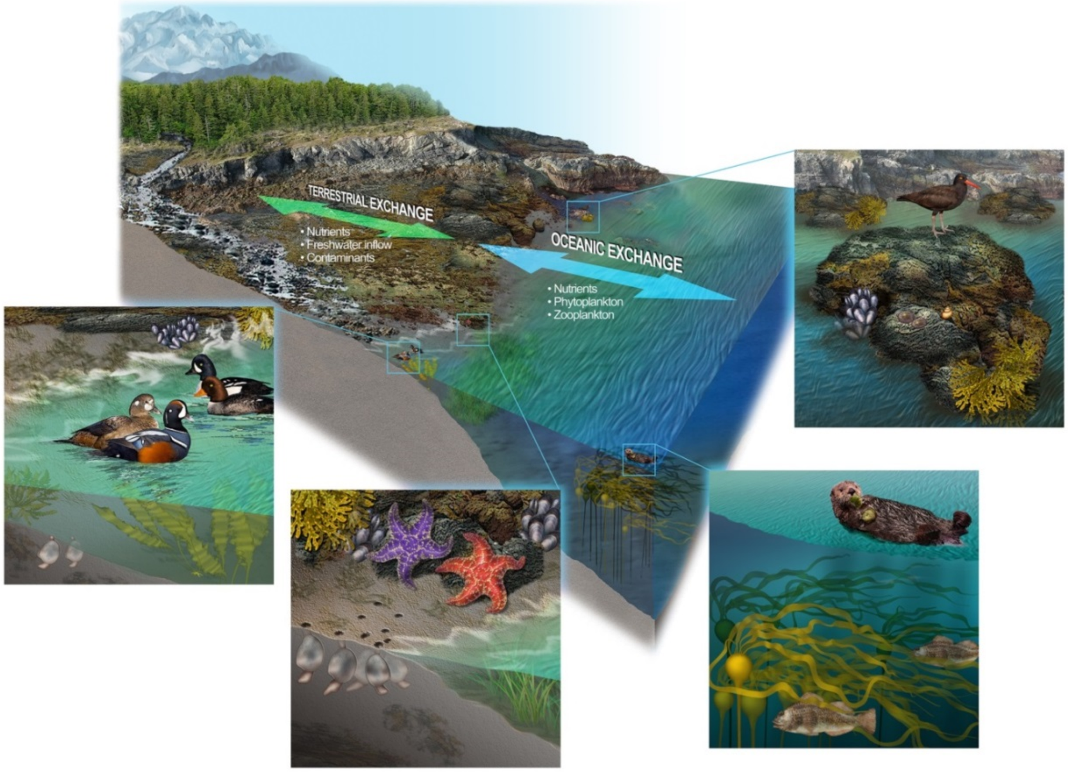

Figure 1. The nearshore ecosystem monitored by Gulf Watch Alaska in the northern Gulf of Alaska.

The nearshore ecosystem was strongly affected by the *Exxon Valdez* oil spill (EVOS), and many nearshore species showed evidence of both acute and chronic injury as a result of the spill. Of the nearly 11 million gallons of crude oil spilled (Wolfe et al. 1994), an estimated 40% landed on beaches in Prince William Sound (Galt et al. 1991), contaminating nearly 800 km of nearshore ecosystem shoreline (Short et al. 2004). The oil also moved along the Kenai and Alaska Peninsulas, with an estimated total of 2,100 km of nearshore beaches affected throughout the northern GOA (Owens 1991). Although the extent and degree of oiling declined rapidly over the first few years after the spill (Neff et al. 1995), oil remained for decades in subsurface sediments of a small number of beaches in Prince William Sound and the GOA (Michel et al. 2010, Irvine et al. 2014), and remains in some beaches at the present (Lindeberg et al. 2018). The spilled and lingering oil had disproportionately large effects on nearshore species (Michel et al. 2016), and recovery of some nearshore wildlife required decades (Ballachey et al. 2014, Esler et al. 2016, Iverson and Esler 2010).

As one of several components of Gulf Watch Alaska, the nearshore monitoring described in this document offers a window into the health of the marine environment, one that will yield important insights that may be different from those gleaned from pelagic ecosystems.

Given the social, economic, and ecological importance of nearshore systems and their inhabitants, as well as the protracted process of recovery from the EVOS observed in nearshore species, the nearshore monitoring offers an important opportunity to disentangle factors influencing Alaska's marine environment.

OBJECTIVES

The fundamental objective of this work is the long-term monitoring of a suite of nearshore species at multiple locations across the GOA, with an overall goal of identifying important processes regulating or causing changes within the GOA nearshore ecosystem. The specific objectives for the period 2012-2016 included:

1. Continue restoration monitoring in the nearshore to evaluate the current status of injured resources in oiled areas.
2. Identify if those injured resources being monitored may be considered recovered from EVOS effects.
3. Identify potential factors that could inhibit recovery of injured resources, and recommend potential restoration actions.

METHODS

The nearshore ecosystem marine monitoring work described in this document was designed to detect changes in abundance and distribution of numerous nearshore species, and to lend insight into underlying drivers of change, including the relative influences of oil spill injury versus other natural or anthropogenic effects. The consistently-measured metrics collected simultaneously at a broad geographic scale across the spill-affected region of northern GOA allow unprecedented insights into the spatial and temporal scales of change in nearshore ecosystems. Also, because the program is coordinated and designed to quantify attributes of the food web at multiple trophic levels within the same sites and regions, we can better understand the physical and biological mechanisms leading to observed changes. The nearshore monitoring design and underlying rationale are detailed by Dean et al. (2014) and Coletti et al. (2016; Appendix A of this document), and are described briefly below.

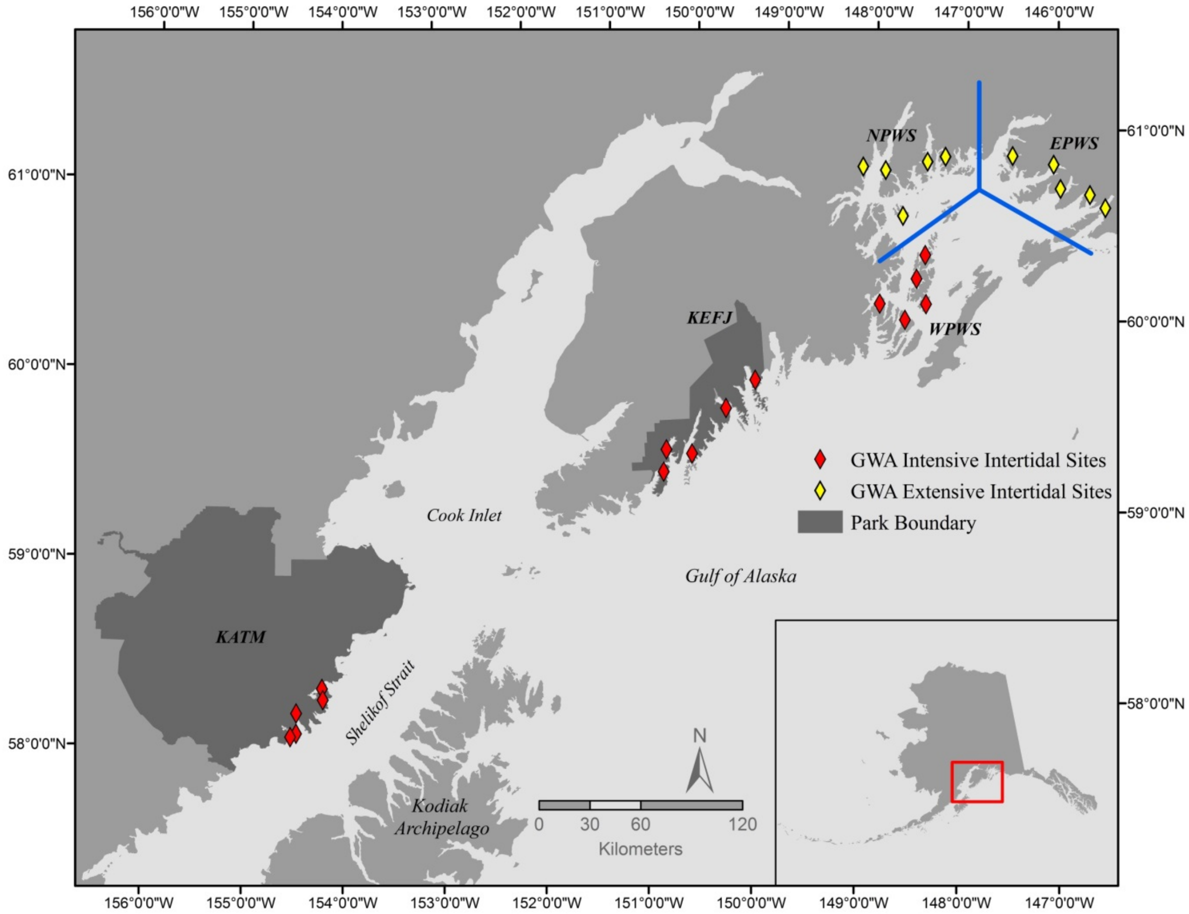

Figure 2. Gulf Watch Alaska nearshore sampling sites within the Katmai National Park and Preserve (KATM), Kenai Fjords National Park (KEFJ), and western, northern, and eastern Prince William Sound (WPWS, NPWS, and EPWS, respectively).

Our nearshore monitoring program employs a spatially nested design, with sampling within several approximately equal sized "blocks" that include KATM, KEFJ and WPWS (Fig. 2). For most vital sign metrics, sampling is conducted at randomly selected sites within each block. For those species that are spatially constrained (e.g., intertidal algae and invertebrates) sampling is conducted at randomly selected sampling units within each site. Sampling is generally conducted annually for each metric. Exceptions are the sampling of water and air temperatures (hourly), bivalves on mixed sediment shorelines (biennial sampling), surveys of sea otter abundance (approximately every 3 years), and contaminant sampling (7-10 years). This design allows us to make inferences about the scale of changes that may occur over the entire region, within a specific block or blocks within the region, and for some vital signs, for specific sites within each block. Matching the spatial extent of observed changes with scales of potential drivers of change will allow us to gain insights as to the importance of those drivers over time. For example, a region-wide reduction in a given vital sign could be interpreted as resulting from more global drivers (e.g., region-wide increases in sea surface temperature), while more localized site-specific changes may to be attributed to site specific drivers such as a point source introduction of contaminants. We note that the first 5 years of GWA included biennial sampling of a subset of attributes at "extensive" sites in northern and eastern Prince William Sound (Fig. 2); these will serve as baseline blocks that can be re-sampled in subsequent years if a compelling need emerges. Also, we reiterate that nearshore monitoring of some metrics also occurs in Kachemak Bay (KBAY; Konar et al. 2018) and those data can be incorporated when addressing some objectives or questions.

Sampling of all vital signs is temporally and spatially coordinated to allow for more seamless integration of observed changes over the entire food web (Fig. 3). Sampling is centered on the randomly selected rocky intertidal monitoring site, and other metrics are sampled nearby, following a set of protocols that have been established (Dean et al. 2014).

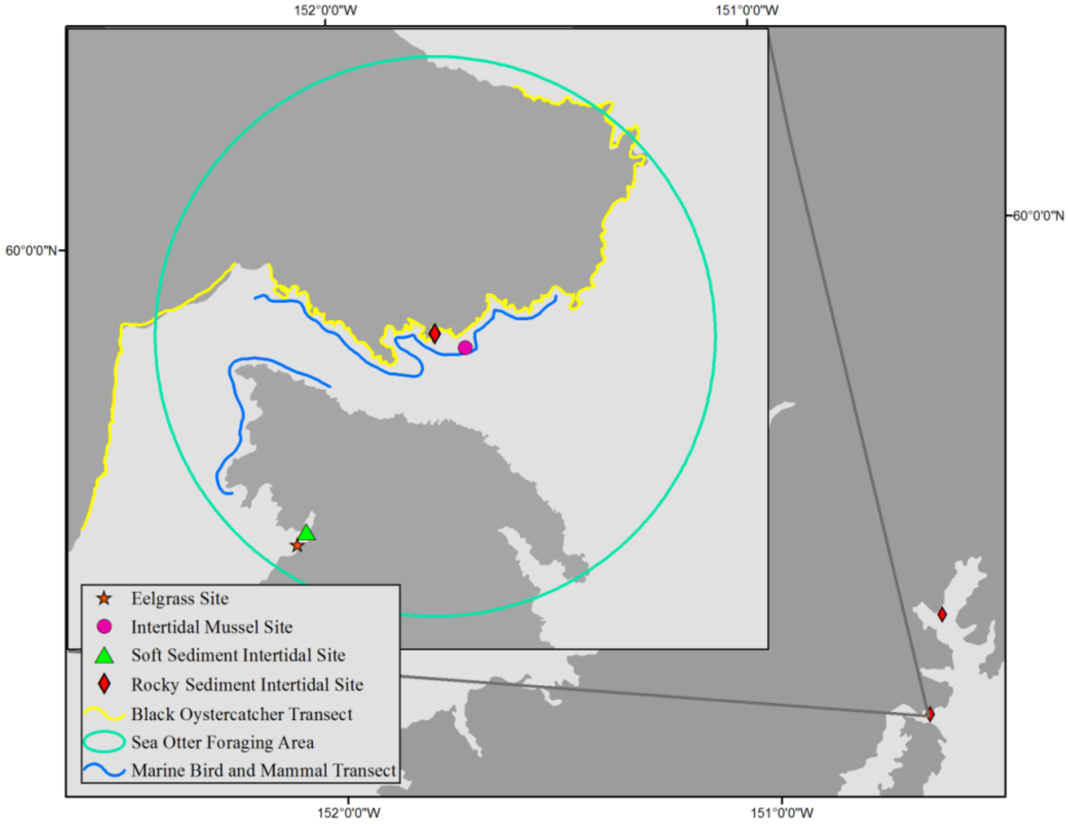

Figure 3. Example of the spatially integrated sampling of multiple metrics that occurs at each GWA nearshore sampling site within KATM, KEFJ, and WPWS.

Vital Signs

The nearshore monitoring protocol focuses on sampling of multiple components of nearshore ecosystems in the Gulf of Alaska that are both numerically and functionally important to the system's health. These are termed "vital signs" by the National Park Service (NPS) Inventory &Monitoring (I&M) program and include kelps (and other marine algae), seagrasses, marine intertidal invertebrates, marine birds, black oystercatchers, sea otters, and marine water quality (Bennett et al. 2006).

Kelp, other seaweeds, and seagrass are "living habitats" that serve as a nutrient filter, provide understory and habitat for planktivorous fish, clams, urchins, and a physical substrate for other invertebrates and algae. Kelps and other seaweeds are the major primary producers in the marine nearshore and because they are located in shallow water they could be significantly impacted by human activities. These include spills of oil or other contaminants, dredging and disturbance from anchoring of vessels, and increased turbidity caused by runoff of sediments or nutrients.

Marine Intertidal Invertebrates provide critical food resources for shorebirds, ducks, fish, bears, sea otters, and other marine invertebrate predators, as well as spawning and nursery habitats for forage fish and juvenile crustaceans. Benthic invertebrates and algae are ecologically diverse in terms of habitat and trophic requirements; have a wide range of physiological tolerances; are relatively sedentary, and have varied life-histories. As a result, they are good biological indicators of both short-term (e.g., annual) and long-term (e.g., decadal scale) changes in environmental conditions.

Marine Birds are predators near the top of marine nearshore food webs. Marine birds are long-lived, conspicuous, abundant, widespread members of the marine ecosystem and are sensitive to change. Because of these characteristics marine birds are good indicators of change in the marine ecosystem. Many studies have documented that their behavior, diets, productivity, and survival changed when environmental conditions change. Public concern exists for the welfare of seabirds because they are affected by human activities like oil pollution and commercial fishing.

Black Oystercatchers are well suited for inclusion into a long-term monitoring program of nearshore habitats because they are long-lived; reside and rely on intertidal habitats; consume a diet dominated by mussels, limpets, and chitons; and provision chicks near nest sites for extended periods. Additionally, as a conspicuous species sensitive to disturbance, the black oystercatcher would likely serve as a sentinel species in detecting change in nearshore community resulting from human or other disturbances.

Sea Otters are a keystone species that can dramatically affect the structure and complexity of their nearshore ecological community. They cause well described top-down cascading effects on community structure by altering abundance of prey (e.g., sea urchins) which can in turn alter abundance of lower trophic levels (e.g., kelps). Sea otters generally have smaller home ranges than other marine mammals; eat large amounts of food; are susceptible to contaminants such as those related to oil spills; and have broad appeal to the public. Recent declines in sea otters have been observed in the Aleutian Islands. Currently declines are documented in areas to the western edge of our study area. As a result of these declines, the Western Alaska stock of sea otters (which includes populations in KATM as well as Aniakchak National Monument and Preserve), was federally listed as threatened on September 2005 under the Endangered Species Act.

Marine Water Chemistry and Water Quality including temperature and salinity, are critical to intertidal fauna and flora and are likely to be important determinants of both long-term and short-term fluctuations in the intertidal biotic community. Basic water chemistry parameters provide a record of environmental conditions at the time of sampling and are used in assessing the condition of biological assemblages. Water quality (including water temperature, salinity, and levels of contaminants such as heavy metals and organic pollutants) are also critical in structuring nearshore marine ecosystems and can cause both acute and chronic changes in nearshore populations and communities.

Table 1. Overview of the variables measured as part of the Nearshore Component of Gulf Watch Alaska in WPWS, KEFJ, and KATM, 2012-2016.

Vital Sign	**Metric**	**Sampling unit**	**Number sampled per sampling period and block**
Eelgrass	Eelgrass percent cover	Fixed polygon in eelgrass habitat - (approximately 1 km$^{2)}$	5 sites
Intertidal invertebrates and algae	Sea star density on sheltered rocky shores (by species)	Transect - 200 m^2	5 sites
	Predatory whelk (*Nucella* spp.) and chiton (*Katharina tunicata*) density on sheltered rocky shores	Quadrat - 2 m^2	12 quadrats per site at each of 2 tidal elevations, 5 sites
	Sessile invertebrate and algae percent cover (by species) on sheltered rocky shores	Quadrat - 0.25 m^2	12 quadrats per site at each of 2 tidal elevations, 5 sites
	Limpet (*Lottia persona*) density and size distribution on sheltered rocky shores	Quadrat - 0.25 m^2	6 quadrats per site, 5 sites
	Bivalve density and size distribution (by species) on gravel/sand shores	Quadrat - 0.25 m^2	12 quadrats per site, 5 sites
	Mussel density and size distribution in mussel beds	Quadrat - 0.25 m^2	10 quadrats per site, 5 sites
	Mussel bed size	Mussel bed - area of bed on 50 m long shoreline segment	5 sites

Vital Sign	**Metric**	**Sampling unit**	**Number sampled per sampling period and block**
Marine birds	Density (by species)	Transect - 5 km long by 200 m wide	30 to 43 transects per block (depending on coastal extent of block)
Black oystercatchers	Nest density	Transect - 20 km of shoreline	5 sites
	Productivity – number of eggs and chicks per nest site	Nest site	Variable depending on number of active nest sites per year
	Diet – Relative abundance of prey	Nest site	Variable depending on number of active nest sites per year
Sea otters	Abundance	Transect - variable approximately 1 to many km long by 400 m wide	Variable, depending on area of sea otter habitat in each block
	Relative abundance of prey, prey energy obtained per hour	Feeding bout	Variable, depending on number of sea otters observed feeding per year
	Age at death	Individual carcass	Variable, depending on number of carcasses recovered per year
Water quality	Temperature	Rocky site	5 sites
	Salinity	Rocky site	5 sites (currently not collected)
	Contaminants	Rocky site	5 sites

Sample Collections and Data Analyses

Rocky Intertidal Communities

Intertidal invertebrates and algae were sampled annually at KATM beginning in 2006, and at KEFJ beginning in 2008. WPWS sampling began in 2007 and then again from 2010-2011. Sampling of intertidal invertebrates and algae at these sites is designed to detect changes in these communities over time. In this section, we present highlights of results of sampling conducted in 2006-2016. Sampling was conducted at five sites in sheltered rocky habitats within KATM, KEFJ and WPWS. Descriptions of the study sites and methods used to sample intertidal algae and invertebrates are available in Dean and Bodkin (2011). The following is a general description of the methods employed. Sampling of abundance and species composition for algae and invertebrates was conducted along two 50-m long transects at each site. The percent cover of algae and sessile invertebrates was estimated within 12 evenly spaced ¼ m^2 quadrats placed along transects that ran parallel to the shoreline and originated at permanent markers placed at 0.5 m and 1.5 m tidal elevations, respectively. Quadrats were placed at random start points and at equally spaced intervals thereafter. Percent cover was estimated by noting the presence/absence of species at each of 49 (2006 and 2007) or 25 (2008 through 2016) systematically gridded points within each quadrat. The density of sea stars was measured in a single 50-m long by 4-m wide transect at each site. The transect was placed below the 0.5 m transect used to estimate percent cover and extended from 0.0 m mean low low water (MLLW) to 4 m (linear distance) above. Mean percent cover and associated SE are calculated annually (see below). More detailed analyses of community structure and relationships to static habitat features are presented by Konar et al. (2016).

Eelgrass Beds

We sampled the percent cover of eelgrass (*Zostera marina*) at five designated sites in KATM, KEFJ, and WPWS from 2008 through 2016. All sampling was conducted in early summer when eelgrass beds generally have reached their seasonal maximum in extent and density of plants. All beds sampled were in sheltered bays and in closest proximity to the randomly selected rocky intertidal sites (see intertidal invertebrates and algae section). At each site, we sampled eelgrass within a prescribed area along a shoreline of approximately 200 m in length. The width of each bed examined depended on the depth contour at each site, but was generally on the order of 50 to 100 m. The areas sampled were bounded by an approximately 200 m segment of shoreline over which eelgrass was observed and extended offshore to a distance approximately 15 m beyond the last observed eelgrass. The percent cover of eelgrass within this area was estimated by determining the presence or absence of eelgrass at approximately evenly spaced intervals along a series of transects running perpendicular to shore that were spaced approximately 20 m apart. Presence or absence at each observation point was determined using an underwater video camera lowered from a small inflatable boat and/or a single-beam sonar (Dean and Bodkin 2016). Mean percent cover was calculated based on presence / absence of eelgrass shoots within a given polygon for each eelgrass site within a region.

Unconsolidated Sediment Bivalve Communities

Mixed-sediment bivalve communities were quantified following the GWA Standard Operating Procedure (SOP) for mixed-sediment bivalve communities at five sites, within four blocks (KATM, KBAY, KEFJ, and WPWS) across the GOA (Fig. 2; Dean et al. 2014; Weitzman et al. 2017). Sites were selected based on proximity to rocky intertidal sites and presence of clams (siphons, squirts, and shell liter). Sampling occurred biannually by a predetermined GPS point for the transect start. At each site a 100 m transect was placed along the 0.0 MLLW tide elevation and 12 evenly spaced, 0.25 m^2 quadrats were excavated to a depth of 25 cm. All excavated material was run through a 10 mm sieve to recover all bivalves with a shell length of ≥ 14 mm. All bivalves recovered were measured with Vernier calipers to the nearest mm and recorded in the clam data spreadsheet for quantification of abundance and size distribution (Fig. 4). Mean densities (#/¼m^2) and mean biomass (kg/¼m^2) have been calculated to date.

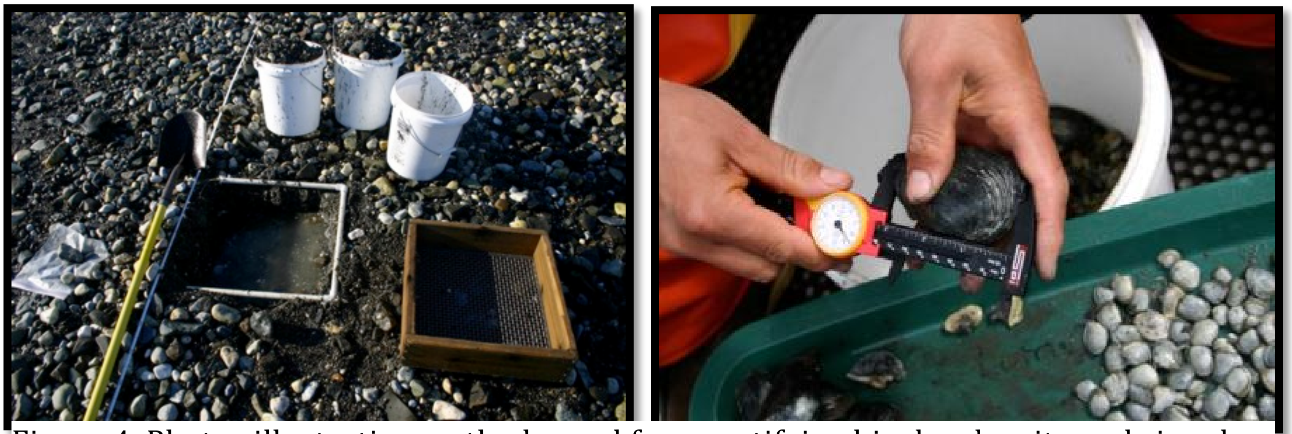

Figure 4. Photos illustrating methods used for quantifying bivalve density and size class in unconsolidated sediment sites.

Mussel Beds

Pacific Blue mussels (*Mytilus trossolus*) were sampled under two nearshore monitoring standard operating procedures that direct sampling of intertidal invertebrate and algal communities (Table 1, Appendix B). At five rocky intertidal sites in each of three regions (Fig. 2, KATM, KEFJ and WPWS) the percent cover of mussels is estimated using point contact methods at two tidal elevations (+0.5 m and +1.5 m) within 24, 0.25 m^2 quadrats evenly spaced along 50 m permanent transects parallel to the shoreline (Dean and Bodkin

2011). Mussel bed size and abundance is estimated at five sites in each of three regions by measuring the distance of contiguous mussels along 10 transects placed perpendicular to the shoreline spaced at five m intervals along 50 m permanent transects parallel to the shoreline (Bodkin et al. 2016). Densities and sizes of mussels and specifically of mussels ≥ 20 mm are estimated within each bed through a quadrat located randomly along each of 10 perpendicular transects. Means and associated SE of several mussel bed metrics are calculated annually. More detailed data analyses of the spatial and temporal patterns in mussel abundance are presented by Bodkin et al. (2017) and Appendix B.

Marine Bird and Mammal Surveys

Standardized surveys of marine birds are conducted in KATM and KEFJ between late June and early July and are generally conducted from small vessels (5-8 m length) traveling at speeds of 8-12 knots along randomly selected sections of coastline that represent independent transects. The survey design consists of a series of transects along shorelines such that a minimum of 20% of a NPS park shoreline is surveyed. Transects are systematically selected beginning at a random starting point from the pool of contiguous 2.5-5 km transects that are adjacent to the mainland or islands. The transect width is 200 – 300 m, depending on the elevation of the observer platform, and the survey boat represents the midpoint. Transects are surveyed by a team of three. The boat operator generally surveys the 100 - 150 m offshore area of the transect, while a second observer surveys the 100 - 150 m nearshore area. The third team member enters the observations into a laptop running program dLOG, specifically designed for this type of surveying, and the third team member can assist with observations when needed. All marine birds and mammals within the 200 - 300 m transect swath are identified and counted. Detailed descriptions of methods and procedures can be found in the Marine Bird and Mammal Survey SOP (Bodkin 2011a). Densities (#/km^2) are calculated annually.

Black Oystercatchers

Nest Density

Black oystercatcher surveys are conducted along five 20 km transects associated with each rocky intertidal site to estimate nest density of black oystercatchers. Survey were conducted at KATM since 2006 (no sampling in 2011), KEFJ since 2007, and WPWS in 2007 and annually in WPWS since 2010. We located nest sites by surveying the shoreline in a small boat using high resolution binoculars (Fig. 5). All accessible nest sites were visited to determine the number of chicks and/or eggs present. Detailed survey methods for estimation of nest density and productivity can be found in the SOP for monitoring black oystercatchers (Bodkin 2011b). Densities (#/ linear km) are calculated annually.

Figure 5. Black oystercatcher breeding pair near their nest in Kenai Fjords National Park.

Chick Diet

We estimated species composition and size distributions of prey fed to chicks during oystercatcher surveys. Upon locating an active nest, we collected all prey remains found near the nest, indicative of adults provisioning their chicks. Prey items were measured and identified to the genus or species level. We also opportunistically collected prey from nests found outside of our survey transects. Detailed methods for estimation of chick diet can be found in the SOP for monitoring black oystercatchers (Bodkin 2011b). Size frequency distributions of select prey species are calculated annually as well as prey proportions by species.

Sea Otters

Aerial Surveys of Abundance

An aerial survey method developed specifically for estimating sea otter abundance (Bodkin and Udevitz 1999) was used to sample each survey area. Sea otter habitat was divided into two strata, high density and low density, distinguished by distance from shore and depth contour. The high density stratum extended from shore to 400 m seaward or to the 40 m depth contour, whichever was greater. The low density stratum extended from the high density line to a line 2 km offshore or to the 100 m depth contour, whichever was greater. However, bays and inlets less than 6 km wide were treated as high density habitat, regardless of depth. Transects were spaced systematically within each stratum according to expected sea otter densities.

For each survey, a pilot flew an airplane over the transects at an altitude of 91m while an observer searched on one side of the plane and recorded sea otter group counts and locations. Sea otters observed within 400 m of each transect were later used to estimate abundance. To estimate the number of sea otters in small groups (<20) not detected along transect swaths (e.g., because they were diving or camouflaged by kelp), 400 m diameter circles were searched intensively by periodically flying 5 concentric circles around an initiating group. These Intensive Search Units (ISUs) were distributed throughout the survey area to reflect the full range of observation conditions encountered during the survey and were later used to adjust the abundance estimate of sea otters in small groups. Large groups of sea otters (≥20) sighted on transect were circled until a complete count was made and were not adjusted for detection.

Carcass Collections

We examined the age-at-death distributions of beach-cast sea otters in KATM and WPWS. We systematically collected beach cast carcasses at KATM each summer (July) from 2006-2016, except for 2011 (no field work conducted in KATM) and in WPWS each spring (April) from 2006-2016 except for 2009. The WPWS collections added to data from identical carcasses surveys conducted between 1976-1989 and 1990-2005 (Monson et al. 2000, Monson et al. 2011). We also attempted to collect carcasses at KEFJ each summer (June), though numbers recovered were very low. We estimated the age of dying otters by aging teeth collected from the recovered carcasses (Bodkin et al. 1997) and binned the age distribution into three age-classes including young (< 2 yrs), prime-age (2-8 yrs) and old (> 8 yrs). These age-class distributions were compared with a "baseline" distribution collected in WPWS before the *Exxon Valdez* Oil Spill (1976-1989; Monson et al. 2000).

Foraging Observations

We estimated rates of food consumption by sea otters in KATM, KEFJ, and WPWS based on the: 1) time of an average foraging dive, 2) time interval between dives, 3) proportion of dives that were successful in obtaining food, 4) type, number, and size of prey obtained on each successful dive, and 5) average energy content of each prey (Dean et al. 2002). We estimated the first four measurements based on direct foraging observations made from sites along the shoreline using a 50 to 80 power spotting scope (Questar Corp. New Hope, PA). Average energy content of prey was estimated based on published or calculated values from prey species tissues. Forage observations were made annually at KATM (2006 to 2016, except for 2011), and KEFJ (2007 through 2016), while in WPWS observations were made in 2007, and then annually from 2010 through 2016. We conducted all foraging work during daylight hours with the bulk of the observations made between late May and late July. We based energy conversions on expressions given in Table 3 of Dean et al. (2002) or from values given in Cummins and Wuycheck (1971) or Wacasey and Atkinson (1987). For dives where prey type was not identified, we used maximum likelihood methods to assign the most likely prey type based on the dive attributes associated with identified prey types, which removes the potential biases that may occur if the known dive data are not representative of missing data (Tinker et al. 2012, Tinker 2015). We estimated 95% confidence intervals for each recovery rate using Monte-Carlo simulations (Manly 1991, Dean et al. 2002). We used MATLAB (MathWorks, Inc., Natick, MA) for all likelihood analysis and Monte-Carlo simulations.

Detailed analyses of sea otter metrics are presented by Coletti et al. (2016) and in Appendix A, and inferences are drawn from the suite of metrics with regard to the factors that influence sea otter population dynamics within each block.

Marine Water Chemistry and Water Quality

We measured water and air temperature at five sites in sheltered rocky habitats within each of three areas including KATM, KEFJ and WPWS. HOBO temperature loggers (Onset Computer Corp., Bourne, MA) were first deployed at KATM in June 2006, at KEFJ in June 2007 and in WPWS in June 2010. Loggers were mounted within PVC pipe bolted to intertidal rocks at ~0.5 m tidal elevation and programmed to recorded temperature at 20, 30 or 60 min intervals depending on location and year of deployment. These recording intervals generally allowed the HOBOs to log one to nearly two years of continuous temperature readings with most HOBOs recovered and data downloaded after one year. HOBOs deployed in 2009 at both KATM and KEFJ were erroneously programed to record temperature at 1 min intervals and all logger's memory capacity filled and quite logging after ~18 days. We did not conduct field work at KATM in the summer of 2011 thus no loggers were deployed in that year at these sites. Data were downloaded using Onset's HOBOware software and then brought into SAS (SAS Institute Inc., Cary, NC,) for further processing. Data were standardized by fitting a spline function to each temperature time series and assigning temperature values at 10 min intervals starting at the top of each hour. Temperature values at each 10-min interval were merged with tidal height from the nearest tide station using tide information exported from Tides & Currents software (Nobeltec, Inc., Beaverton, OR). To obtain water temperature information, we limited readings to those where tide level for the site was > 2 m (i.e., loggers submerged to ~1.5 m depth). We determined the over-all mean monthly water temperatures (all years of data combined) for each area separately and subtracted this from each area-level monthly mean to calculate mean monthly water temperature anomalies.

Contaminant loads at our intertidal sampling sites were evaluated by collection of mussels for analyses of soft tissues, utilizing protocols developed for the NOAA National Status and Trends (NS&T) Mussel Watch Program (https://coastalscience.noaa.gov/). In summer 2007, mussels were collected from our five sampling sites at KEFJ and KATM, plus at one additional site at KATM. In summer 2012, mussels were collected from the five intertidal sampling sites in WPWS, and at four sites in EPWS, and two sites in KBAY. In summer 2013, mussels were collected from three intertidal sampling sites in NPWS. Mussels were collected according to NS&T protocols (Lauenstein and Cantillo 1993) and submitted for analysis of a suite of contaminants including polycyclic aromatic hydrocarbons (PAH) by GC/MS-SIM, organochlorine pesticides (OC) and polychlorinated biphenyls (PCBs) by GC/ECD, butyltins (BT) by GC/MS-SIM, polybrominated diphenyl ethers (PBDE) by GC/MS-NCISIM, polybrominated biphenyls (PBB) by GC/MS-SIM, trace metals (TM) and mercury. Details on collection, shipping and analytical procedures, including quality assurance and quality control, and a listing of specific analyses, are presented in three technical reports received from the contract laboratory overseeing analyses (TDI-Brooks International, Inc. 2008, 2013, 2014).

RESULTS

Over the first five years of GWA Program, we have successfully completed the nearshore ecosystem sampling as prescribed (Dean et al. 2014). Table 2 describes the effort, by location, metric, and year. Results from each of the metrics are described in more detail below.

Table 2. Nearshore component metrics measured by location and year, 2012-2016.

Location and Metric	**2012**	**2013**	**2014**	**2015**	**2016**
Western PWS, intertidal invertebrates and algae	x	x	x	x	x
Western PWS, kelps and sea grass	x	x	x	x	x
Western PWS, black oystercatchers	x	x	x	x	x
Western PWS, contaminants/water quality	x				
Western PWS, sea otter carcass recovery	x	x	x	x	x
Western PWS, sea otter foraging observations	x	x	x	x	x
Western PWS, water / air temperature	x	x	x	x	x
Eastern PWS, intertidal invertebrates and algae	x		x		
Eastern PWS, kelps and sea grass	x		x		
Eastern PWS, contaminants/water quality	x				
Northern PWS, intertidal invertebrates and algae		x		x	
Northern PWS, kelps and sea grass		x		x	
Northern PWS, contaminants/water quality		x			
Katmai NP, intertidal invertebrates and algae	x	x	x	x	x
Katmai NP, kelps and sea grass	x	x	x	x	x
Katmai NP, black oystercatchers	x	x	x	x	x
Katmai NP, sea otter carcass recovery	x	x	x	x	x
Katmai NP, sea otter foraging observations	x	x	x	x	x
Katmai NP, water / air temperature	x	x	x	x	x
Kenai NP, intertidal invertebrates and algae	x	x	x	x	x
Kenai NP, kelps and sea grass	x	x	x	x	x
Kenai NP, black oystercatchers	x	x	x	x	x
Kenai NP, sea otter carcass recovery	x	x	x	x	x
Kenai NP, sea otter foraging observations	x	x	x	x	x
Kenai NP, water / air temperature	x	x	x	x	x
PWS, sea otter aerial survey			x		
Kenai NP, sea otter aerial survey		x			x
Katmai NP, sea otter aerial survey	x			x	
PWS Nearshore marine bird survey*	x		x		x
Katmai nearshore marine bird survey	x	x	x	x	x
Kenai nearshore marine bird survey	x	x	x	x	x

*Under Pelagic component Restoration Project 16120114-K

Rocky Intertidal Communities

The analyses presented here focus on percent cover estimates of mussels (*Mytilus trossulus*), the dominant perennial alga (*Fucus distichus*) and of bare substrate as a measure of disturbance. We also present analyses on the abundance of sea stars. Results for percent cover of blue mussels are also reported in detail in Bodkin et al. (2017; Appendix B). Trends for the percent cover of mussels were similar in all regions. Cover of mussels was high in 2007 and 2008, declined to a low in 2012/2013, increased to a second peak in 2014, and declined since. In contrast, temporal trends in cover by *Fucus* differed substantially between regions. Peaks in *Fucus* cover were in 2010 in KEFJ, 2014 in WPWS, and 2009/2014 in KATM. These patterns (Fig. 6) suggest that trends in cover by mussels were influenced by factors operating on a large, GOA-wide scale while trends in *Fucus* cover were influenced by factors operating at the regional scale.

While temporal trends in *Fucus* differed between regions, all regions showed a decline in cover between 2014 and 2016. This decline was coincident with an increase in bare substrate (no algae or sessile invertebrates observed). The reason for the decline in *Fucus* and increase in bare substrate is unclear, but may have been the result of mortality caused by especially high temperatures observed during this period.

Density of sea stars varied considerably over years and between regions (Fig. 7). Declines in the density of *Evasterias troshelii* (in KATM), *Pisaster ochraceus* (in KEFJ), and *Pycnopodia helianthoides* (in both KEFJ and WPWS) were observed from 2015 to 2016. The cause of this decline is unclear. Observations made during our summer sampling period did not indicate a high incidence of sea star wasting disease and we have little evidence indicating that the disease, which has been widely observed from California to Southeast Alaska, was the cause of these declines. However, we only made observations in early summer and cannot rule out that animals were dying from disease later in the summer or fall.

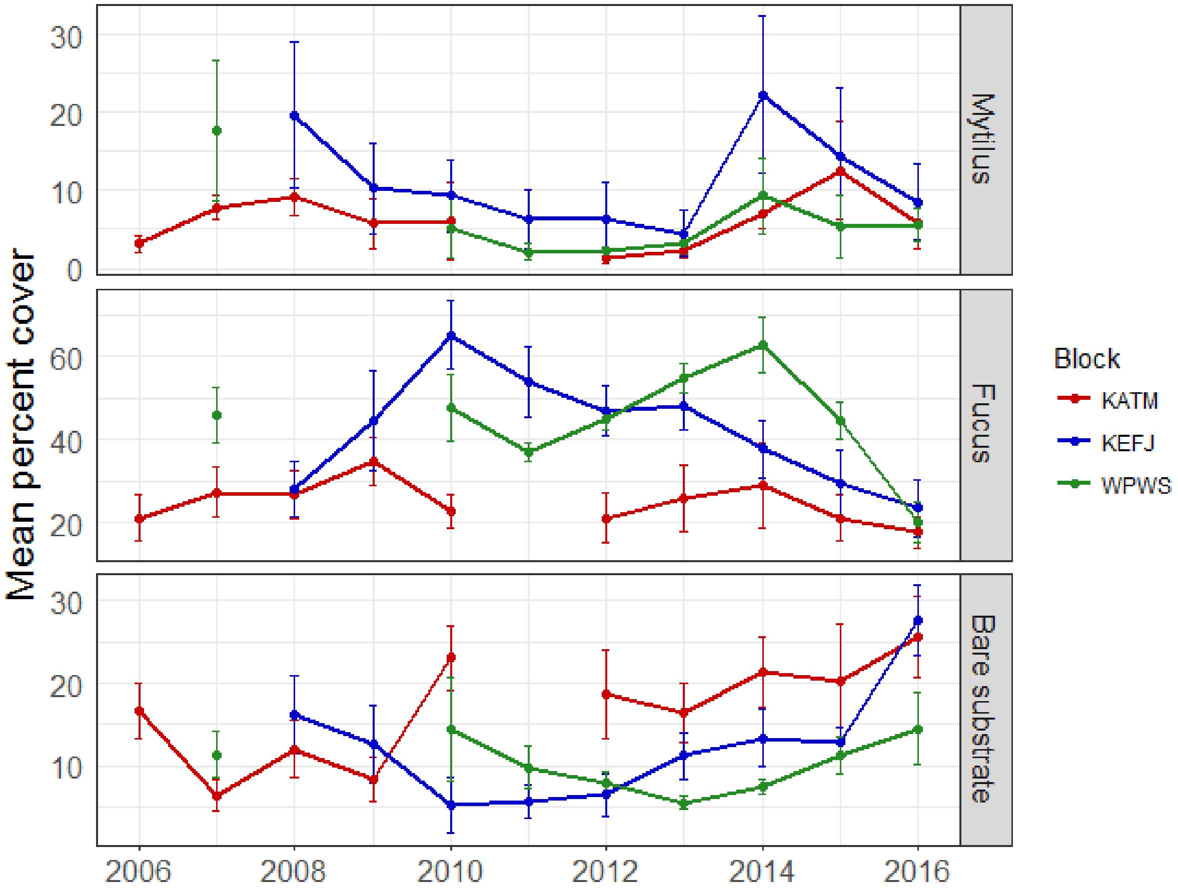

Figure 6. Mean percent cover of *Mytilus trossulus*, *Fucus distichus*, and bare substrate at 0.5 and 1.5 m MLLW in KATM, KEFJ, and WPWS during 2006-2016. Error bars represent ± 1SE.

Percent cover data for algae and invertebrates were also utilized to examine the role of six static drivers (physical attributes that do not appreciably change from year to year) on the structure of the intertidal communities in the northern GOA (Konar et al. 2016). Static attributes included distance to freshwater streams, tidewater glacial presence, wave exposure, fetch, beach slope, and substrate composition. Five to six sites in each of the six regions in the mid and low intertidal strata were examined. Across regions, static attributes were not consistently different and only small clusters of sites had similar attributes. Additionally, intertidal communities were less similar at the site compared with the region level. These results suggest that these biological communities were not strongly influenced by the local static attributes measured.

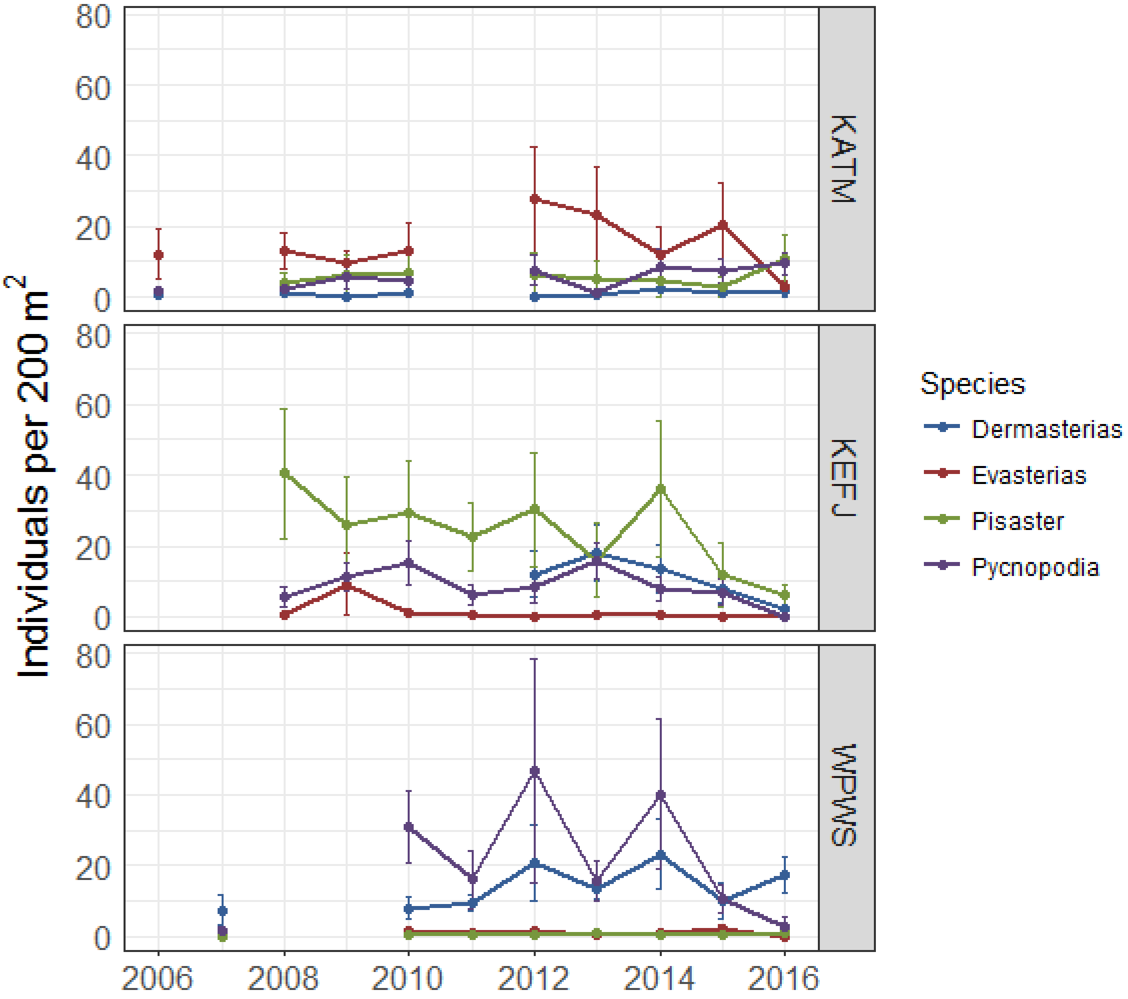

Figure 7. Mean density (individuals per 200 m^2) of the four most common species of sea stars (*Dermasterias imbricata, Evasterias trishelii, Pisaster ochraceus* and *Pycnopodia helianthoides*) in KATM, KEFJ, and WPWS during 2006-2016. Error bars represent ± 1SE.

Eelgrass Beds

Eelgrass cover varied widely among sites and years (Fig. 8). Overall, percent cover of eelgrass within sampling transects ranged from 12% (Kaflia, 2014) to 90% (Iktua, 2013). At the block level, KEFJ and WPWS exhibited similar trends with mean eelgrass cover peaking in 2013 (Fig. 9). Trends in KATM were consistent with KEFJ for the first three years of sampling and then diverged in 2012. Despite high inter-annual variability, long-term trends in eelgrass bed cover appears to be relatively stable based on calculated means of percent cover.

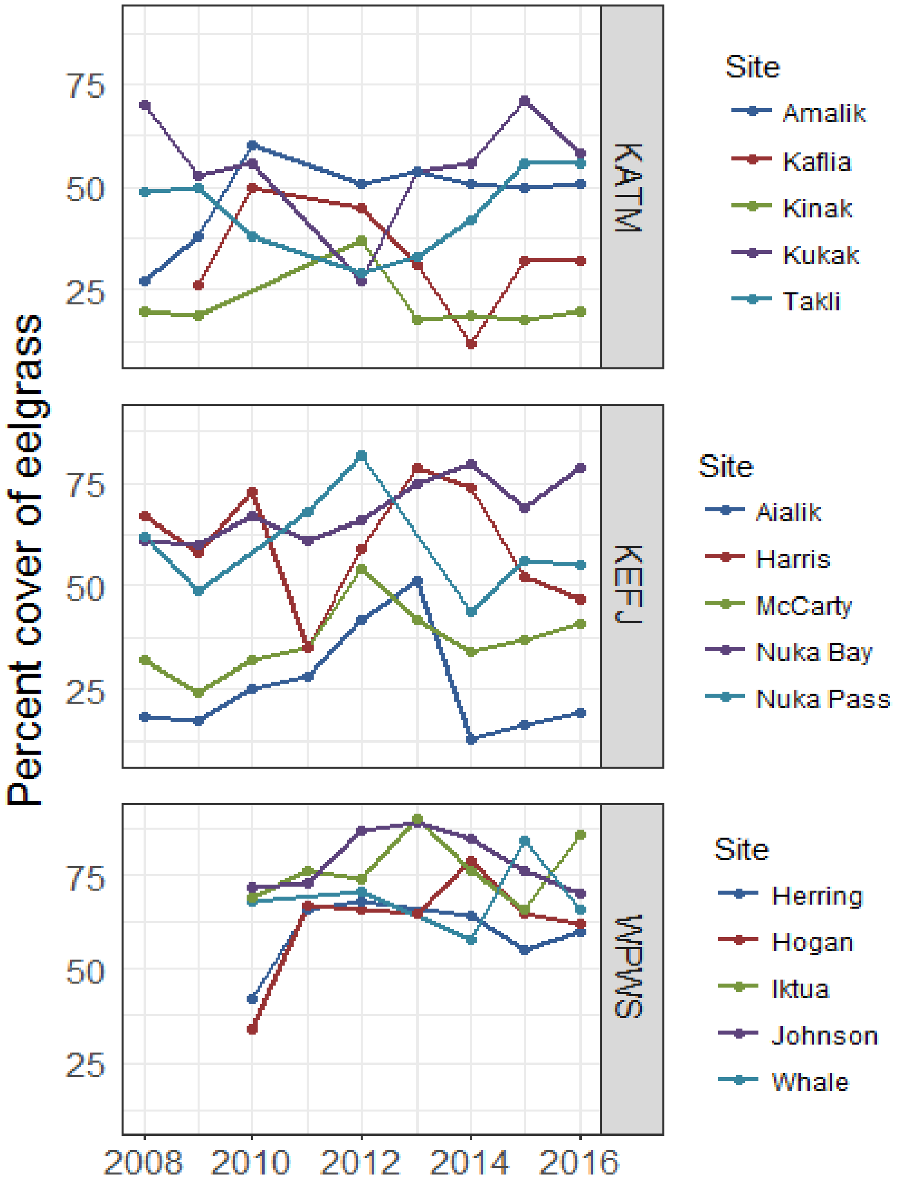

Figure 8. Percent cover of eelgrass within sampling transects for sites in KATM, KEFJ, and WPWS during 2008-2016. KATM and WPWS were not sampled in 2011 and 2008-2010, respectively.

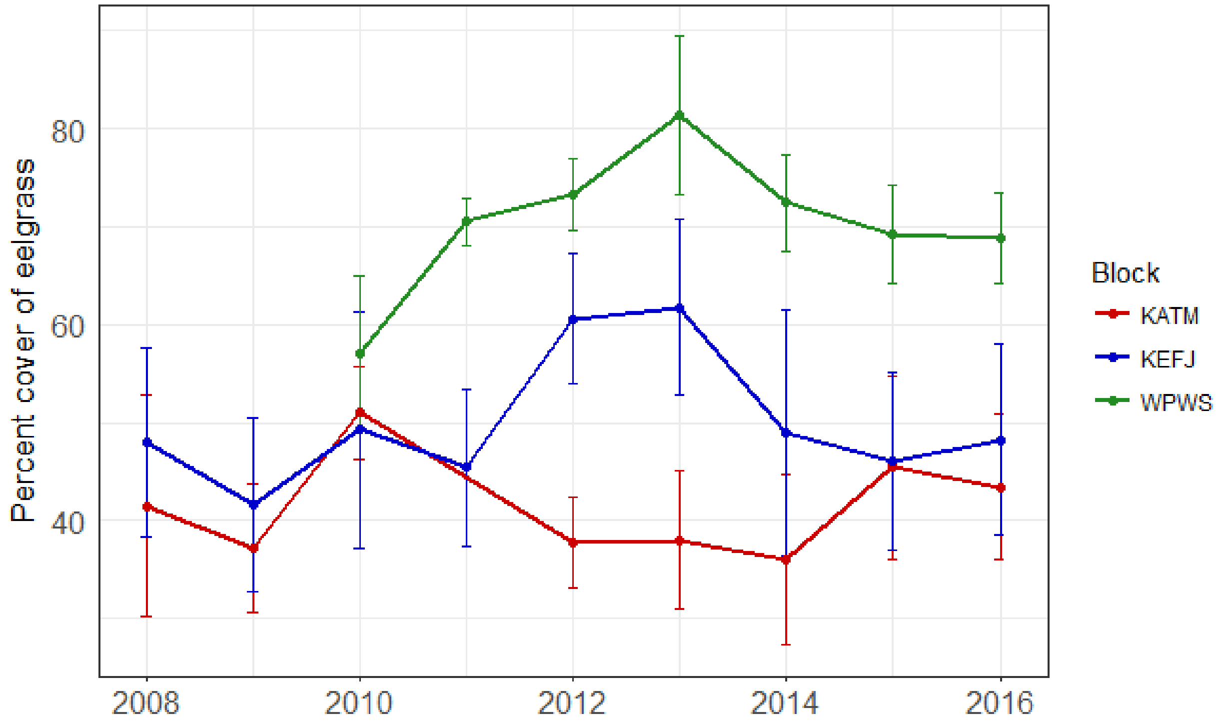

Figure 9. Mean percent cover of eelgrass within sampling transects in KATM, KEFJ, and WPWS during 2008-2016. KATM and WPWS were not sampled in 2011 and 2008-2010, respectively. Error bars represent ± 1SE.

Unconsolidated Sediment Bivalve Communities

Bivalve assemblages within mixed-sediment beaches were successfully sampled from 2007-2015 in KATM, KEFJ, WPWS, and 2013-2015 in KBAY. Thirteen distinct taxa were quantified, where several genera were pooled as spp. (*Clinocardium nuttallii*, *Diplodonta* spp. [*D. impolita*, *D. orbella*], *Hiatella arctica*, *Leukoma staminea*, *Lucinoma annulatum*, *Macoma* spp. [*M. balthica*, *M. calcarea*, *M. inquinata*, *M. nasuta*, *M. obliqua*], *Modiolus modiolus*, *Mya* spp. [*M. arenaria*, *M. truncata*], *Mytilus trossulus*, *Neaeromya compressa*, *Saxidomus gigantea*, *Serripes groenlandicus*, and *Siliqua patula*). Of these taxa encountered, six species of clam and one species of mussel comprised the majority of species assemblages across all regions: *C. nuttallii*, *H. arctica*, *L. staminea*, *Macoma* spp., *Mya* spp., *S. gigantea*, (Fig. 10) and *Mytilus trossulus.* .

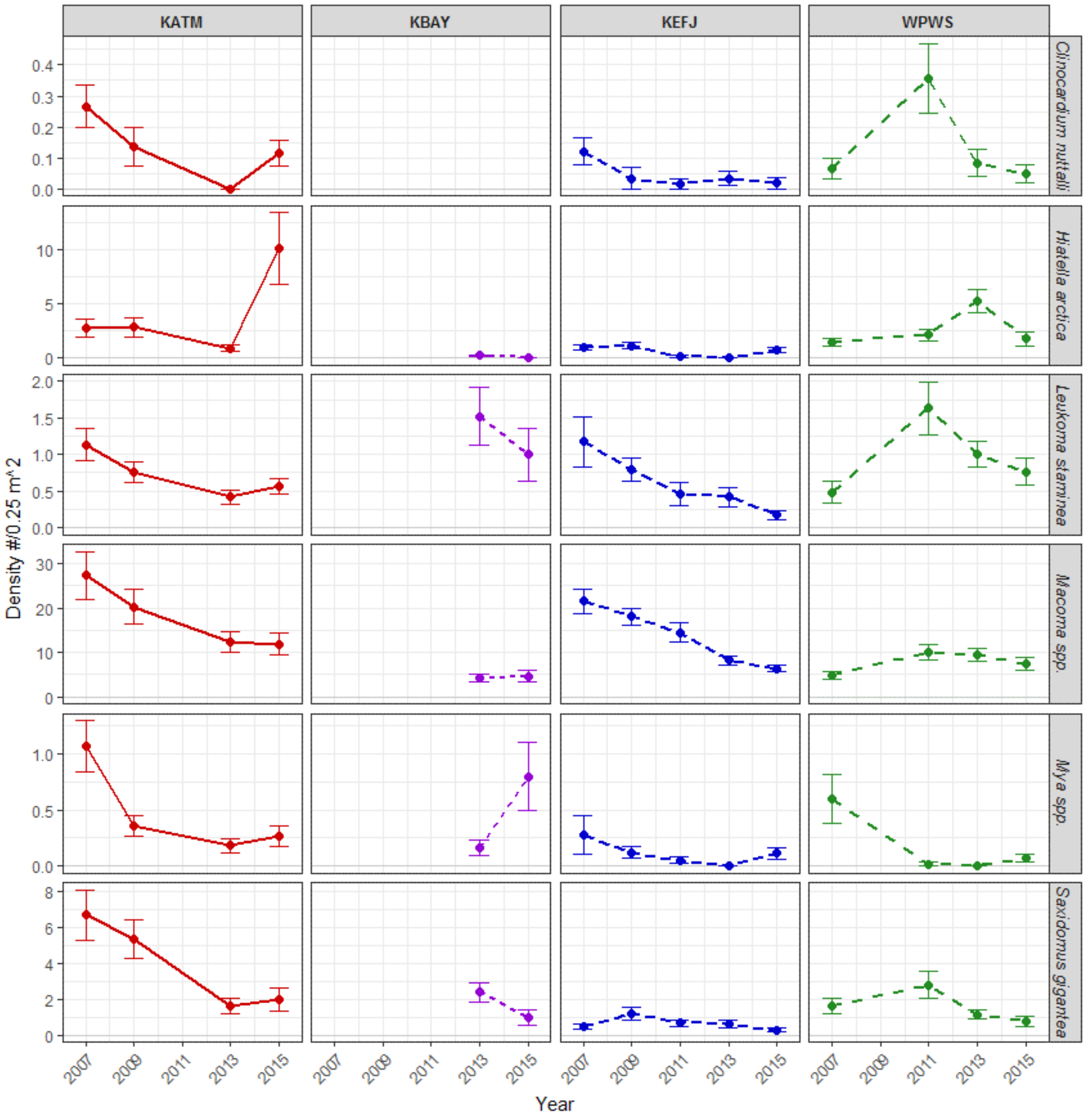

Figure 10. Mean clam densities of taxa per ¼m² in mixed-sediment beaches across the Gulf of Alaska from 2007-2015. Vertical lines indicate ± 1SE.

The most abundant taxa were *Macoma* spp. and *H. arctica*. The largest taxa were *L. staminea*, *Mya* spp., and *S. gigantea*, occurring at biomass densities in excess of 1kg/¼ m². When occurring in high abundance *Macoma* spp. and *H. arctica* also amounted to similar levels of available biomass (Fig. 11). Mussels were not routinely monitored at mixed-sediment beaches prior to 2015, but occurred at markedly high densities at some sites. Regionally, KATM had the highest abundance and biomass of most taxa, particularly *S. gigantea*. However, a general pattern of decline in clam abundance and biomass has been observed across the GOA, and this pattern varied among WPWS, KEFJ, and KATM. Trends at KBAY will be determined following a third year of sampling in 2017.

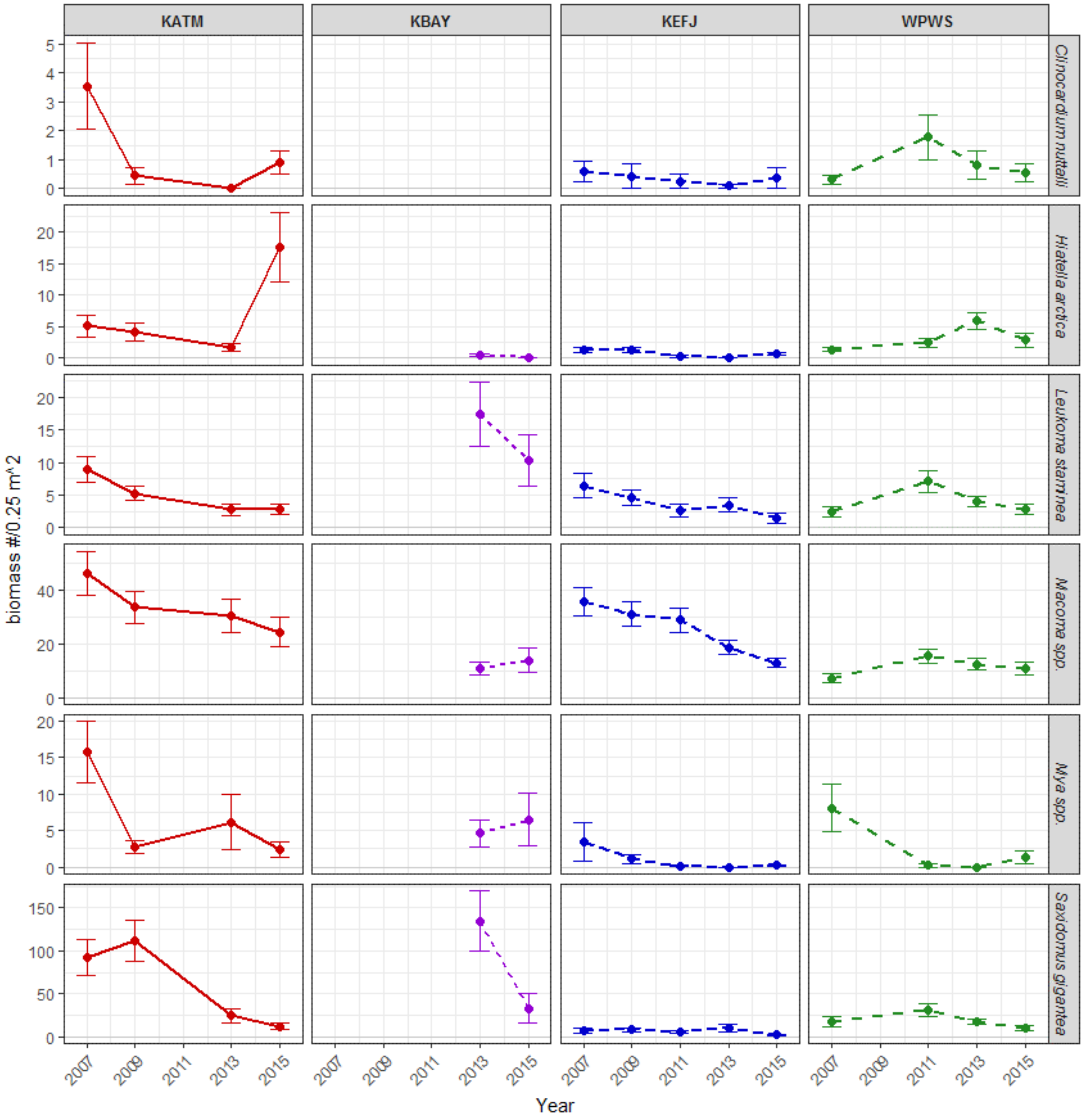

Figure 11. Mean clam biomass per ¼m^2 of taxa across the Gulf of Alaska from 2007-2015. Vertical lines indicate ± 1SE.

Mussel Beds

Since 2006 we have monitored mussel abundance in the northern GOA. We report the results of monitoring 7 metrics that describe mussel abundance and size at three regions (KATM, KEFJ and WPWS) from 2006-2015 in Bodkin et al. (in press; Appendix B). Through 2015 we found that, for all metrics, mussel abundance varied on a site-by-site basis (Fig. 12). After accounting for site differences, we found similar temporal patterns in several measures of abundance (% cover at +0.5 and +1.5 m tidal elevations, large mussel density, large mussel abundance, and core mussel abundance), in which abundance was initially high, declined significantly over several years, and subsequently recovered (Fig. 13).

Averaged across all sites, we documented declines of more than 80% in total large mussel abundance through 2013 with recovery to about 40% of initial abundance by 2015. These findings suggest that factors operating across the northern GOA were affecting mussel survival and subsequently abundance. In contrast, density of primarily small mussels obtained from cores (as an index of settlement), varied markedly by site, but did not show meaningful temporal trends. We interpret this to indicate that settlement was driven by site-specific features rather than broad-scale drivers. By extension, we hypothesize that temporal changes observed in mussel abundance were not a result of temporal variation in larval supply leading to variation in recruitment or settlement, but rather suggest mortality as a primary demographic factor driving mussel abundance.

Preliminary analysis of 2016 data are generally consistent with the findings summarized above, that mussel abundance varied among sites and there are consistent trends in mussel abundance across most sites. In 2016 most estimates of mussel abundance generally continued the pattern of recovery observed since 2012-2013, while a lack of consistent trend in abundance of small mussels remains evident.

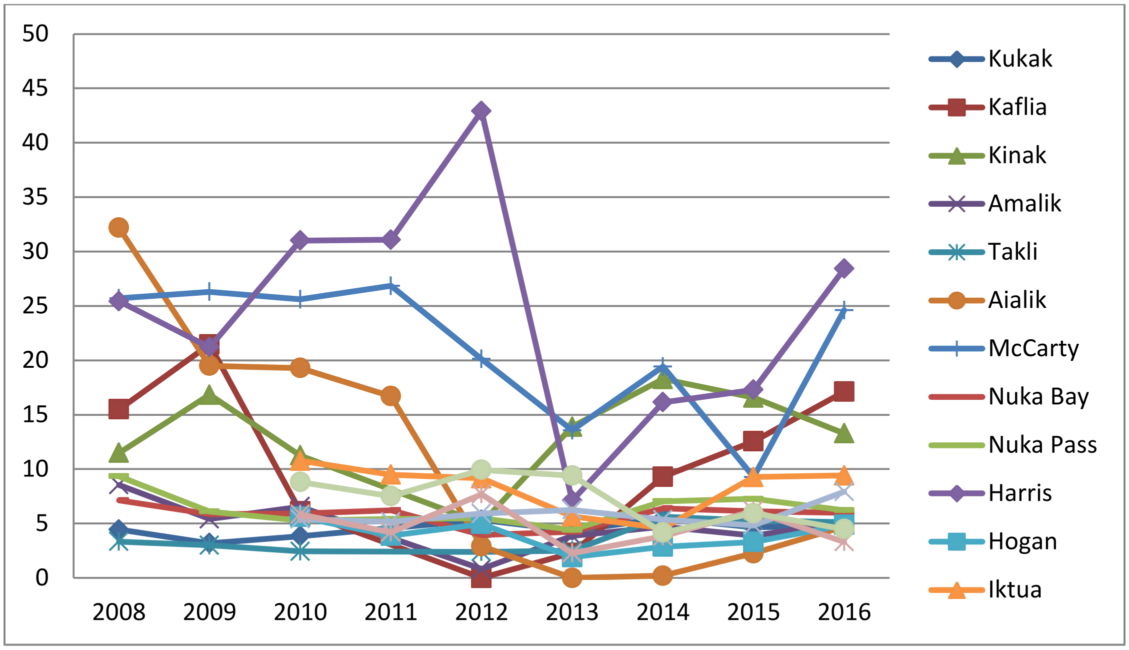

Figure 12. Mussel bed width by site across years (2008 – 2016) illustrating variation.

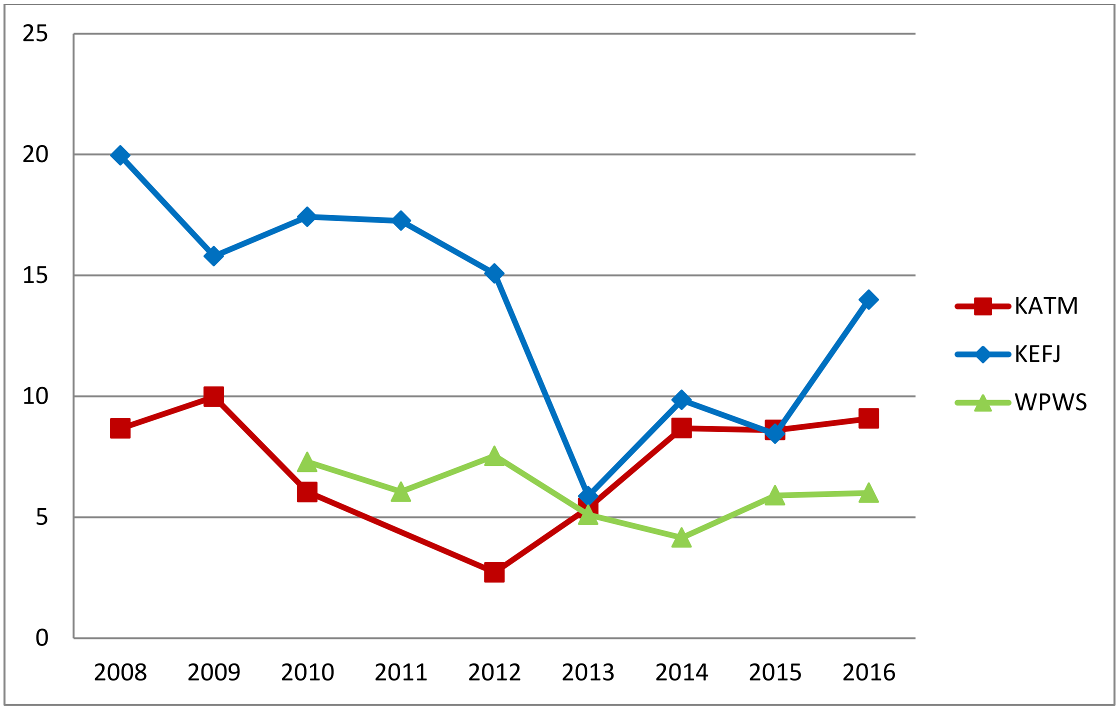

Figure 13. Average mussel bed width by region. When differences across sites are accounted for, a temporal trend is observed.

Marine Bird and Mammal Surveys

Skiff-based marine bird and mammal surveys along coastal (nearshore) transects have been conducted annually in KATM since 2006 (with the exception of 2011) and annually in KEFJ since 2007. During the summer of 2015, we observed large increases in common murres relative to previous years. This increase was particularly evident in KATM (Fig. 14). KEFJ does have common murre colonies, however we observed an increase of these birds moving into coastal areas not associated with colonies (Fig. 15). Our documentation of unusual murre distributions corresponded to observations of large die-offs of murres throughout the north Pacific in winter of 2015-2016. We speculate that high water temperature may have disrupted prey abundance or availability, leading to changes in murre distribution, behavior, condition, and mortality rates. Our results contributed to observations across GWA components that demonstrated that 2015 was an anomalous year. Common murre density and distribution have returned to pre-anomalous values in 2016. Observations from KEFJ in 2016 were slightly lower than expected, but due to inclement weather, many transects in close proximity to colonies were not surveyed.

We have observed interesting trends in black oystercatcher density in KATM and KEFJ over time. Black oystercatcher trends appear to correlate with mussel abundance data to date, where a decline in black oystercatcher density in both KATM and KEFJ beginning in 2009 coincided with increases in density in both parks beginning in 2012-2013 with continued growth through 2016 (Fig. 16). Other marine bird species, while highly variable, tend to have had relatively stable densities over time with little evidence of increasing or decreasing trends over time, although average densities (#/km ^{2}) with ± 1SE are the only values examined to date (Table 3).

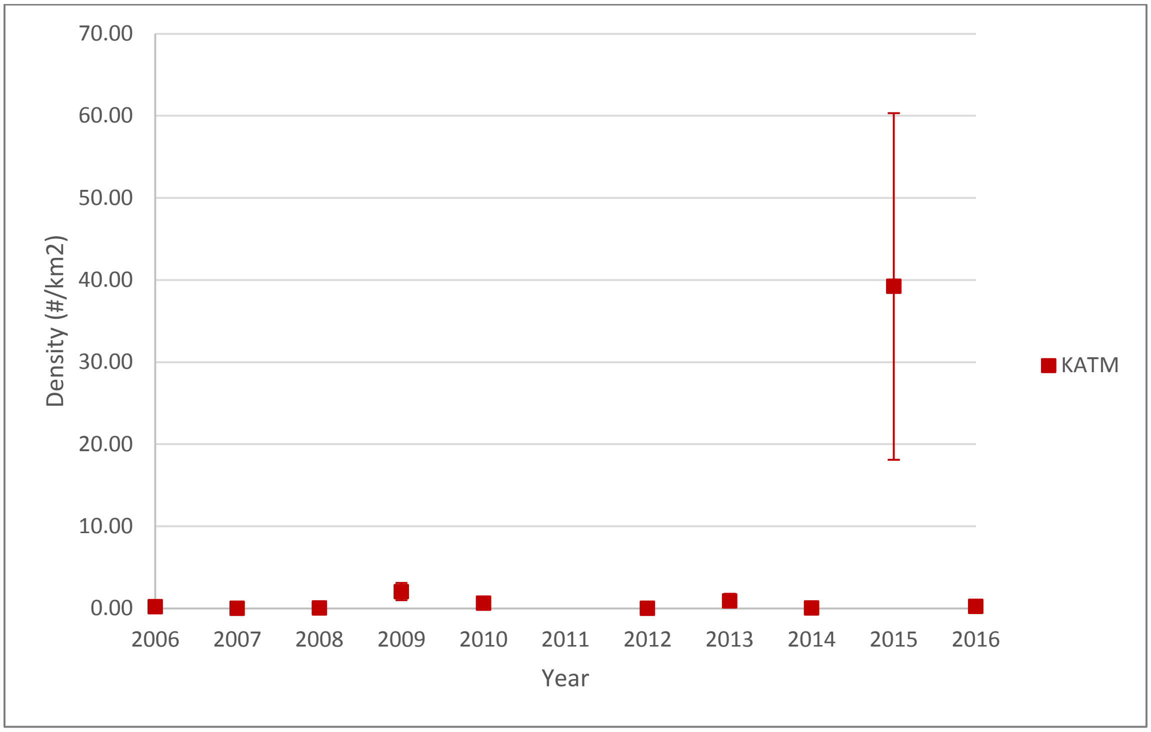

Figure 14. Common murre density in KATM. 2011 was not surveyed. Error bars indicate ± 1SE.

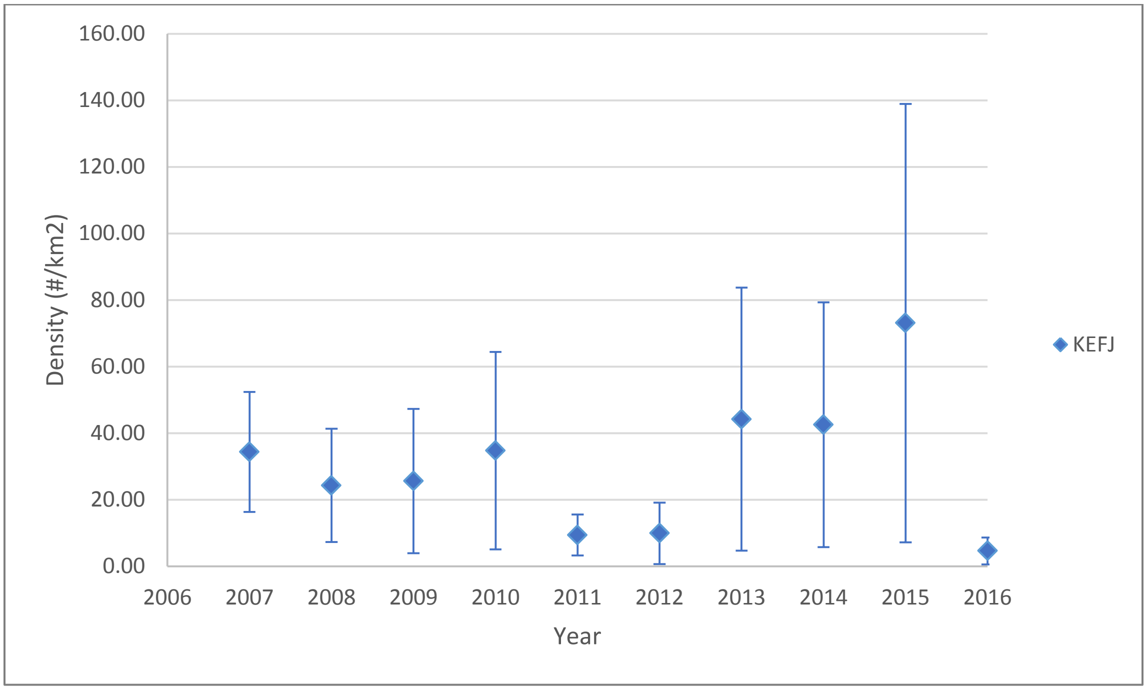

Figure 15. Common murre density in KEFJ. 2006 was not surveyed. Error bars indicate ± 1SE.

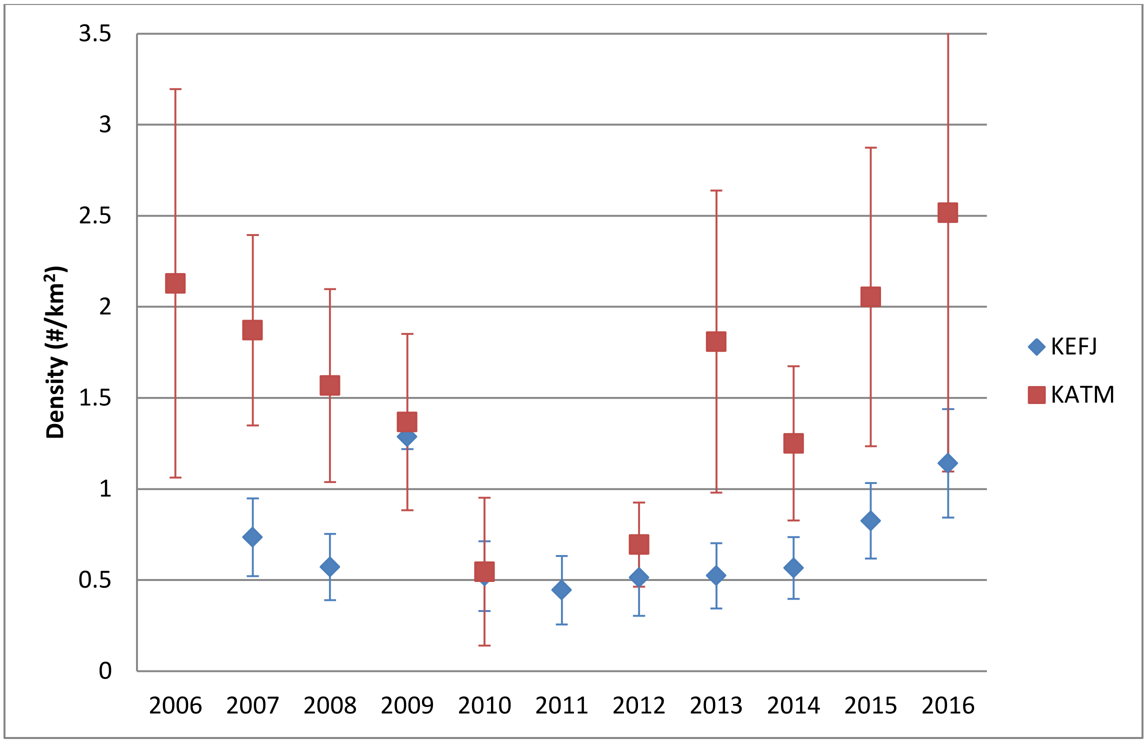

Figure 16. Black oystercatcher density in KATM and KEFJ. 2011 was not surveyed in KATM while KEFJ was not surveyed in 2006. Error bars indicate ± 1SE.

Table 3. Select marine bird survey results from KATM (2006-2016; 2011 was not sampled) and KEFJ (2007-2016). Numbers shown are average densities (number of birds/km²) and (± 1SE). Bird table headings: BLKI (Black-legged kittiwake), BLOY (Black oystercatcher), GWGU (Glaucous-winged gull), HADU (Harlequin duck), PIGU (Pigeon guillemot), Corm (Cormorant species pooled and include Double-crested, Red-faced and Pelagic), Scot (Scoter species pooled and include Surf, Black and White-winged), and Merg (Merganser species pooled and include Common and Red-breasted).

Park	Year	BLKI	BLOY	GWGU	HADU	PIGU	Corm	Scot	Merg
KATM	2006	62.44 (31.04)	2.13 (1.07)	74.68 (23.42)	16.32 (3.44)	8.02 (2.20)	75.49 (35.17)	2.30 (1.30)	5.66 (3.80)
KATM	2007	77.80 (37.79)	1.87 (0.52)	103.11 (29.52)	30.19 (7.92)	7.30 (2.67)	42.03 (23.70)	6.62 (4.72)	5.72 (3.29)
KATM	2008	3.34 (3.25)	1.57 (0.53)	49.04 (30.26)	38.38 (17.51)	9.85 (3.55)	0.50 (0.24)	9.01 (6.79)	14.67 (12.77)
KATM	2009	59.93 (19.05)	1.37 (0.48)	110.68 (38.34)	36.86 (13.30)	16.35 (4.74)	46.70 (26.75)	50.39 (22.88)	1.73 (0.79)
KATM	2010	67.80 (28.71)	0.55 (0.41)	122.10 (47.80)	25.61 (9.85)	15.56 (9.35)	33.08 (17.05)	17.37 (5.81)	26.83 (18.07)

Park	Year	BLKI	BLOY	GWGU	HADU	PIGU	Corm	Scot	Merg
KATM	2012	44.41 (13.09)	0.69 (0.23)	127.95 (40.08)	23.92 (5.78)	8.50 (2.99)	12.88 (5.90)	5.28 (3.60)	4.55 (2.25)
KATM	2013	33.74 (14.66)	1.81 (0.83)	92.12 (26.98)	38.73 (14.29)	15.25 (5.70)	7.61 (2.77)	20.88 (8.23)	5.39 (3.10)
KATM	2014	35.28 (15.18)	1.25 (0.42)	85.48 (28.11)	29.64 (11.25)	12.04 (4.57)	40.60 (24.30)	1.92 (1.25)	11.92 (11.15)
KATM	2015	485.00 (366.43)	2.05 (0.82)	141.56 (37.02)	44.15 (18.73)	10.81 (5.58)	34.33 (11.67)	18.43 (11.65)	10.78 (8.80)
KATM	2016	37.71 (14.26)	2.52 (1.42)	73.09 (25.25)	24.62 (9.02)	13.81 (4.84)	50.01 (35.88)	16.96 (9.40)	14.39 (8.27)
KEFJ	2007	45.78 (21.59)	0.74 (0.21)	180.19 (56.86)	12.45 (8.87)	6.49 (1.34)	34.33 (15.43)	1.17 (0.59)	1.40 (0.69)
KEFJ	2008	31.00 (25.48)	0.57 (0.18)	126.84 (40.16)	17.53 (13.31)	5.49 (1.34)	21.14 (6.97)	2.30 (1.66)	0.00 (0.00)
KEFJ	2009	81.82 (76.05)	1.29 (0.07)	119.19 (40.06)	15.92 (8.26)	4.63 (1.31)	29.19 (10.70)	0.11 (0.08)	0.00 (0.00)
KEFJ	2010	38.32 (28.21)	0.52 (0.19)	106.00 (22.62)	28.84 (24.88)	5.69 (1.36)	31.98 (10.41)	10.85 (8.03)	4.71 (3.10)
KEFJ	2011	45.18 (39.76)	0.44 (0.19)	117.74 (25.12)	11.38 (5.84)	5.01 (1.07)	30.90 (9.94)	2.85 (1.78)	0.54 (0.40)
KEFJ	2012	12.25 (4.33)	0.51 (0.21)	78.09 (18.28)	20.49 (11.01)	6.87 (1.91)	16.58 (8.09)	3.95 (3.69)	0.22 (0.13)
KEFJ	2013	68.03 (66.50)	0.52 (0.18)	176.66 (71.90)	12.59 (6.68)	7.75 (1.31)	9.36 (2.55)	0.00 (0.00)	1.01 (0.66)
KEFJ	2014	104.65 (99.36)	0.57 (0.17)	111.69 (26.23)	12.93 (6.61)	7.79 (2.13)	7.39 (1.83)	0.39 (0.31)	0.06 (0.04)
KEFJ	2015	105.53 (80.11)	0.83 (0.21)	106.99 (28.61)	12.57 (6.09)	4.30 (1.24)	15.52 (6.57)	1.01 (0.68)	2.49 (1.96)
KEFJ	2016	22.14 (12.18)	1.14 (0.30)	109.23 (28.28)	12.15 (8.16)	4.08 (0.75)	11.68 (2.82)	0.41 (0.22)	0.94 (0.94)

Black Oystercatchers

Nest Density

All five black oystercatcher transects were analyzed at the regional level for nest density (nest/km) and productivity ((eggs + chicks)/nest) by year in KATM, KEFJ and WPWS. The mean density of active black oystercatcher nest sites at KATM ranged from 0.06 to 0.12 per km of shoreline from 2006-2016. The mean density of active black oystercatcher nest sites at KEFJ ranged from 0.05 to 0.09 per km of shoreline from 2007-2016 and from 0.06 to 0.13 per km of shoreline in WPWS between 2007 and 2016 (Fig. 17). Although highly variable in all three regions, active nest density continues to be similar across time with little evidence of a trend (Fig. 17). However, in 2016, there was evidence of a decline in KEFJ nest density, although the decline appears to be not significant.

The mean productivity ((eggs + chicks) / nest) ranged from 1.13 to 2.2 for KATM from 2006-2016 while in KEFJ, mean productivity ranged from 0.12 to 1.87 from 2007- 2016 and from 0.6 to 2.22 in WPWS from 2007-2016 (Fig. 18). Mean productivity also tends to be highly variable across all regions. However, in KEFJ and WPWS, we observed a decline in productivity that appears to correlate with a decline in mussel abundance (see mussel section) beginning in 2009 with subsequent increases in both regions beginning in 2012-2013. Because we only visit a nest once per year in our monitoring program, results reflect productivity at the time of the survey, adding to the variability in the results.

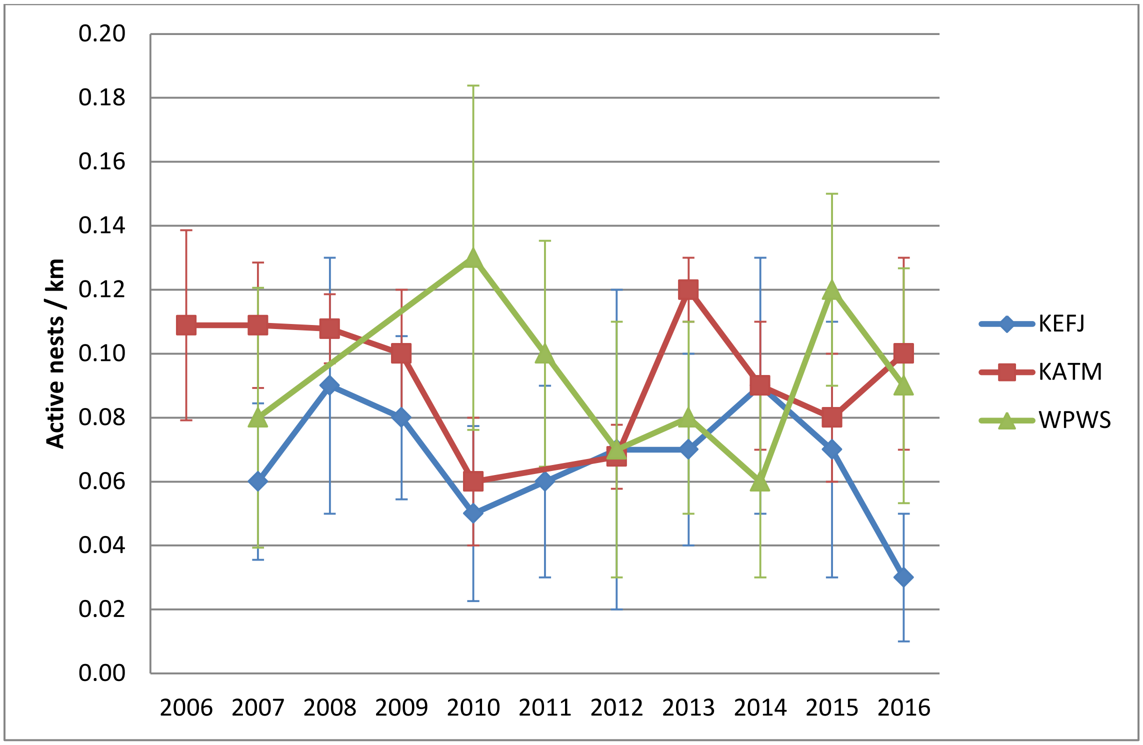

Figure 17. Number of active black oystercatcher nests/km in KATM, KEFJ, and WPWS during 2006-2016. Error bars indicate ± 1SE.

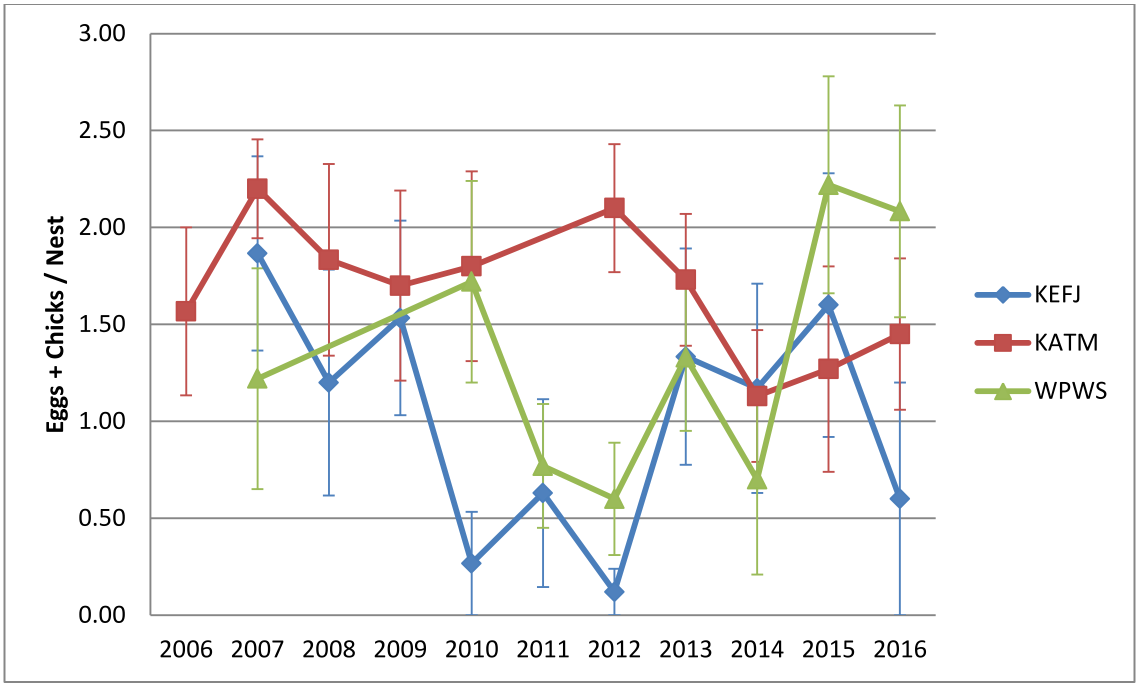

Figure 18. Productivity ((eggs + chicks)/nest) of active black oystercatcher nests in KATM, KEFJ, and WPWS during 2006-2016. Error bars indicate ± 1SE.

Chick Diet

We collected 17,898 prey items, representing at least 26 different prey species, at 154 black oystercatcher nest sites in KATM, KEFJ and WPWS. Although prey size is measured for all species, here we report only on the mean size of the three most predominate species: *Lottia pelta*, *L. persona*, and *Mytilus trossulus*. Three species of limpets (*Lottia pelta*, *L. persona*, and to a lesser extent *L. scutum*) and the Pacific blue mussel (*Mytilus trossulus*) were the predominant prey items found at nest sites (Fig. 19). Together, these four species represented 84, 92, and 97% of prey items found at KATM, KEFJ, and PWS, respectively, for all sampling years. The size of *M. trossulus* prey varied widely across blocks and years, ranging from 19.37 ± 6.39 (mean ± 1SD; KEFJ 2008) to 41.88 ± 8.66 mm (KATM 2006; Fig. 20). Limpet prey sizes did not vary as widely; *L. pelta* prey ranged from 18.63 ± 2.96 (mean ± 1SD; WPWS 2007) to 26.10 ± 5.17 mm (KEFJ 2013) and *L. persona* prey ranged from 17.71 ± 2.81 (WPWS 2012) to 23.74 ± 4.37 mm (KATM 2008).

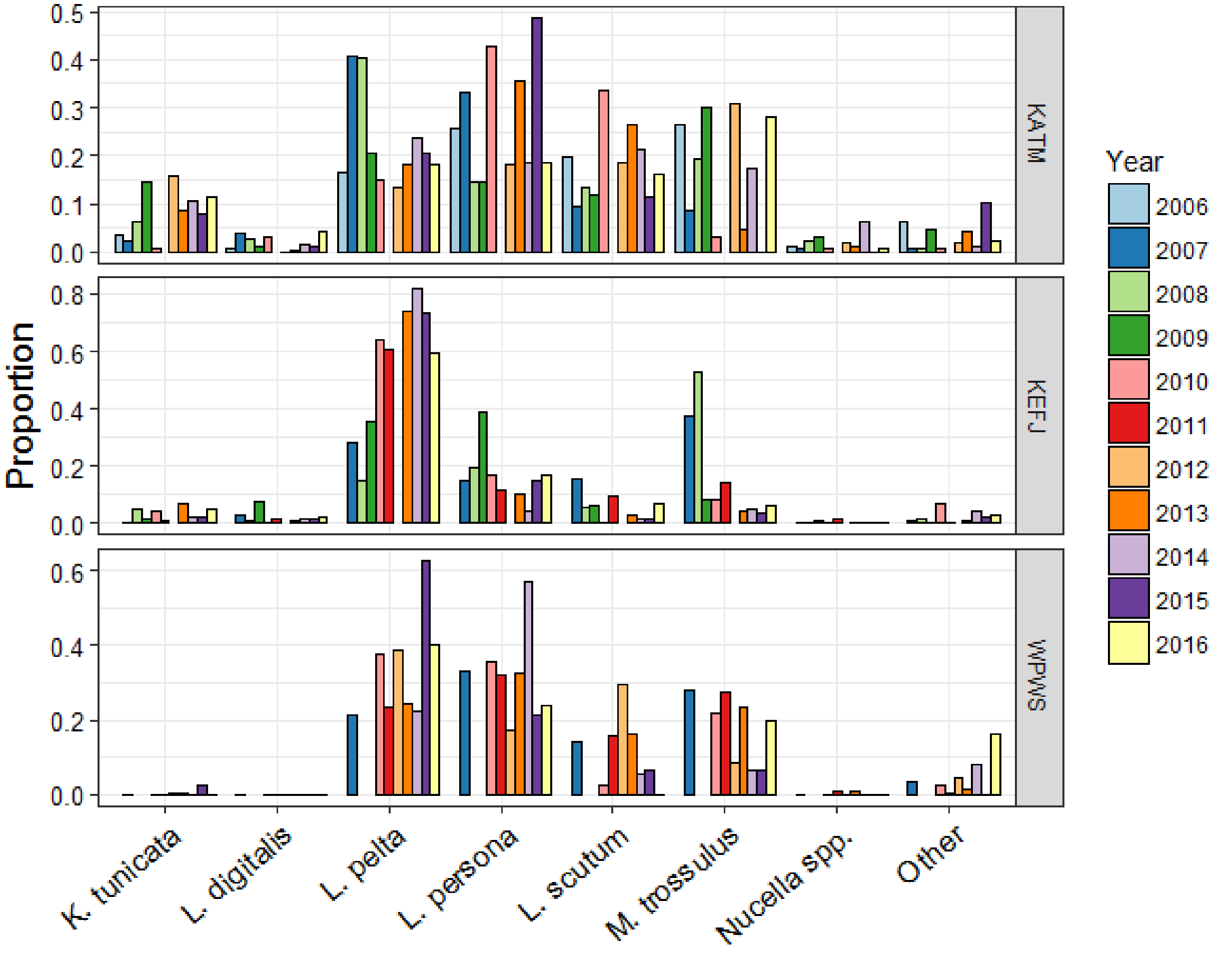

Figure 19. Species composition of prey items collected at active black oystercatcher nests in KATM, KEFJ, and WPWS during 2006-2016. KATM was not sampled in 2011. KEFJ was not sampled in 2006 and 2012. WPWS was not sampled in 2006, 2008, and 2009.

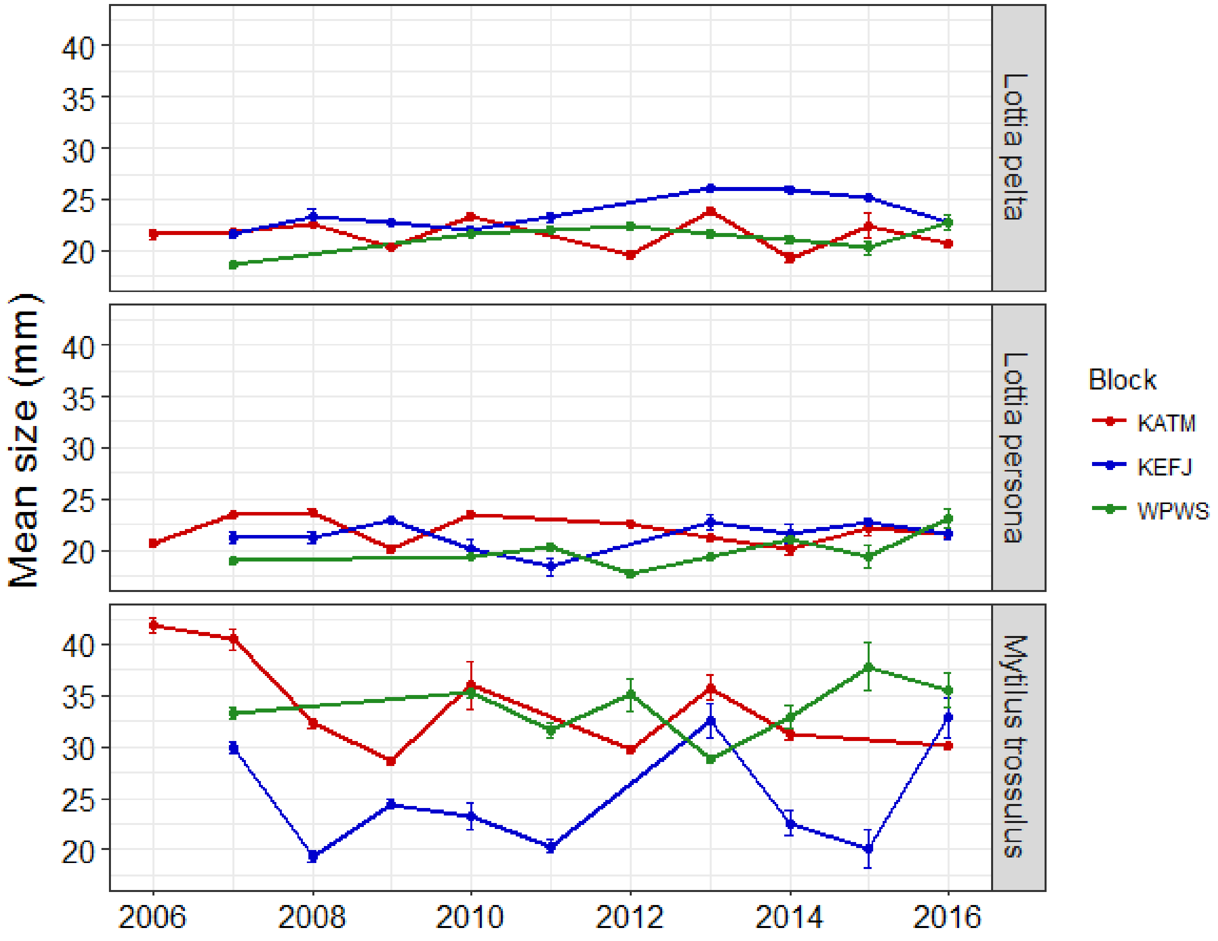

Figure 20. Mean size (mm) of the three most common species of prey found at black oystercatcher nest sites in KATM, KEFJ, and WPWS during 2006-2016. KATM was not sampled in 2011. KEFJ was not sampled in 2006 and 2012. WPWS was not sampled in 2006, 2008, and 2009. Error bars represent ± 1SE.

Sea Otters

Aerial Surveys of Abundance

Based on aerial surveys in 2012 and 2015, sea otter abundance in KATM appears to have stabilized following more than a decade of population growth (Appendix A). In KEFJ, 3 surveys between 2002 and 2010 suggest a stable sea otter population (Appendix A). However, sea otter numbers in KEFJ declined from 1,322 (1SE=494) in 2010 to 866 (1SE=214) in 2016. Sea otter abundance in WPWS increased at 3% per year from 1993-2013 (Ballachey et al. 2014, Appendix A) (Fig. 21).

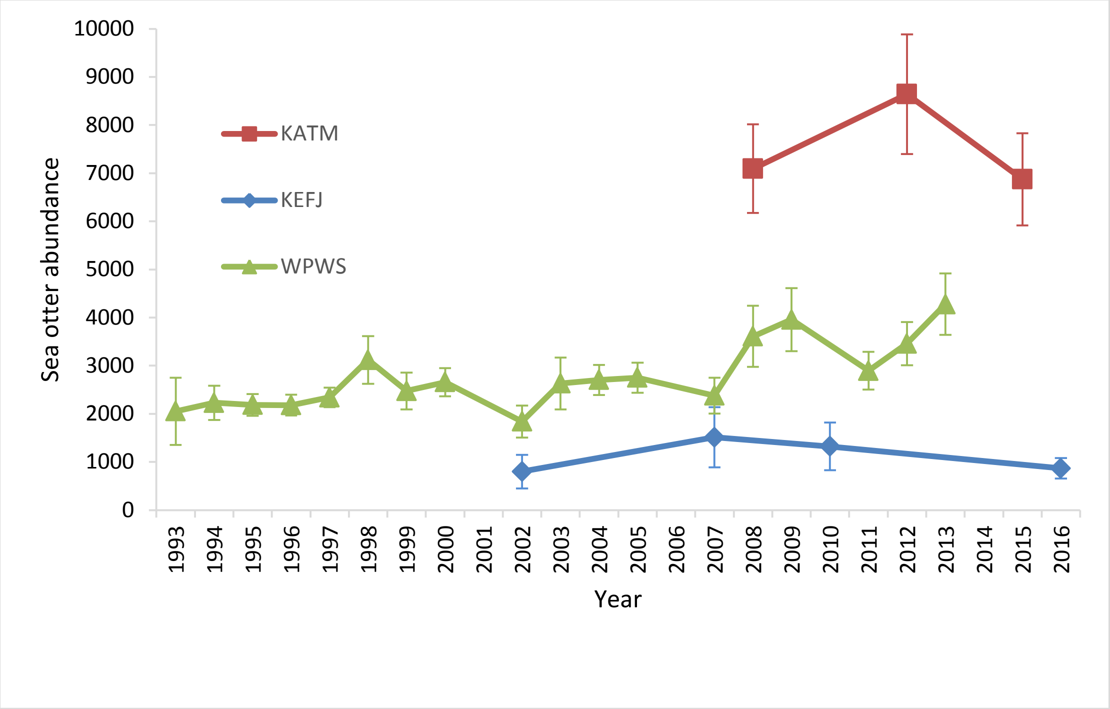

Figure 21. Sea otter abundance in KATM, KEFJ and WPWS during 1993 – 2016. Error bars indicate ± 1SE.

Carcass Collections

We collected 302 carcasses at KATM between 2006 and 2015. The KATM age-at-death distributions had high proportions of prime-age animals and relatively low proportions of young and old age-classes when compared to the baseline age-class distribution (Appendix A). We collected an additional 59 carcasses at KATM in 2016, and teeth have been submitted for aging. We collected 329 carcasses from the beaches of WPWS between 2006 and 2015. However, until at least 2010, the age-at-death distribution was still significantly affected by EVOS-related mortality (Monson et al. 2011, Ballachey et al. 2014). In general, the recent WPWS age-at-death distributions (2010 to 2015) contained low proportions of prime-age animals similar to pre-spill collections reflecting the generally low mortality rates of this age-class (Appendix A). Aging results are pending for an additional 32 carcasses collected in WPWS in 2016.

Foraging Observations

From 2006 to 2016, we observed a total of 1,498 summer (late May to early August) forage bouts, including 534 bouts at KATM, 443 bouts in KEFJ, and 527 bouts in WPWS. Most forage observations focused on adult animals (94% of all bouts including 98%, 89% and 94% for KATM, KEFJ and WPWS respectively). Adult foraging success averaged 91% and was similar among areas averaging 89%, 92% and 92% for KATM, KEFJ and WPWS respectively.

At KATM, sea otter energy recovery rates steadily declined from a high of 11.6 kcal/min when first measured in 2006, to levels observed in sea otters at the other two areas by 2012 (overall average = 8.1 kcal/min) and continued to decline through 2016 (results up to 2015 presented in Appendix A). Clams are the predominant item in the diet of KATM otters averaging 63% of recovered biomass. The declining energy recovery rates at KATM presumably reflects generally decreased abundance and size of available clams with the rate of prey tissue mass gain from clam foraging declining from a high of about 14 g/min during 2006 to 2008 to approximately 5.3 g/min in 2016. Energy recovery rates were low but fairly stable at KEFJ and WPWS. Overall, recovery rates averaged 5.8 kcal/min at both KEFJ and WPWS. However, the values in WPWS represent a decline from the mid-1990's recovery rates (mean = 9.0 kcal/min; 95% CI = 7.9 to 10.2) measured while sea otter densities were still depressed from the EVOS (Dean et al. 2002). Clams are also the predominant item in the diet in WPWS averaging 57% of recovered biomass. The high energy recovery rate documented in the mid 1990's in WPWS otters appeared to be driven by the relaxation of predation pressure on the clam population while the sea otter population was depressed (Bodkin et al. 2002, Dean et al. 2002). Similar to KATM, the subsequent decline in energy recovery rates in WPWS during the period of this study presumably reflect reductions in clam numbers and size, with mass gain from clam foraging averaging 6.2 g/min from 2007 to 2015). In contrast, mussels were a much more important component of sea otter diet at KEFJ averaging 58% of recovered biomass. Interestingly, energy recovery rates at KEFJ appear to track changes in intertidal mussel (*Mytilus trossulus*) biomass at rocky intertidal sites (Appendix A). Overall, mass gain from mussel foraging at KEFJ averaged 8.6 g/min from 2007 to 2016 with highs of 17.7 g/min and 14.4 g/min in 2008 and 2015 respectively and a low of 4.1 g/min in 2011.

Marine Water Chemistry and Water Quality

Mean monthly water temperatures (2006-2016) were coolest at KATM and warmest in WPWS (Fig. 22). KEFJ had intermediate water temperatures with values similar to WPWS during winter months but staying cooler and becoming more similar to KATM values during summer (Fig. 22). In general, water temperatures among sites within KATM and KEFJ were less variable than among sites within WPWS. Coincident with a warm water mass (the BLOB) that entered the Gulf of Alaska in 2014, intertidal water temperatures became anomalously warm during the spring of 2014 and remained high through the summer of 2016 with winter water temperatures 1.5 °C to 2 °C above average in all three areas (Fig. 23).

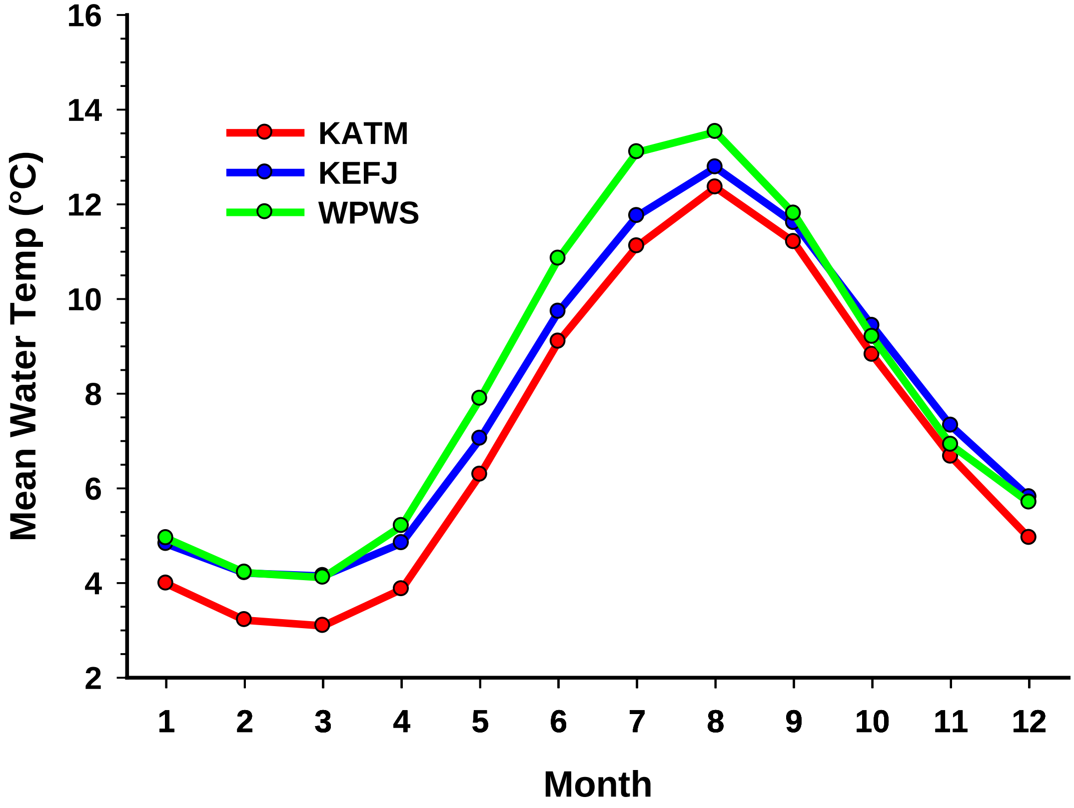

Figure 22. Mean monthly water temperatures (2006-2016) at KATM, KEFJ and WPWS rocky intertidal sites as measured by HOBOs placed at the 0.5 m tidal elevation. Month 1 corresponds to January, month 2 to February, etc.

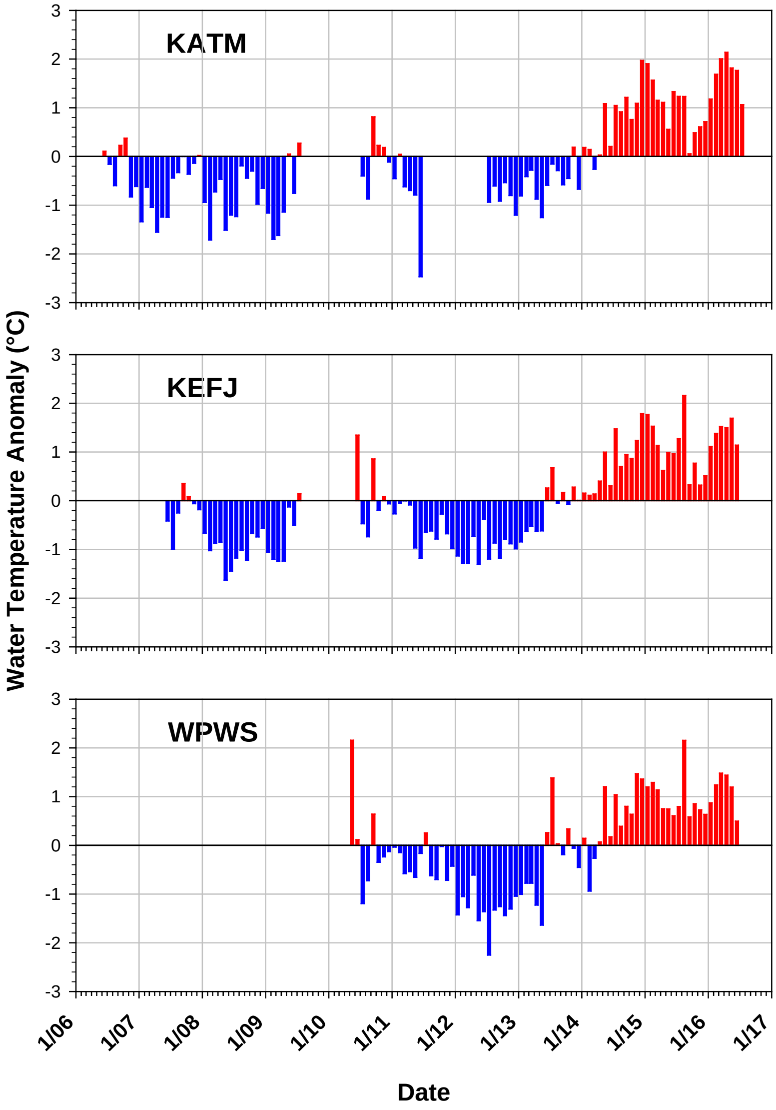

Figure 23. Monthly mean water temperature anomalies from 2006 to 2016 at KATM, KEFJ and WPWS rocky intertidal sites as measured by HOBOs placed at the 0.5 m tidal elevation.

Results of the contaminant analyses on mussels sampled in 2007, 2012 and 2013 (from 25 intertidal sites) are provided in three technical reports received from the contract laboratory overseeing analyses (TDI-Brooks International, Inc. 2008, 2013, 2014). Data provided include presentation of quality assurance and quality control measures, and for each sample analyzed, concentration for each specific compound tested. A preliminary examination of the data has not identified outliers or unanticipated findings. A comprehensive statistical analysis of the contaminant data will be conducted subsequent to collection and testing of additional mussel samples, planned for the second 5-year cycle of the GWA Program (2017-2021).

DISCUSSION

Our overarching objective for the nearshore component was to detect change and identify important processes regulating or causing changes within the nearshore ecosystem across portions of the northern GOA. Several examples have been given throughout this report and are summarized below. Specific objectives also included: continued restoration monitoring in the nearshore to evaluate the current status of injured resources in oiled areas, identify if those injured resources being monitored may be considered recovered from EVOS effects, identify potential factors that could inhibit recovery of injured resources, and recommend potential restoration actions.

As highlighted in the Results section above, our nearshore ecosystem monitoring has provided spatially-extensive data on a wide array of nearshore metrics, many of which were considered injured resources from the EVOS, and builds whenever possible on longer-term data streams that pre-date GWA. In terms of status and recovery, our data have been critical for evaluating recovery status for nearshore species injured by the EVOS (Ballachey et al. 2014, 2015, Bodkin et al. 2014, Esler et al. 2015, Michel et al. 2016). For example, both contaminants and gene expression information from mussels confirms findings from other studies concluding that lingering oil is no longer a source of bioavailable contamination (Bowen et al. 2017). Similarly, GWA lingering oil studies have shown that harlequin ducks were exposed to oil through 2011, but that exposure has since abated (Esler and Ballachey 2014, Esler et al. 2016). Our GWA sea otter surveys have contributed to understanding long-term trends in oiled areas of WPWS; even in the heavily-oiled area of northern Knight Island, sea otter abundance has returned to pre-spill levels (Ballachey et al. 2014). Taken together, these results indicate that, for nearshore species, recovery from the oil spill has occurred, despite the continuing presence of lingering oil. The timeline over which recovery of nearshore species occurred was long, spanning decades in some cases (Iverson and Esler 2010, Ballachey et al. 2014, Michel et al. 2016). Now that recovery is complete, however, other natural and anthropogenic influences will be the most significant drivers of change in nearshore ecosystems. We note that some pelagic species are not considered recovered from the spill, although lack of recovery is not related to continued exposure to oil (Bodkin et al. 2014, Esler et al. in press, Michel et al. 2016).

Data streams from GWA as well as from programs that pre-date GWA, but are being continued through this effort, have already revealed many interesting patterns, processes and potential causes for change. For example, we see that different metrics vary at substantially different spatial and temporal scales. Some physical (e.g., water temperature) and biological (e.g., large mussel densities) attributes show consistent temporal variation at the scale of the northern GOA, suggestive of broad-scale drivers. Other metrics show variation at the regional level (e.g., proportions of mussels in sea otter diets), indicating regional-scale differences in ecological conditions. Other metrics vary on a site-by-site basis (e.g., mussel recruitment and eelgrass cover), which indicates responses to local conditions. Potential drivers and the scales at which they operate, both temporal and spatial, are critical for managers as they engage in scenario planning in anticipation of climate change effects (National Park Service 2013) and oil spill response. Through a variety of outlets, we have provided managers with updates on the status of these vital signs and their various metrics over the entire study period.

For example, one important result has been recognition of divergent population trajectories and differing equilibrium densities of sea otters at our various sampling regions. When population data is coupled with sea otter foraging data, this information provides important insights on the factors that influence sea otter populations at each region. Sea otter numbers in KATM have increased dramatically in recent decades and are now substantially higher than in KEFJ and WPWS, which is likely due to more extensive and potentially more productive habitat at KATM. Sea otters in WPWS have increased in abundance since 1993, as they recovered from injury resulting from the EVOS. Sea otter densities in KEFJ have been consistent and low. Interestingly, foraging data indicate that otters in all three regions currently appear to be near a food-limited equilibrium density, suggesting that managers should not expect substantial increases in any of these regions in sea otter abundance and that region-specific drivers have influenced past population trajectories and dictate current abundance. These results, including explicit management implications, are reported in detail by Coletti et al. (2016), which is included as Appendix A of this report.

As another example of completed work, in collaboration with Restoration Project 16120114-K, we evaluated the role of selected physical factors in dictating rocky intertidal community structure across our study regions (Konar et al. 2016). Surprisingly, these static drivers were not strongly related to intertidal communities. This may have resulted from our selection of similar, sheltered rocky sites throughout the region. However, this may provide an ideal situation for subsequently understanding the role of dynamic drivers of intertidal community structure across the region, which we intend to pursue during the next five-year program. Understanding drivers of community change will allow agencies to make informed management decisions for marine areas.

We also have analyzed mussel data collected as part of our nearshore monitoring efforts (Bodkin et al. in press; Appendix B of this document). All mussel metrics varied considerably on a site-by-site basis, which highlights the importance of local conditions for mussel recruitment and abundance. However, after accounting for site differences, we also found patterns in several measures of abundance that indicated synchronous variation across the entire northern GOA, suggesting an influence of broad-scale drivers. Because mussels are an important food resource for nearshore predators such as sea stars, black oystercatchers, sea ducks and sea otters, understanding mussel dynamics may also allow us to predict predator responses to changing prey resources. These tools will be invaluable to managers as local and regional stressors continue to impact nearshore resources.

In addition to the detailed findings reported in the attached Appendices, we also have seen a number of interesting patterns in other metrics, as described in Results. For example, our water temperature data confirm that the warm water anomalies that are well-established in offshore measurements also are expressed in intertidal regions across the northern Gulf of Alaska. Nearshore biological effects of abnormally warm water remain under investigation. As another example, in response to the well-publicized common murre die-offs during the winter of 2015-2016, we examined our marine bird survey data, and determined that we also observed anomalous distributions and numbers of murres preceding the winter die-off. Also, we have discovered, in collaboration with Restoration Project 16120114-K, that sea star abundance and species dominance varies markedly among regions, suggesting broad-scale rather than site-specific drivers of these patterns. With continuing data collection in upcoming years, we will continue to see and explore patterns in the data, to understand causes of variation and the spatial scales over which they operate.

In conjunction with core monitoring work, we also were engaged in several collaborative efforts to understand nearshore processes, leveraging the field presence facilitated by GWA. These collaborations included stable isotope analyses of nearshore communities, collection of mussels for growth and energetics analyses, evaluation of the prevalence of sea star wasting disease, and collection of clams as part of an evaluation of gene expression and other biomarkers as tools for monitoring health of nearshore ecosystems.

As an example of the value of these collaborations, we surveyed sea stars at our nearshore sites for sea star wasting disease, which has been widely observed in stars along the California, Oregon, Washington and British Columbia coasts. We initially collaborated with an experienced star observer from the University of California Santa Cruz on our first GWA trip in 2014. In 2014, we conducted a concerted effort to look for wasting disease at all GWA nearshore monitoring sites in southcentral Alaska. We detected only 9 diseased stars out of 1,588 counted across 30 sites (0.6%), far fewer than expected given the prevalence of wasting disease further south. In 2015, we recorded 69 diseased stars out of 2,016 stars observed (3.4%); almost all of these (67) were observed in KBAY (Iken and Konar pers comm.). Although there was a slight increase in 2015, the occurrence of diseased stars is still low in contrast to southeast Alaska and the Lower 48.

Through collaboration and a multi-agency approach to monitoring, the nearshore component of GWA has met the objectives defined for this study period. We have concurrently provided valuable information to management agencies (NPS, USFWS, BOEM) that has been used in spill response actions as well as in planning documents. We have also provided data streams that originated prior to the start of the GWA program as part of other EVOSTC projects and the NPS SWAN I&M program. The data sets, including data collected under GWA, have been made publicly available in order to preserve the opportunity for other researchers, managers and the public to access these data in the future.

CONCLUSIONS

This work provides unprecedented spatial and temporal coverage of nearshore ecosystem dynamics in the northern GOA. Results to date are showing compelling patterns, and are leading to insights about the drivers of observed patterns in the nearshore communities. In a broader context, our findings are providing interesting comparisons with and contrasts to those of the Pelagic Component of GWA (Restoration Project 16120114-O). For example, biological responses to recent, anomalous warm water conditions have been stronger in pelagic species, perhaps reflecting adaptation by nearshore species to temperature and salinity conditions that naturally vary widely. In contrast, nearshore systems may be more vulnerable to other kinds of changes (e.g., ocean acidification, upland habitat modification, contamination), highlighting the value of multiple windows into overall marine health. We anticipate that the GOA is likely to be affected by projected changes in ocean condition across the Northeast Pacific as well as by oceanographic changes in the arctic. As the GWA Program progresses and matures, we are confident that further insights into the marine environment will become apparent, and will be valuable for improving understanding and management of marine natural resources of high societal and ecological value.

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Appendix A

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esa ECOSPHERE

SPECIAL FEATURE: SCIENCE FOR OUR NATIONAL PARKS' SECOND CENTURY

Detecting and inferring cause of change in an Alaska nearshore marine ecosystem

Heather A. Coletti,[1],† James L. Bodkin,[2] Daniel H. Monson,[2]
Brenda E. Ballachey,[2] and Thomas A. Dean[3]

[1]*National Park Service, 4175 Geist Road, Fairbanks, Alaska 99709 USA*
[2]*United States Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508 USA*
[3]*Coastal Resources Associates Inc., 5190 El Arbol Drive, Carlsbad, California 92008 USA*

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Abstract. Community composition, species abundance, and species distribution are expected to change while monitoring ecosystems over time, and effective management of natural resources requires understanding mechanisms contributing to change. Marine ecosystems in particular can be difficult to monitor, in part due to large, multidimensional spatial scales and complex dynamics. However, within the temperate marine ecosystems, the nearshore food web is reasonably well described. This food web is ecologically and socially important, spatially constrained, and has been the focus of extensive experimental research that describes the underlying mechanisms important to system dynamics. Here, we describe a monitoring program initiated in 2006 that focuses on the nearshore benthic food web in the Gulf of Alaska, whose design anticipates potential causes of ecosystem change to improve rigor, resolution, and confidence in understanding the mechanisms underlying change. We established 15 long-term monitoring sites across more than 1000 km of coastline, including 10 within two national parks and 5 within Prince William Sound, area of the 1989 *Exxon Valdez* oil spill. The program evaluates six ecological indicators and more than 200 species that range from primary producers to top-level consumers, and is designed to examine both bottom-up and top-down dynamics. Employing a design that allows broad spatial inference and selecting species with direct food-web linkages, we demonstrate the ability of our monitoring program to simultaneously detect change and assess potential mechanisms underlying that change. Detecting change and understanding mechanisms can help guide management and conservation policy. Specifically, we provide an example focusing on the sea otter (*Enhydra lutris*) that illustrates how (1) analytical methods are used to evaluate changes on various scales and infer potential mechanisms of change, (2) food-web linkages can enhance the understanding of changes and their effects, and (3) data can be used to inform management.

Key words: abundance; ecosystem dynamics; energy recovery rates; *Enhydra lutris*; Gulf of Alaska; long-term monitoring; mortality; nearshore marine food web; sea otter; Special Feature: Science for Our National Parks' Second Century; vital signs.

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† **E-mail:** Heather_Coletti@nps.gov

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INTRODUCTION

Ecosystems are inherently complex, with temporal and spatial variabilities reflecting that complexity (Darwin 1859, Elmqvist et al. 2003, Parr et al. 2003, Coppin et al. 2004). Consequently, we anticipate that as we monitor an ecosystem, change will be observed over time. In fact, ecological monitoring often aims to document how ecosystems change, typically accomplished by quantifying the presence, abundance, and attributes of species over time (Magurran et al. 2010). However, understanding what causes change in species abundance or community composition can be problematic, particularly if the question is asked from the retrospective perspective of "What caused an observed change?" (Lindenmayer and Likens 2009). Answers to such questions are often couched with high levels of uncertainty and little confidence, potentially impairing management and policy decisions. Spatially explicit data collection and anticipation of potential causes of ecosystem change in the design phase of long-term monitoring programs can improve the rigor and confidence in understanding the mechanisms underlying change.

Marine ecosystems in general are well known for high spatial and temporal variabilities in the composition, distribution, and abundance of species (Hughes et al. 2005, Levin and Lubchenco 2008). Due to large spatial scales, fluid boundaries, and complex dynamics, marine ecosystems are often difficult to sample, constraining our ability to identify the underlying cause of change (Botsford et al. 1997).

Although nearshore marine ecosystems can be distinguished from the terrestrial and oceanic environments that they border, functionally these three environments are intricately linked in important ways (Fig. 1). The high productivity, species diversity, and unique food webs found in nearshore systems are supported by contributions of matter and energy from terrestrial watersheds and the sea (Estes 2015). However, adverse inputs from watersheds (e.g., contaminants and disease) and oceans (e.g., oil spills and harmful algal blooms) threaten the continued health and function of the nearshore. More recently, climate change has led to warming, rising sea levels, and ocean acidification (Mann and Lazier 1996, Feely et al. 2004, Wei et al. 2009, Doney et al. 2012), with the potential to disrupt entire marine food webs (Kurihara and Shirayama 2004, Kurihara et al. 2008, Widdicombe and Spicer 2008), including those in the nearshore.

Potential changes from anthropogenic causes are set against a backdrop of a naturally variable environment. In the North Pacific, ocean environments can change over scales of years to decades due to teleconnections such as the Pacific Decadal Oscillation and El Niño (Emery and Hamilton 1985, Mantua et al. 1997), which may impact the nearshore environments (Gunnil 1985, Wootton et al. 1996, Navarrete et al. 2002). Changes also may result from earthquakes, volcanic activity, landslides, and tsunamis that are important agents of change in this seismically active region (Rigg 1914, Baxter 1971, Haven 1971, Hubbard 1971, NRC 1971, DeGange et al. 2010). A challenge in monitoring is to identify and partition the relative contributions of natural and anthropogenic sources in system changes.

Our objectives in this study were to provide a general description of the nearshore system in the central Gulf of Alaska (GOA), historical causes of change, and illustrate how corresponding monitoring data, spatial contrasts, and food-web linkages from our monitoring program can be used to inform the cause of change. We use multiple data sets collected on the sea otter to illustrate the evaluation of trends in abundance and the interpretation of these trends. We also provide examples of how ongoing monitoring data and inferences based on our sampling design have facilitated management and policy decisions in and adjacent to national parklands.

Description of the GOA nearshore system

The structure of nearshore communities in the GOA is largely governed by the same forces recognized as controlling the distribution and abundance of organisms in the more widely studied temperate rocky shores at lower latitudes (reviewed in Peterson 2005). Important physical factors include substrate composition, slope, temperature (both water and air), desiccation (for the intertidal), light, exposure to waves, the degree of freshwater input (i.e., salinity), currents, and ice scour. Particularly important are ecological processes, including predation by certain keystone predators whose influences on community structure are disproportionate to

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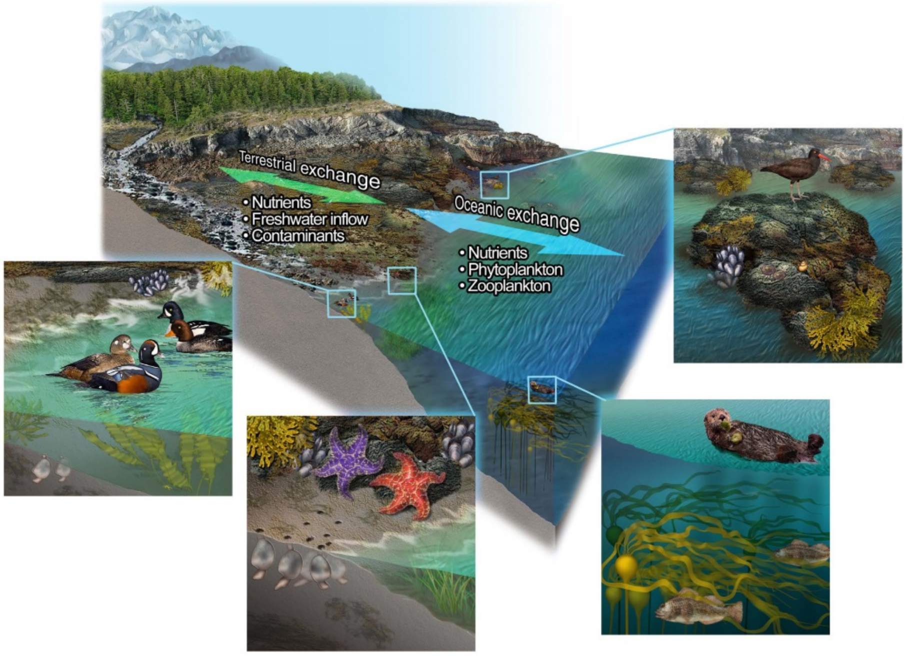

Fig. 1. Conceptual model of the nearshore food web with terrestrial and oceanic influences illustrated. In this model, sea otters, black oystercatchers, sea ducks, and sea stars act as the top-level consumers in a system where primary productivity originates mostly from the macroalgae and seagrass and moves through to the benthic invertebrates to the top-level consumers.

their abundance (Paine 1969). In the GOA, keystone predators include sea otters (Riedman and Estes 1990, Lowry and Bodkin 2005), certain sea stars (e.g., *Pycnopodia helianthoides, Pisaster ochraceus, and Evasterias troschelii*) (O'Clair and Rice 1985), black oystercatchers (*Haematopus bachmani*) (Marsh 1986, Power et al. 1996), and predatory snails (*Nucella* spp.) (Carroll and Highsmith 1996). Changes in the abundance of these keystone species can produce intense direct and indirect effects that can cascade through the ecosystem (Paine 1980).

The food web in the nearshore system of the GOA is relatively complex (Fig. 1). Most animals derive a large proportion of their energy from sources that can be traced to benthic-based primary production from seaweeds (especially kelps), eelgrass, and unicellular algae (especially benthic diatoms) (Duggins et al. 1989, Fredriksen 2003, Tallis 2009, Dunton et al. 2012, von Biela et al. 2013). Additional energy is derived from offshore planktonic sources. Plankton and nearshore detritus are food for filter- and suspension-feeding benthic invertebrates, including clams, mussels, barnacles, and some crabs (especially hermit crabs). Other benthic invertebrates are herbivorous and feed primarily on diatoms or small encrusting algae (e.g., limpets, littorines, and some crabs) or larger seaweeds and eelgrass (e.g., sea urchins, helmet crabs, and some larger herbivorous snails). The predators in this food web comprise a large and diverse group that include sea stars, predatory snails, fishes, birds, sea otters, and occasionally killer whales (*Orcinus orca*).

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Large mobile predators that reside in or spend some critical phase of their life cycle within the nearshore zone include a variety of mammals (both terrestrial and marine), birds, fishes, and invertebrates. The sea otter is perhaps the most recognized nearshore marine mammal (Kenyon 1969, Lowry and Bodkin 2005). Sea otters spend their entire life cycle principally within the nearshore zone and rely on intertidal and subtidal invertebrates (primarily clams and mussels) for food. Birds commonly encountered include bald eagles (*Haliaeetus leucocephalus*), gulls, shorebirds, seabirds, and sea ducks (Irons et al. 2000). Among those most closely linked to the nearshore are the black oystercatcher and several sea ducks including harlequin ducks and Barrow's goldeneye (Vermeer 1982, 1983, Andres and DeZeeuw 1991, O'Clair and O'Clair 1998, Robertson and Goudie 1999). Several commercially valuable fishes including Pacific herring and salmon also rely on the nearshore, particularly for spawning (Brown et al. 1996). Larger predatory invertebrates common in the nearshore include several species of sea stars, crabs, octopus, and snails that prey on smaller invertebrates.

Historical causes of change in the GOA nearshore

Three major events have resulted in long-term change in the nearshore community in the GOA: the extirpation and subsequent recolonization by sea otters, the 1964 earthquake, and the 1989 *Exxon Valdez* oil spill (EVOS).

Commercial harvest of sea otters began in the late 18th century, and by the early 20th century, sea otters in the North Pacific were nearly extinct, leaving only a few isolated populations (Kenyon 1969). Based on the observations of nearshore ecosystems in the presence and absence of sea otters, it is evident that the near extinction likely caused a dramatic shift in nearshore community structure across the coastal North Pacific (Estes and Palmisano 1974, Estes and Duggins 1995, Watson and Estes 2011). With sea otters present, the rocky nearshore is dominated by an abundant and diverse assemblage of kelps and seagrasses that are a dominant source of primary productivity into the system (Duggins et al. 1989, Wilmers et al. 2012). When sea otters are removed, herbivorous sea urchins (*Strongylocentrotus* spp.) proliferate and may functionally eliminate these primary producers, with cascading effects to other kelp-associated species (Estes 2015). At the same time, other invertebrates, including abalone, clam, crab, and urchins themselves, are released from sea otter predation and can increase in abundance and size and support important 20th-century fisheries.

Since the cessation of large-scale harvest of sea otters in the early 20th century, sea otter populations in the North Pacific have been recovering at various rates (Bodkin 2015). Recovery has been characterized by initial periods of low population density, followed by relatively rapid increases in population size as populations expand their range and recolonize vacant habitats. Expansion of sea otters across the Pacific eventually led to a reduction in sea urchin abundance and herbivory, and the recovery of kelp forests, associated species, and restoration of ecosystem effectiveness (Estes et al. 2010). Concurrently, expansion of sea otters led to declines in invertebrate prey species (e.g., abalone, crab, clam, and urchin) often to the point of fisheries collapse (Stephenson 1977, Garshelis et al. 1986, Kvitek et al. 1992). Cascading effects on other parts of the system (e.g., reduction in populations of animals that compete with sea otters for clam and crab resources) likely occurred, but were not documented. Sea otters now occupy most of the nearshore GOA from the Aleutians to Prince William Sound (PWS), although declines in the Aleutians late in the 20th century were sufficient to warrant listing under the U.S. Endangered Species Act, as well as lead to the collapse of the kelp forest ecosystem (Estes et al. 2010).

The 1964 Great Alaska Earthquake, with a magnitude of 9.2, had its epicenter near Perry Island in northern PWS (NRC 1971). The quake generated a tsunami that resulted in extensive physical damage and the loss of life in towns and villages that border PWS. Postquake surveys documented the complete destruction of the intertidal community in areas of maximum uplift (nearly 10 m in some areas) as the land and associated attached fauna and flora were thrust upward into the supratidal zone (Baxter 1971, Haven 1971, Hubbard 1971). In addition, the quake caused an estimated 35% reduction in intertidal hard-shell clam populations in PWS (Baxter 1971). Recovery of some intertidal communities apparently occurred within several years or less, but it was estimated that recovery of some clam

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populations took considerably longer (Hubbard 1971). Kenyon (1969) reported an estimated 40% decline in sea otter abundance postearthquake based on surveys in 1959 and 1964.

In March 1989, the T/V *Exxon Valdez* ran aground in PWS spilling almost 11 million gallons of crude oil. The oil contaminated nearly 2400 km of coastline in the GOA region extending from PWS to Kodiak Island, including coastlines along Katmai National Park and Preserve (KATM) and Kenai Fjords National Park (KEFJ). Hundreds of thousands of birds and mammals were killed, including several thousand sea otters and an untold numbers of fishes and invertebrates (Spies et al. 1996). The spill and the associated cleanup of shorelines resulted in a major restructuring of the intertidal community (Highsmith et al. 1994, Dean et al. 1996, Jewett et al. 1999, Dean and Jewett 2001). While some of the nearshore system communities within much of the spill area recovered within several years (e.g., Dean and Jewett 2001), some impacts in heavily oiled portions of PWS persisted for 18 yr or more (Fukuyama 2000, Peterson et al. 2003, Short et al. 2006). Exposure to lingering oil continued through 2005 for Barrow's goldeneyes (*Bucephala islandica*) (Esler et al. 2011) and through 2011 for harlequin ducks (*Histrionicus histrionicus*) (Esler and Ballachey 2014). For sea otters and harlequin ducks, exposure to oil was linked to lower survival, as population densities remained suppressed in oiled areas of PWS through at least 2007 for sea otters (Monson et al. 2000*a*, 2011, Ballachey et al. 2014) and 2005 for harlequin ducks (Iverson and Esler 2010).

Over the past decades, there have undoubtedly been additional changes in the nearshore GOA that resulted from both human activities (e.g., logging activity, shoreline development, fishing pressure) and natural events (e.g., ice scour, storm events, and ocean climate). We suspect that many of these changes have largely gone undocumented or have occurred over smaller spatial and/or temporal scales than those related to recolonization by sea otters, earthquakes, or the EVOS.

METHODS

Designing the monitoring plan

The vital signs monitoring program was initiated by the National Park Service (NPS) to provide long-term monitoring of a key set of high-priority natural resource conditions. Vital signs are defined as a "subset of physical, chemical, and biological elements and processes of park ecosystems that are selected to represent the overall health or condition of NPS resources, known or hypothesized effects of stressors, or elements that have important human values" (Bennett et al. 2006). The following sections provide an overview of the nearshore monitoring program in the central GOA initiated in 2006 under the NPS Southwest Alaska Network Inventory and Monitoring Program and subsequently adopted by the Gulf Watch Alaska Program and the EVOS Trustee Council (Dean et al. 2014). The goals of this program are to detect changes that occur within the central GOA nearshore system over the next several decades, to help identify the potential causes for change, and to provide this information to resource managers and to the public in order to preserve the nearshore resources. The program focuses on the portion of central GOA from KATM eastward to KEFJ and western PWS (WPWS) (Fig. 2), areas previously affected by EVOS. The program is designed to detect changes that occur on spatial scales of several kilometers of coastline or larger, and on temporal scales of one year or more.

A food-web-based approach

The monitoring program focuses on the marine nearshore food web (Fig. 1) and encompasses key species or groups of species (i.e., vital signs) that represent all trophic levels, from primary producers to apex vertebrate and invertebrate predators. Water quality parameters (temperature and salinity) are also included in the design. Species identified as vital signs are numerically abundant, functionally important, and amenable to sampling that allows for cost-effective detection of ecologically significant levels of change over time. Where possible, we selected species with historical time series of data, thereby enhancing our ability to detect future changes. In addition, the selected species are known to be susceptible to change from a variety of anthropogenic and natural causes, and many are viewed as important by resource managers. They include macroalgae and seagrass; marine intertidal invertebrates; marine birds (in particular

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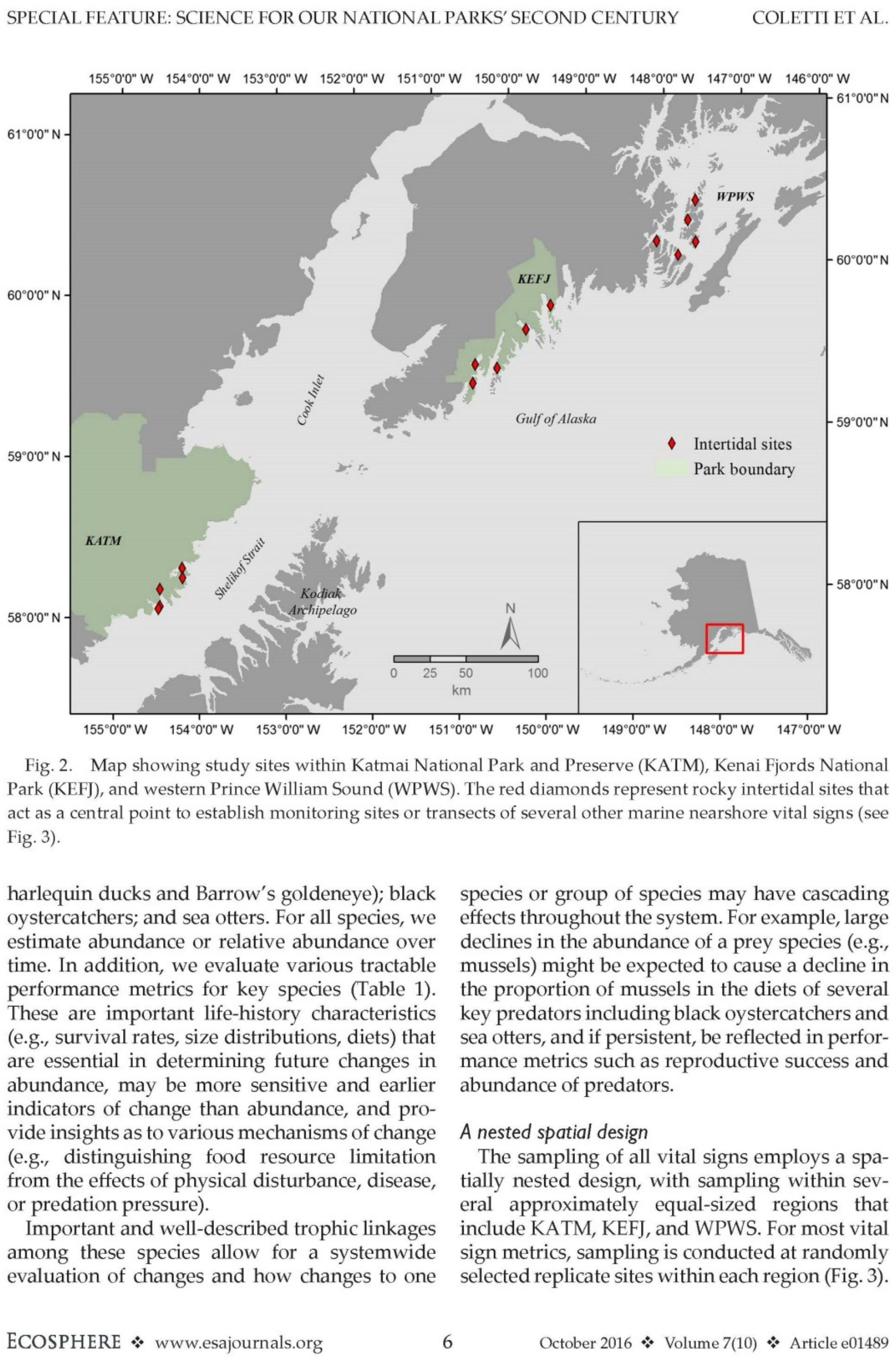

Fig. 2. Map showing study sites within Katmai National Park and Preserve (KATM), Kenai Fjords National Park (KEFJ), and western Prince William Sound (WPWS). The red diamonds represent rocky intertidal sites that act as a central point to establish monitoring sites or transects of several other marine nearshore vital signs (see Fig. 3).

harlequin ducks and Barrow's goldeneye); black oystercatchers; and sea otters. For all species, we estimate abundance or relative abundance over time. In addition, we evaluate various tractable performance metrics for key species (Table 1). These are important life-history characteristics (e.g., survival rates, size distributions, diets) that are essential in determining future changes in abundance, may be more sensitive and earlier indicators of change than abundance, and provide insights as to various mechanisms of change (e.g., distinguishing food resource limitation from the effects of physical disturbance, disease, or predation pressure).

Important and well-described trophic linkages among these species allow for a systemwide evaluation of changes and how changes to one species or group of species may have cascading effects throughout the system. For example, large declines in the abundance of a prey species (e.g., mussels) might be expected to cause a decline in the proportion of mussels in the diets of several key predators including black oystercatchers and sea otters, and if persistent, be reflected in performance metrics such as reproductive success and abundance of predators.

A nested spatial design

The sampling of all vital signs employs a spatially nested design, with sampling within several approximately equal-sized regions that include KATM, KEFJ, and WPWS. For most vital sign metrics, sampling is conducted at randomly selected replicate sites within each region (Fig. 3).

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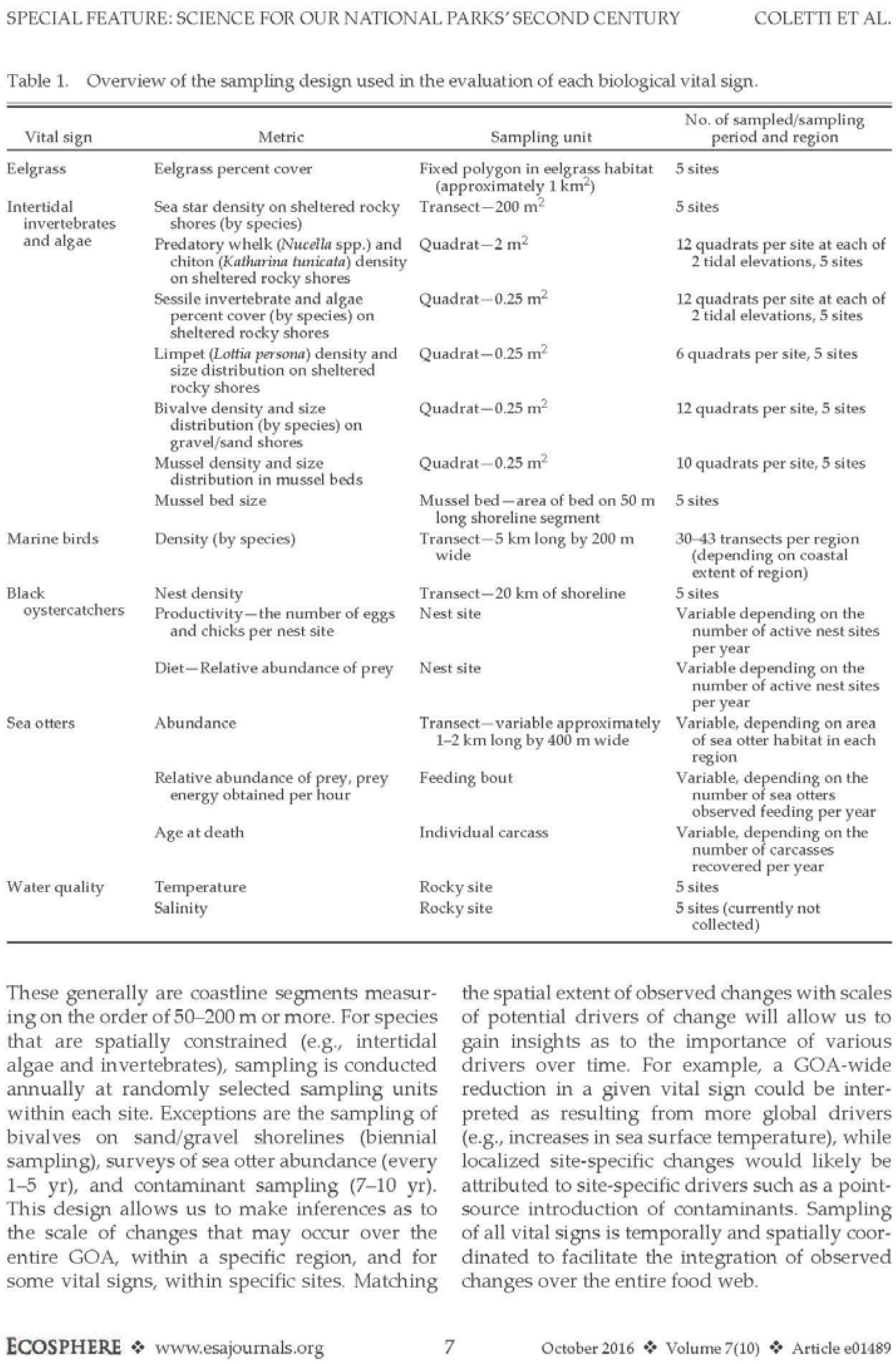

Table 1. Overview of the sampling design used in the evaluation of each biological vital sign.

Vital sign	Metric	Sampling unit	No. of sampled/sampling period and region
Eelgrass	Eelgrass percent cover	Fixed polygon in eelgrass habitat (approximately 1 km^2)	5 sites
Intertidal invertebrates and algae	Sea star density on sheltered rocky shores (by species)	Transect—200 m^2	5 sites
	Predatory whelk (*Nucella* spp.) and chiton (*Katharina tunicata*) density on sheltered rocky shores	Quadrat—2 m^2	12 quadrats per site at each of 2 tidal elevations, 5 sites
	Sessile invertebrate and algae percent cover (by species) on sheltered rocky shores	Quadrat—0.25 m^2	12 quadrats per site at each of 2 tidal elevations, 5 sites
	Limpet (*Lottia persona*) density and size distribution on sheltered rocky shores	Quadrat—0.25 m^2	6 quadrats per site, 5 sites
	Bivalve density and size distribution (by species) on gravel/sand shores	Quadrat—0.25 m^2	12 quadrats per site, 5 sites
	Mussel density and size distribution in mussel beds	Quadrat—0.25 m^2	10 quadrats per site, 5 sites
	Mussel bed size	Mussel bed—area of bed on 50 m long shoreline segment	5 sites
Marine birds	Density (by species)	Transect—5 km long by 200 m wide	30–43 transects per region (depending on coastal extent of region)
Black oystercatchers	Nest density	Transect—20 km of shoreline	5 sites
	Productivity—the number of eggs and chicks per nest site	Nest site	Variable depending on the number of active nest sites per year
	Diet—Relative abundance of prey	Nest site	Variable depending on the number of active nest sites per year
Sea otters	Abundance	Transect—variable approximately 1–2 km long by 400 m wide	Variable, depending on area of sea otter habitat in each region
	Relative abundance of prey, prey energy obtained per hour	Feeding bout	Variable, depending on the number of sea otters observed feeding per year
	Age at death	Individual carcass	Variable, depending on the number of carcasses recovered per year
Water quality	Temperature	Rocky site	5 sites
	Salinity	Rocky site	5 sites (currently not collected)

These generally are coastline segments measuring on the order of 50–200 m or more. For species that are spatially constrained (e.g., intertidal algae and invertebrates), sampling is conducted annually at randomly selected sampling units within each site. Exceptions are the sampling of bivalves on sand/gravel shorelines (biennial sampling), surveys of sea otter abundance (every 1–5 yr), and contaminant sampling (7–10 yr). This design allows us to make inferences as to the scale of changes that may occur over the entire GOA, within a specific region, and for some vital signs, within specific sites. Matching the spatial extent of observed changes with scales of potential drivers of change will allow us to gain insights as to the importance of various drivers over time. For example, a GOA-wide reduction in a given vital sign could be interpreted as resulting from more global drivers (e.g., increases in sea surface temperature), while localized site-specific changes would likely be attributed to site-specific drivers such as a point-source introduction of contaminants. Sampling of all vital signs is temporally and spatially coordinated to facilitate the integration of observed changes over the entire food web.

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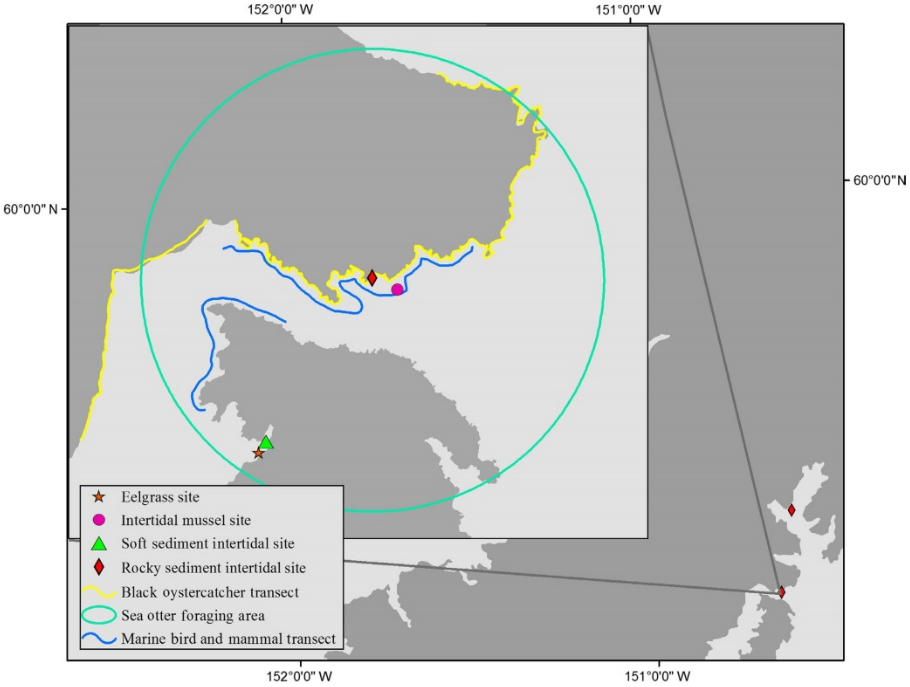

Fig. 3. A hypothetical example of the nested spatial design of the nearshore monitoring program.

Evaluation of key drivers

In addition to the biological measures, we also directly measure or evaluate data gathered by others for several key potential drivers of nearshore community structure. These include the measurement of temperature and concentrations of a suite of organic and inorganic contaminants at each intertidal site; wind, wave, and temperature data from nearby moored buoys; and estimates of sea surface temperature and chlorophyll *a* concentrations derived from satellite data. It is anticipated that temporal changes in some or all of these factors may contribute to change in the nearshore biological system. We also directly measure several relatively static physical measures. For example, we estimate the available sea otter foraging habitat (the area within each region of shallow [<40 m] water habitat where sea otters feed), slope, and substrate type within intertidal habitats, and the relative exposure to waves at intertidal sampling sites. Accounting for these relatively static physical differences (i.e., using them as covariates in future analyses) will help to improve our ability to detect meaningful temporal changes.

Detecting trends and inferring cause: sea otter populations—an example of analysis of monitoring data and its use by resource managers

The sea otter is a keystone predator in the North Pacific nearshore food web (Estes and Duggins 1995). Because of the history of human exploitation and recovery, the role sea otters play in the nearshore, and the uncertainty of their future, sea otters are an important component of the nearshore monitoring plan. Several sea otter-specific metrics, including abundance and distribution, diet and energy recovery rates, and mortality are described here. These metrics provide important information on the status of sea

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otter populations relative to the available food resources (Monson and Bowen 2015), which will enable us to differentiate top-down from bottom-up mechanism of change, and localized from broad-scale drivers of change (e.g., point-source pollutant vs. ocean climate-driven changes in prey resources).

Measurement of sea otter abundance

We estimated sea otter abundance using aerial surveys conducted from a small single engine aircraft (Bodkin and Udevitz 1999). Surveys consist of two components: (1) strip transects and (2) intensive search units to estimate the probability of detection of otters along strips. We sampled sea otter habitat in two strata: a stratum characterized by high sea otter densities generally between the shore and 40 m depth contour (although this stratum includes deepwater within the protection of bays) and a deeper water stratum offshore between the 40 and 100 m depth contours, where sea otter densities are usually lower. Survey effort is allocated proportional to expected sea otter abundance by systematically adjusting spacing of transects within each stratum. We generate population estimates by adjusting strip counts for animals not observed using the intensive searches within strips and extrapolate resulting density estimates to areas not surveyed.

Since initiating vital signs monitoring in 2006, we conducted annual summer (June to August) surveys in WPWS from 2007 through 2009 and from 2011 through 2013. We also conducted summer surveys at KATM in 2008, 2012, and 2015 and KEFJ surveys in 2007 and 2010 (Fig. 2). The area surveyed included approximately 1500 km^2 in the two NPS units and more than 2000 km^2 in WPWS. We compared sea otter abundance through time in WPWS with information from identical surveys conducted annually from 1993 through 2005 as part of EVOS studies (Bodkin et al. 2002), and in KEFJ with an identical survey conducted in 2002. In addition, while not strictly comparable, we compared sea otter abundance through time at KATM with information from helicopter surveys flown in 1989 after the EVOS (DeGange et al. 1995).

We calculated the trends in abundance over time by linear regression on the natural logs of survey counts. The slope of the line was back-transformed by the antilog to yield a discrete growth rate. Analyses were conducted in SAS statistical software (SAS Institute, Cary, North Carolina, USA).

Energy recovery rates of sea otters

We estimated the rates of food consumption by sea otters in KATM, KEFJ, and WPWS based on the (1) time of an average foraging dive; (2) time interval between dives; (3) proportion of dives that were successful in obtaining food; (4) type, number, and size of prey obtained on each successful dive; and (5) the average energy content of each prey (Dean et al. 2002). We estimated the first four measurements based on direct foraging observations made from sites along the shoreline using a 50- to 80-power spotting scope (Questar, New Hope, Pennsylvania, USA). Average energy content of prey was estimated based on published or calculated values from prey species tissues. Forage observations were made annually at KATM (2006–2015, except for 2011) and KEFJ (2007 through 2015), while in WPWS observations were made in 2007 and then annually from 2010 through 2015. We conducted all foraging work during daylight hours with the bulk of the observations made between late May and late July. We based energy conversions on expressions given in Table 3 of Dean et al. (2002) or from the values given in Cummins and Wuycheck (1971) or Wacasey and Atkinson (1987). For dives where prey type was not identified, we used maximum-likelihood methods to assign the most likely prey type based on the dive attributes associated with identified prey types, which removes the potential biases that may occur if the known dive data are not representative of missing data (Tinker et al. 2012, Tinker 2015). We estimated 95% confidence intervals for each recovery rate using Monte Carlo simulations (Manly 1991, Dean et al. 2002). We used MATLAB (MathWorks, Natick, Massachusetts, USA) for all likelihood analyses and Monte Carlo simulations.

Mortality estimates of sea otters

We estimated survival rates of sea otters in KATM and WPWS based on the age at death of beach-cast sea otters. We systematically collected beach-cast carcasses at KATM each summer (July)

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from 2006 to 2015, except for 2011, and in WPWS each spring (April) from 2006 to 2008 and from 2010 to 2015. The WPWS collections added to data from the identical carcass surveys conducted between 1976–1989 and 1990–2005 (Monson et al. 2000*a*, 2011). We also attempted to collect carcasses at KEFJ each summer (June); however, the numbers recovered were very low. We estimated the age distribution of dying otters by aging teeth collected from the recovered carcasses (Bodkin et al. 1997), and used the age-at-death distributions to estimate l_x (relative number alive at age$_x$), d_x (relative number dying between age$_x$ and age$_{x+1}$), and q_x (proportion of animals alive at age$_x$ that died between age$_x$ and age$_{x+1}$) values from life-table analysis (Caughley 1966) from which a survival function was constructed. Because of potential bias in the collection of age-0 sea otters, survival to age 1 $(1 - \mathrm{q}_x)$ was conservatively adjusted by setting it equal to an assumed preweaning survival rate (Monson et al. 2000*b*) and solving for the expected number of zero-age carcasses that could have been found had a representative number been recovered. We used life-table analysis to calculate age-specific l_x values for each year of carcasses collections, and then used the average age-specific l_x value over all years as the input into a survival model (Siler 1979). The model produced a smoothed nonlinear survival function along with 95% CIs. Models were constructed using PROC NLIN in SAS statistical software (SAS Institute). We present modeled q_x values as they are less affected by bias or assumptions concerning age-0 carcass recovery (Caughley 1966).

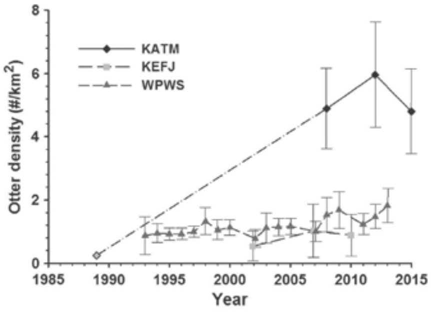

Fig. 4. Density (estimated abundance/available suitable habitat) of sea otters living in the Katmai National Park and Preserve (KATM), Kenai Fjords National Park (KEFJ), and western Prince William Sound (WPWS) study blocks. Available habitat = 1450, 1485, and 2360 km^2 for KATM, KEFJ, and WPWS, respectively. All abundance estimates are based on fixed-wing aerial surveys (Bodkin and Udevitz 1999) except for a 1989 survey of KATM (source of broken line) based on a helicopter survey (DeGange et al. 1995). The dashed line represents the rapid growth of the population. Actual trajectory is unknown between 1989 and 2008.

RESULTS

Abundance

At KATM, our first fixed-wing aerial survey in 2008 provided an abundance estimate of 7095 (SE = 922) animals, indicating that the population had expanded rapidly since 1989 when helicopter surveys estimated well below 1000 animals in the same area (DeGange et al. 1995). While not directly comparable, the 1989 population estimate indicated that the KATM population was still recovering from historical commercial fur harvest prior to 1989 (Coletti et al. 2009). The KATM sea otter population potentially peaked ca. 2012 (Fig. 4) with abundance estimates of 8644 (SE = 1243) and may have potentially declined some by 2015 when abundance was estimated at 6873 (SE = 959) otters. Overall, the KATM population has grown significantly ($P = 0.03$) at an average rate of 13% per yr since 1989. The population estimates between 2012 and 2015 are suggestive of a recent decline, but may also be interpreted as a stabilization of the population between 2008 and 2015 ($P = 0.97$). The three surveys conducted in KEFJ indicate a fairly stable, low-density population with no significant change ($P = 0.37$) between 2002 (year of first survey) and 2010. Overall, abundance estimates at KEFJ averaged 1211 (SE = 489). Abundance in WPWS reflected a continued recovery following the EVOS. We estimated a population size of 4277 (SE = 638) in 2013, which represented a doubling of sea otter densities in WPWS because the first surveys were conducted in 1993 when surveys estimated a population of 2054 (SE = 698; Bodkin et al. 2002). However, due to a lag in population recovery due to the spill (Monson et al. 2000*a*, 2011), population growth was slow although significant ($P < 0.001$), averaging 3% per

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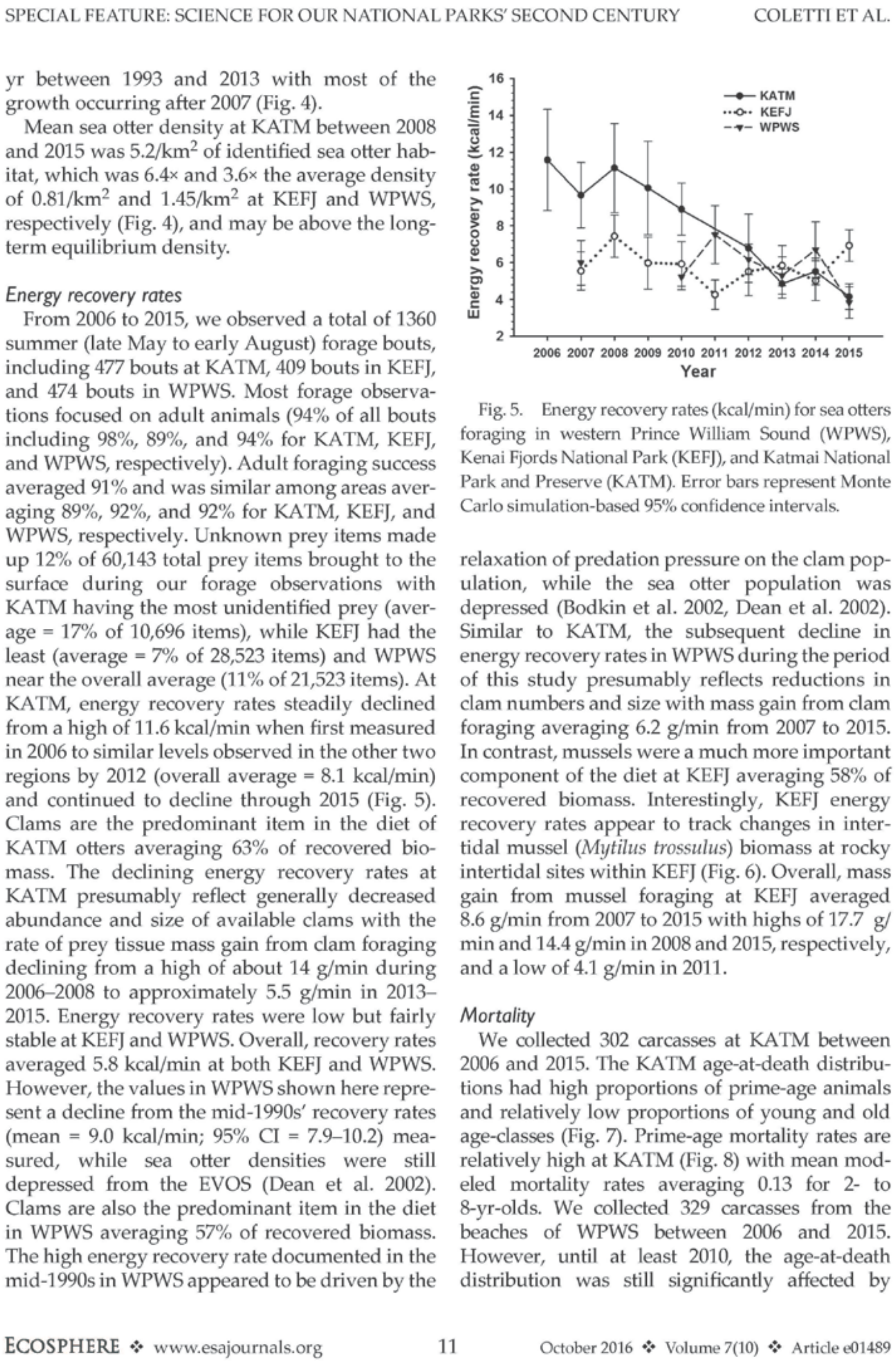

yr between 1993 and 2013 with most of the growth occurring after 2007 (Fig. 4).

Mean sea otter density at KATM between 2008 and 2015 was 5.2/km^2 of identified sea otter habitat, which was 6.4× and 3.6× the average density of 0.81/km^2 and 1.45/km^2 at KEFJ and WPWS, respectively (Fig. 4), and may be above the long-term equilibrium density.

Energy recovery rates

From 2006 to 2015, we observed a total of 1360 summer (late May to early August) forage bouts, including 477 bouts at KATM, 409 bouts in KEFJ, and 474 bouts in WPWS. Most forage observations focused on adult animals (94% of all bouts including 98%, 89%, and 94% for KATM, KEFJ, and WPWS, respectively). Adult foraging success averaged 91% and was similar among areas averaging 89%, 92%, and 92% for KATM, KEFJ, and WPWS, respectively. Unknown prey items made up 12% of 60,143 total prey items brought to the surface during our forage observations with KATM having the most unidentified prey (average = 17% of 10,696 items), while KEFJ had the least (average = 7% of 28,523 items) and WPWS near the overall average (11% of 21,523 items). At KATM, energy recovery rates steadily declined from a high of 11.6 kcal/min when first measured in 2006 to similar levels observed in the other two regions by 2012 (overall average = 8.1 kcal/min) and continued to decline through 2015 (Fig. 5). Clams are the predominant item in the diet of KATM otters averaging 63% of recovered biomass. The declining energy recovery rates at KATM presumably reflect generally decreased abundance and size of available clams with the rate of prey tissue mass gain from clam foraging declining from a high of about 14 g/min during 2006–2008 to approximately 5.5 g/min in 2013–2015. Energy recovery rates were low but fairly stable at KEFJ and WPWS. Overall, recovery rates averaged 5.8 kcal/min at both KEFJ and WPWS. However, the values in WPWS shown here represent a decline from the mid-1990s' recovery rates (mean = 9.0 kcal/min; 95% CI = 7.9–10.2) measured, while sea otter densities were still depressed from the EVOS (Dean et al. 2002). Clams are also the predominant item in the diet in WPWS averaging 57% of recovered biomass. The high energy recovery rate documented in the mid-1990s in WPWS appeared to be driven by the relaxation of predation pressure on the clam population, while the sea otter population was depressed (Bodkin et al. 2002, Dean et al. 2002). Similar to KATM, the subsequent decline in energy recovery rates in WPWS during the period of this study presumably reflects reductions in clam numbers and size with mass gain from clam foraging averaging 6.2 g/min from 2007 to 2015. In contrast, mussels were a much more important component of the diet at KEFJ averaging 58% of recovered biomass. Interestingly, KEFJ energy recovery rates appear to track changes in intertidal mussel (*Mytilus trossulus*) biomass at rocky intertidal sites within KEFJ (Fig. 6). Overall, mass gain from mussel foraging at KEFJ averaged 8.6 g/min from 2007 to 2015 with highs of 17.7 g/min and 14.4 g/min in 2008 and 2015, respectively, and a low of 4.1 g/min in 2011.

Fig. 5. Energy recovery rates (kcal/min) for sea otters foraging in western Prince William Sound (WPWS), Kenai Fjords National Park (KEFJ), and Katmai National Park and Preserve (KATM). Error bars represent Monte Carlo simulation-based 95% confidence intervals.

Mortality

We collected 302 carcasses at KATM between 2006 and 2015. The KATM age-at-death distributions had high proportions of prime-age animals and relatively low proportions of young and old age-classes (Fig. 7). Prime-age mortality rates are relatively high at KATM (Fig. 8) with mean modeled mortality rates averaging 0.13 for 2- to 8-yr-olds. We collected 329 carcasses from the beaches of WPWS between 2006 and 2015. However, until at least 2010, the age-at-death distribution was still significantly affected by

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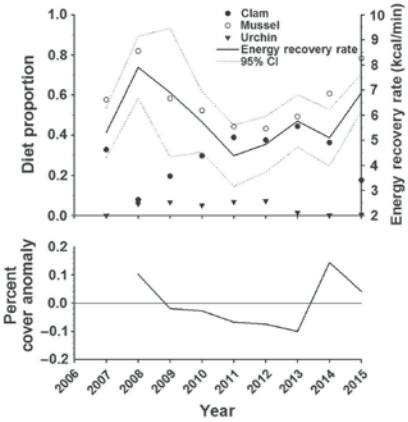

Fig. 6. Proportion of mussels in sea otter diets in Kenai Fjords National Park (KEFJ), 2007–2015 (upper graph), and percent cover anomaly of mussels in KEFJ, 2008–2015 (lower graph).

EVOS-related mortality (Monson et al. 2011, Monson 2014). Thus, we calculated survival rates only on the 263 carcasses collected from 2010 on. We also calculated a prespill survival rate from the 215 carcasses collected between 1976 and 1989 in WPWS. In general, the recent WPWS age-at-death distributions contained low proportions of prime-age animals (Fig. 7), reflecting the generally low mortality rates of this age-class (mean modeled rate = 0.08) and higher mortality rates associated with the young and old age-classes (Fig. 8).

Discussion

Conservation and management of natural resources commonly share goals of restoring or maintaining populations or ecosystems, and accomplishing these goals requires documentation of the composition and abundance of species over time. Long-term ecological monitoring provides a path toward achieving the conservation and management objectives of detecting change, with increasing power over time. In addition, ecological monitoring allows for the evaluation of mechanisms potentially responsible for that change. Appropriate management actions are predicated on the accuracy of this understanding. Above, we describe our approach in nearshore marine habitats to monitor species over time, and the use of spatial and ecological design features within the monitoring program to inform conservation and management of both the magnitude and the underlying mechanisms of change. Use of sea otter abundance, diet, and mortality data

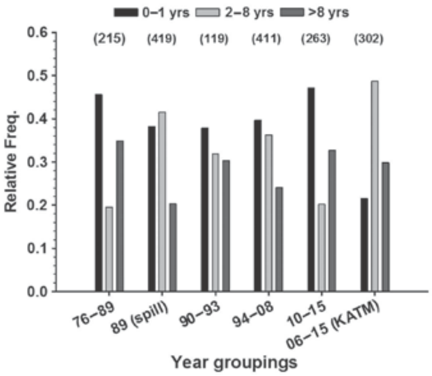

Fig. 7. Age-class structure of sea otters found dead on beaches in Western Prince William Sound prior to and after the *Exxon Valdez* oil spill (1976–2015, first five groupings; Monson 2014) and on beaches in Katmai National Park (2006–2015, last grouping). Note the number of carcasses in each grouping in parentheses above each set of bars.

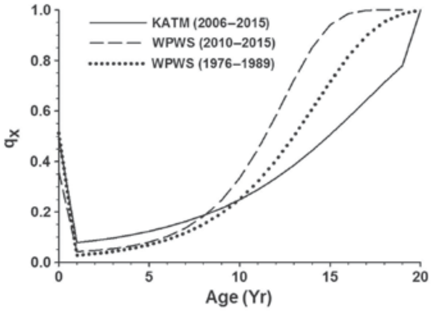

Fig. 8. Estimated mortality rates of sea otters at Katmai National Park and Preserve (KATM) 2006–2015, at western Prince William Sound (WPWS) 2010–2015, and at WPWS pre-*Exxon Valdez* oil spill (1976–1989) based on the age-at-death distributions from beach-cast carcasses.

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provides a specific example of monitoring design elements and application of complementary metrics to infer the cause(s) of a trend.

Our analysis of recent sea otter abundance at three locations in the GOA indicates populations with divergent trajectories, including growth, stability, and perhaps most recently, decline, although this will require additional surveys to verify. This spatial contrast among locations is one of the key design features of our monitoring program and suggests that mechanisms influencing sea otter abundance and trend can differ at relatively small scales. Further, these data suggest that sea otter population dynamics in the GOA currently are not being driven by large-scale (GOA-wide) factors operating more broadly. The divergent trends in sea otter abundance allow us to evaluate those trends independently, using the diet and mortality data collected concurrently at each region.

Sea otter abundance at KATM indicated a rapidly increasing population since 1989, consistent with a population expanding into the previously unoccupied habitat (Estes 1990, Bodkin et al. 1999). The increase can be explained as a consequence of the long-term recovery of sea otters in the North Pacific following their near extirpation around 1900 (Bodkin 2015). Abundance appeared quite low in 1989 when a population of only a few hundred was estimated from helicopter surveys (DeGange et al. 1995). The 1989 survey results are consistent with other historical information, indicating that very few otters occupied this habitat prior to 1989 (Coletti et al. 2009). While the overall trend for recent surveys flown between 2008 and 2015 was flat, the 2015 population estimate represented a 20% decline from 2012, when we estimated over 8600 animals inhabited the area. Additional surveys will be required to confirm whether an actual decline is in progress or whether the population is stabilizing at an equilibrium density.

Although a variety of factors can affect sea otter abundance, including harvests, fisheries, oil spills, and predation (Ballachey and Bodkin 2015), the availability of food resources is recognized as a common factor governing population status (Kenyon 1969, Monson et al. 2000*b*, Monson and Bowen 2015). While direct measurement of in situ food availability for a predator consuming more than 150 different prey species is nearly impossible, it is feasible to directly observe otters foraging. These observations allow estimation of the rate of caloric intake, which can be used to evaluate the status of the population relative to prey availability (Dean et al. 2002, Bodkin et al. 2007, Monson and Bowen 2015). Coincident with the stabilization and possible decline in sea otter abundance at KATM, we documented a decline of energy recovery of more than 50%, from 11 to 4 kcal/min of forage time. These supporting data strongly suggest that food has become a limiting resource at KATM over the past decade.

The age-at-death data derived from beach-cast sea otter carcasses from KATM suggest an underlying mechanism behind the possible decline. Generally, prime-age survival is high both in increasing and in relatively stable sea otter populations (Kenyon 1969, Monson et al. 2000*b*). However, sea otter population dynamics are quite sensitive to prime-age survival (due to female reproductive potential), and even small decreases can have a negative effect (Tinker et al. 2008). Estimated prime-age survival at KATM was 0.82, a level below that observed in California when the sea otter population ceased growing (Tinker et al. 2008). Kenyon (1969) and Bodkin et al. (2000) describe recovering populations (at Amchitka and Bering Islands, respectively) that grew to exceed carrying capacity and, after an adjustment period, stabilized. High prime-age mortality characterized the adjustment at Bering Island, where over 700 carcasses were collected in one winter (Bodkin et al. 2000). At Amchitka, a similar phenomenon of large numbers of beach-cast prime-age carcasses was coincident with a declining population (Kenyon 1969). In both cases, lack of food resources was identified as the proximate cause of the increased mortality rates based on the poor body condition of freshly recovered carcasses.

However, the age-at-death distributions have been fairly consistent through time in KATM, which is at odds with the survey and energy recovery rate data. That is, we would have expected prime-age survival to be high when we began our study and to decrease through time as energy recovery rates declined and abundance stabilized. This mismatch warrants further investigation. Regardless, at KATM, we have age-at-death distributions indicating relatively high prime-age mortality that, in combination with declining energy recovery rates (to levels typical

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of food-limited populations), suggests a population that has reached or exceeded carrying capacity. At best, the population is stabilizing near a state of equilibrium with prey populations, and at worst, it has exceeded carrying capacity and may decline in future years to some new equilibrium density. The energy recovery rate information was particularly informative in this case as it suggests that the stabilization or potential decline in abundance is likely not related to the top-down driven declines that have affected sea otter populations living further west along the Aleutian Archipelago (Estes et al. 1998).

Sea otter abundance surveys conducted in KEFJ indicate a fairly stable, low-density population with no significant change between 2002 (year of first survey) and 2010. We also have shown that energy recovery rates at KEFJ have been low, but stable since 2007, consistent with a population near carrying capacity. Interestingly, the diet composition of the KEFJ sea otter population contains a uniquely high proportion of intertidal mussels compared with other populations. Presumably, this unique diet is explained in part by the limited amount of suitable soft sediment subtidal habitat within the steep and deep fjord habitats of KEFJ. Consistent with the sea otter diet data, intertidal mussel densities and standing stock biomass we have observed are a magnitude higher at KEFJ in comparison with KATM and WPWS (Coletti et al. 2014). Thus, KEFJ appears to both provide optimal mussel habitat capable of supporting at least a low-density sea otter population with relatively limited subtidal clam habitat available as alternate prey when mussel densities are at their lowest (Fig. 6). This result suggests that a local disturbance (e.g., an oil spill) or a large-scale environmental change (e.g., due to ocean acidification) that reduces intertidal mussel abundance in KEFJ could have a profound effect on the sea otter carrying capacity.

The monitoring program we describe here is in part the result of long-term studies of the effects and recovery of the nearshore from the 1989 EVOS. Many design features employed in our program resulted from efforts to understand the underlying mechanisms responsible for the protracted recovery of sea otters in WPWS from the 1989 spill. Although prespill abundance data were lacking, total sea otter mortality may have been several thousand (Garrott et al. 1993, DeGange et al. 1994, Garshelis and Estes 1997), with most mortality and delayed recovery limited to a relatively small area in WPWS. This reduction in sea otter numbers appeared to lessen the predation pressure on primary prey species, and by the mid-1990s, clam numbers and size distributions were greater in the areas with depressed numbers of sea otters compared with an unaffected (unoiled) area (Dean et al. 2002). As a result of increasing prey populations, energy intake rates of sea otters were also higher and suggested that the lack of recovery within the most heavily oiled areas was not due to the lack of food resources (Bodkin et al. 2002, Dean et al. 2002). Age-at-death data further demonstrated that higher-than-normal prime-age mortality rates observed in areas most affected by oil could explain the lack of recovery (Monson et al. 2000*a*, 2011). Sea otter abundance in WPWS began to increase in the mid-2000s, eventually resulting in an approximate doubling of sea otter densities in WPWS since 1993 (Bodkin et al. 2014). Coincident with the numerical recovery of sea otters, we report here a subsequent decline in energy recovery rates similar to the rates elsewhere in the GOA, and a return to age-at-death distributions observed prior to the spill. Collectively, these findings indicate that sea otters in WPWS are now driven more by food limitation and less by the lingering effects of the oil spill.

Management implications

Conservation of natural resources is typically aimed at restoring or maintaining populations or ecosystems, which requires ongoing documentation of the composition, distribution, and abundance of species over time. Long-term ecological monitoring provides a path toward achieving management goals of detecting change, with increasing power over time. In addition to detecting change, a desirable attribute of ecological monitoring is acquisition of information that allows the evaluation of mechanisms potentially responsible for observed change. Appropriate management actions are predicated on the accuracy of this understanding.

In addition to illustrating analytical approaches and the value of utilizing multiple metrics in ecological monitoring, we also demonstrate here how our nearshore monitoring program has provided analyses and interpretation to meet

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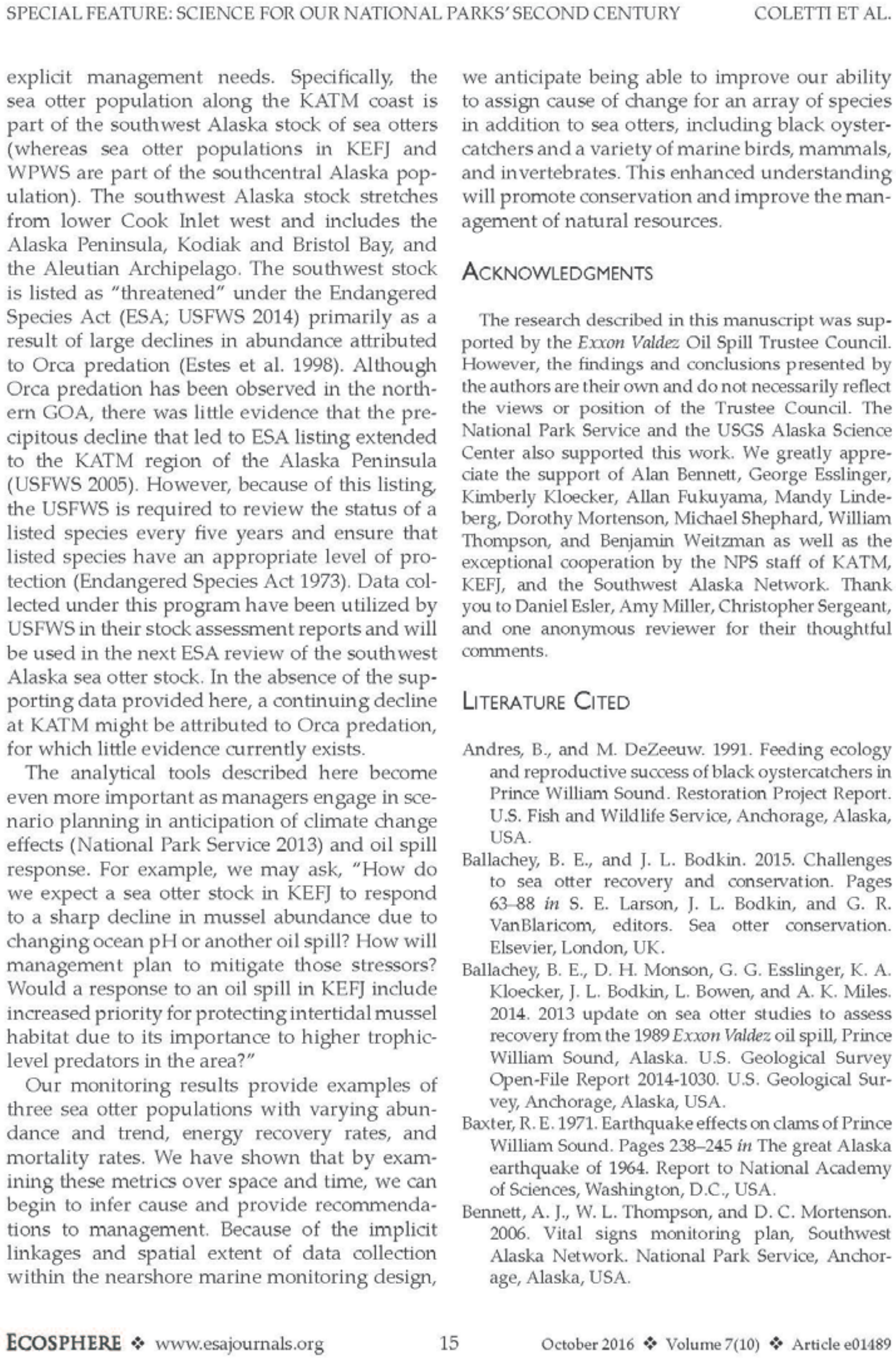

explicit management needs. Specifically, the sea otter population along the KATM coast is part of the southwest Alaska stock of sea otters (whereas sea otter populations in KEFJ and WPWS are part of the southcentral Alaska population). The southwest Alaska stock stretches from lower Cook Inlet west and includes the Alaska Peninsula, Kodiak and Bristol Bay, and the Aleutian Archipelago. The southwest stock is listed as "threatened" under the Endangered Species Act (ESA; USFWS 2014) primarily as a result of large declines in abundance attributed to Orca predation (Estes et al. 1998). Although Orca predation has been observed in the northern GOA, there was little evidence that the precipitous decline that led to ESA listing extended to the KATM region of the Alaska Peninsula (USFWS 2005). However, because of this listing, the USFWS is required to review the status of a listed species every five years and ensure that listed species have an appropriate level of protection (Endangered Species Act 1973). Data collected under this program have been utilized by USFWS in their stock assessment reports and will be used in the next ESA review of the southwest Alaska sea otter stock. In the absence of the supporting data provided here, a continuing decline at KATM might be attributed to Orca predation, for which little evidence currently exists.

The analytical tools described here become even more important as managers engage in scenario planning in anticipation of climate change effects (National Park Service 2013) and oil spill response. For example, we may ask, "How do we expect a sea otter stock in KEFJ to respond to a sharp decline in mussel abundance due to changing ocean pH or another oil spill? How will management plan to mitigate those stressors? Would a response to an oil spill in KEFJ include increased priority for protecting intertidal mussel habitat due to its importance to higher trophic-level predators in the area?"

Our monitoring results provide examples of three sea otter populations with varying abundance and trend, energy recovery rates, and mortality rates. We have shown that by examining these metrics over space and time, we can begin to infer cause and provide recommendations to management. Because of the implicit linkages and spatial extent of data collection within the nearshore marine monitoring design, we anticipate being able to improve our ability to assign cause of change for an array of species in addition to sea otters, including black oystercatchers and a variety of marine birds, mammals, and invertebrates. This enhanced understanding will promote conservation and improve the management of natural resources.

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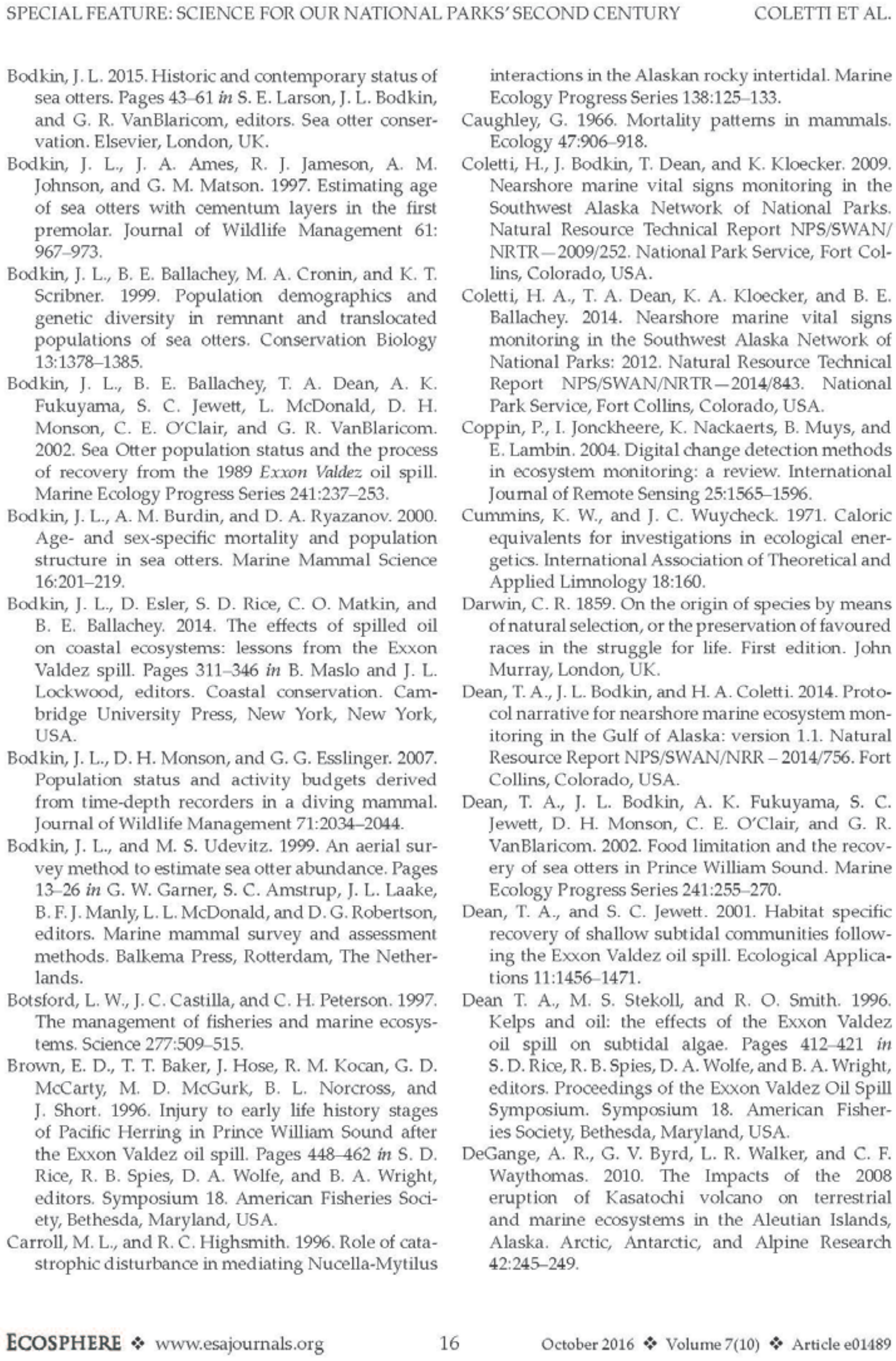

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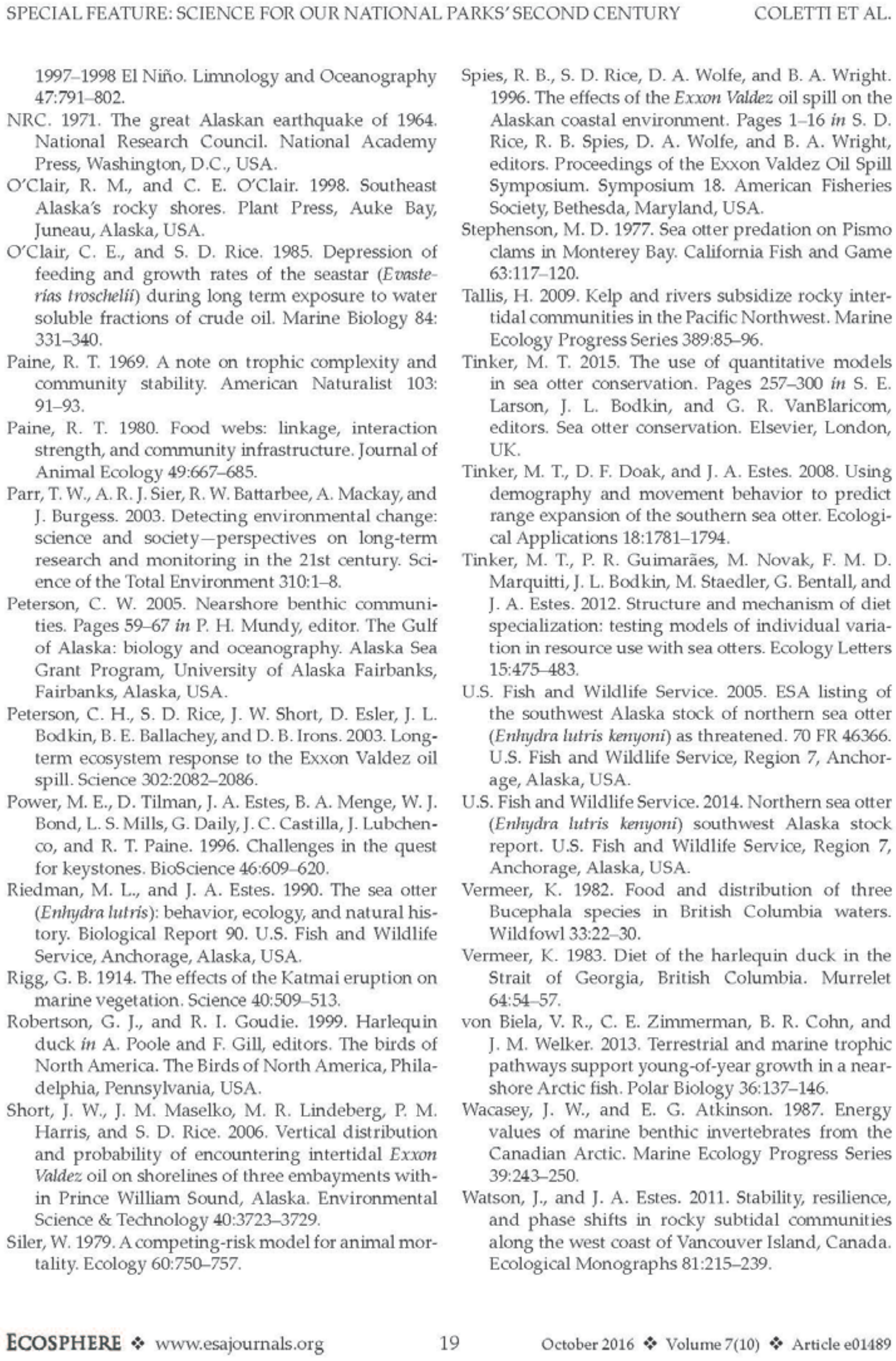

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Appendix A

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Appendix B

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Variation in abundance of Pacific Blue Mussel (*Mytilus trossulus*) in the Northern Gulf of Alaska, 2006–2015

James L. Bodkin[a,*], Heather A. Coletti[b], Brenda E. Ballachey[a], Daniel H. Monson[a], Daniel Esler[a], Thomas A. Dean[c]

[a] *US Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA*
[b] *US National Park Service, Inventory and Monitoring Program, Southwest Alaska Network, 4175 Geist Road, Fairbanks, AK 99709, USA*
[c] *Coastal Resource Associates, 1948 Kellogg Avenue, Carlsbad, CA 92008, USA*

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ABSTRACT

Mussels are conspicuous and ecologically important components of nearshore marine communities around the globe. Pacific blue mussels (*Mytilus trossulus*) are common residents of intertidal habitats in protected waters of the North Pacific, serving as a conduit of primary production to a wide range of nearshore consumers including predatory invertebrates, sea ducks, shorebirds, sea otters, humans, and other terrestrial mammals. We monitored seven metrics of intertidal Pacific blue mussel abundance at five sites in each of three regions across the northern Gulf of Alaska: Katmai National Park and Preserve (Katmai) (2006–2015), Kenai Fjords National Park (Kenai Fjords) (2008–2015) and western Prince William Sound (WPWS) (2007–2015). Metrics included estimates of: % cover at two tide heights in randomly selected rocky intertidal habitat; and in selected mussel beds estimates of: the density of large mussels (≥ 20 mm); density of all mussels ≥ 2 mm estimated from cores extracted from those mussel beds; bed size; and total abundance of large and all mussels, i.e. the product of density and bed size. We evaluated whether these measures of mussel abundance differed among sites or regions, whether mussel abundance varied over time, and whether temporal patterns in abundance were site specific, or synchronous at regional or Gulf-wide spatial scales. We found that, for all metrics, mussel abundance varied on a site-by-site basis. After accounting for site differences, we found similar temporal patterns in several measures of abundance (both % cover metrics, large mussel density, large mussel abundance, and mussel abundance estimated from cores), in which abundance was initially high, declined significantly over several years, and subsequently recovered. Averaged across all sites, we documented declines of 84% in large mussel abundance through 2013 with recovery to 41% of initial abundance by 2015. These findings suggest that factors operating across the northern Gulf of Alaska were affecting mussel survival and subsequently abundance. In contrast, density of primarily small mussels obtained from cores (as an index of recruitment), varied markedly by site, but did not show meaningful temporal trends. We interpret this to indicate that settlement was driven by site-specific features rather than Gulf wide factors. By extension, we hypothesize that temporal changes in mussel abundance observed was not a result of temporal variation in larval supply leading to variation in recruitment, but rather suggestive of mortality as a primary demographic factor driving mussel abundance. Our results highlight the need to better understand underlying mechanisms of change in mussels, as well as implications of that change to nearshore consumers.

1. Introduction

Occupying a thin strip of habitat between expansive oceanic and terrestrial habitats around the globe, we find intertidal ecosystems. These intertidal systems occupy a unique ecological position, being essentially terrestrial for a part of each day as the tide recedes and aquatic as they are covered again by the rising tide. Most of the biological activity associated with growth and reproduction in the community of intertidal organisms occurs while in the aquatic state. However, some of the physical and ecological processes affecting survival, such as predation or environmental stress, also occur within the community in its terrestrial state. In particular, the suite of primary consumers in the intertidal are subjected to an abundant and diverse assemblage of predators, both marine and terrestrial.

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[*] Correspondence to: 92 West Vancouver Drive, Port Townsend, WA 98368, USA.
E-mail address: jldbodkin@gmail.com (J.L. Bodkin).

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The predictable transition between aquatic and terrestrial states in the intertidal has facilitated decades of research on processes that structure communities. Ecological processes clarified through intertidal studies include both abiotic factors [e.g. habitat structure, nutrients, and disturbance (Dayton, 1971; Hunt and Scheibling, 1996; Menge et al., 2003; Menge et al., 2009)] and biotic factors [e.g. recruitment, disturbance, competition, and predation (Connell, 1961; Connell, 1972; Paine, 1966; Estes and Palmisano, 1974; Branch, 1984; Gaines and Roughgarden, 1985; Lewin, 1986; Carroll and Highsmith, 1996)]. The ability to access and impose rigorous experimental design in the intertidal has been instrumental in advancing our understanding of ecosystem dynamics (Connell, 1961; Paine, 1977; Menge, 2000; Menge and Branch, 2001).

Sessile and slightly motile filter-feeding invertebrates such as barnacles and mussels occupy a central place in the food webs of intertidal communities throughout the world (Seed and Suchanek, 1992; Menge and Branch, 2001; Blanchette and Gaines, 2007). They are critical components in energy transfer from primary producers, predominantly nearshore algae but also phytoplankton (Bustamante and Branch, 1996), to larger consumers that include predatory snails, crustaceans, sea stars, fish, sea ducks, shorebirds, and mammals (Webster, 1941; Gaines and Roughgarden, 1987; Menge, 1987; Goudie and Ankney, 1986; Marsh, 1986; Menge, 1992; O'Clair and O'Clair, 1998). In particular, several species of mussel (*Mytilus spp.)* are abundant and conspicuous members of intertidal communities along nearly all North Pacific coastlines. They are widely recognized as foundation species, having the potential to dramatically affect communities and ecosystems, as they can alter habitats through construction of complex three dimensional beds, and can link benthic and pelagic systems through filtration of the water column and deposition in the benthos (Seed and Suchanek, 1992). They are a critical source of food for higher trophic levels and often a dominant competitor for space where substrate is limiting (Paine, 1974; Branch, 1984; Petersen, 1984).

Pacific blue mussels (*Mytilus trossulus*) are widespread in the intertidal zone throughout the Gulf of Alaska (GOA). They occur along sheltered shorelines on both rocky and unconsolidated substrates, where along with a variety of barnacles, the brown alga *Fucus distichus*, and other benthic marine algae, they are dominant occupiers of space (Feder and Keiser, 1980; Klinger and Fukuyama, 2011; O'Clair and Zimmerman, 1986). In the absence of predation or disturbance, *M. trossulus* can form near monotypic stands within the middle intertidal zone (O'Clair and Zimmerman, 1986). However, mussel beds can be highly dynamic due to the competing factors of variation in recruitment processes and subsequent removal by an array of both marine and terrestrial predators and physical disturbance such as strong wave action, ice scour, and stress due to extreme warm or cold temperatures (Seed and Suchanek, 1992; O'Clair and O'Clair, 1998). Blue mussels are a key component of intertidal communities in the northern GOA, as they are potentially dominant in the system and provide critical food resources to nearshore predators, including several species of conservation concern.

Mussel predators in the GOA include the sea otter (*Enhydra lutris*), the black oystercatcher (*Haematopus bachmani*) and Barrow's goldeneye (*Bucephala islandica*). The sea otter is listed under the IUCN as "Endangered" and the SW stock (*E.L. kenyoni*) that occurs along the Katmai coast of Alaska is listed under the ESA as "Threatened" (USFWS, 2013). The black oystercatcher is considered a focal species of conservation concern in the US and Canada, including Alaska (Tessler et al., 2007). Barrow's goldeneye is recognized as a species of special concern in eastern Canada under the Species at Risk Act. Given the central role of mussels as a source of energy for higher trophic level consumers, information on changes of mussel populations over time should lead to an improved understanding of how prey availability contributes to variation in abundance of consumers, particularly those of conservation concern.

Nearshore communities, including intertidal mussels, were impacted by the 1989 Exxon Valdez oil spill, and were important in both injury assessment and recovery monitoring in the Gulf of Alaska (Highsmith et al., 1996). As part of the US National Park Service's Inventory and Monitoring Program and the *Exxon Valdez* Gulf Watch Alaska Program we have been monitoring nearshore ecosystems since 2006 (Dean et al., 2014; Coletti et al., 2016). Here, we evaluate mussel abundance data derived from monitoring conducted in the northern GOA between 2006 and 2015 and discuss potential implications of our findings to mussel predators. Specifically, our objectives are to use multiple data sets to evaluate variation in mussel abundance and determine effects of: (1) space, contrasting site and regional effects, (2) time, considering mussel variation as linear and curvilinear trends, and (3) interactions of space and time, to determine whether observed trends were synchronous across sites, regions, or the northern GOA.

2. Study area

We examined temporal and spatial patterns of mussel abundance using data from three regions: Katmai National Park and Preserve (Katmai), Kenai Fjords National Park (Kenai Fjords) and western Prince William Sound (WPWS, Fig. 1). These regions span > 500 km of the northern GOA and include a diverse geography. Katmai lies on the Alaska Peninsula and is characterized by broad shallow bays, with large tidal influences from Cook Inlet and Shelikof Strait that contribute to high productivity in coastal waters. Kenai Fjords is located on the Kenai Peninsula and contains both open outer coast headlands and deep fjords whose watersheds are predominately glacier fed. Shallow habitats within Kenai Fjords are generally limited to the narrow band along the steep shoreline and glacial moraines near the heads of most fjords. Prince William Sound is a semi-enclosed sea with abundant freshwater inputs, bordered by several large islands that shelter the Sound from the GOA. Western Prince William Sound includes a complex coastline with many islands within its interior and glacial-cut fjords along its northern and western boundaries.

3. Methods

We have been monitoring nearshore ecosystems in the Gulf of Alaska since 2006 (Dean et al., 2014). Included in this program are two standard operating procedures (SOPs) that provide data appropriate for assessing abundance of Pacific blue mussels in the northern Gulf of Alaska (Dean and Bodkin, 2011; Bodkin et al., 2016). Both SOPs were peer-reviewed and published under the National Park Service Inventory and Monitoring Program (Dean et al., 2014) and are summarized below.

3.1. Sampling of mussels at randomly selected rocky intertidal sites

We measured percent cover of mussels (and other sessile invertebrates and algae) at 5 randomly selected sites in sheltered rocky habitats within each of the three regions (Fig. 1). Shorelines categorized as sheltered rocky geomorphologic types were identified based on Environmentally Sensitive Index (ESI) maps produced for each region (RPI 1983a, 1983b, 1985, 1986) and sampling sites within this habitat type were selected using generalized random tessellation stratified (GRTS) sampling (McDonald, 2004; Stevens Jr and Olsen, 2004), which provided a random yet spatially balanced distribution of sites within each of the three regions. Sampling at each site was conducted during spring tides in June and July. Sampling at Katmai began in 2006 and was done annually thereafter through 2015 except for 2011. At Kenai Fjords, annual sampling was done from 2008–2015, while sampling in WPWS occurred in 2007, and then annually from 2010–2015.

At each site and sampling year, we estimated percent cover of mussels within fixed 50 m transects placed at 0.5 m and 1.5 m above mean lower low water (MLLW). In each year, we sampled cover within

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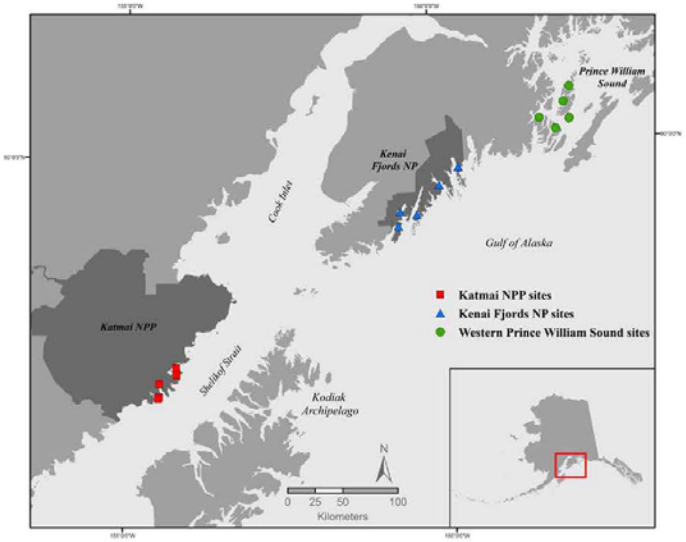

Fig. 1. Location of randomly selected sheltered rocky intertidal sites at three regions within the northern Gulf of Alaska where percent cover of mussels were estimated at tidal elevations of +0.5 and +1.5 m from 2006–2015. Mussel bed sampling occurred at nearby sites where > 50 m of contiguous mussels were present near randomly selected sites.

twelve 0.25 m^2 quadrats at each tidal elevation. The twelve quadrats were systematically positioned along transects starting from a random start point uniquely selected each year (i.e. different quadrats are sampled each year). Within quadrats, we determined presence or absence of mussels, and percent cover was calculated based on the proportion of points occupied by mussels.

For analysis (see below), we averaged the proportion of points with mussels across quadrats at each tidal elevation, within each year and site, added a constant (0.01), and arcsine square-root transformed the result, to avoid violations of assumptions of general linear models when using proportions. Results were back-transformed for presentation.

3.2. *Mussel bed sampling*

In addition to the rocky intertidal sites, we sampled mussel beds in close proximity to the rocky sites. Mussel beds were identified as areas with mussels that were contiguous (< 1 m gap between mussels) over a > 50-m long section of shoreline, and located nearest to the randomly selected rocky sites (generally within 1 km or less, Fig. 1). Within each of these 15 mussel beds (5 per region), we measured mussel density, mussel bed size, and mussel abundance. We began sampling in 2008 at both Katmai and Kenai Fjords and in 2010 at WPWS, and annually thereafter except at Katmai where there was no sampling in 2011. Within selected mussel beds, we estimated the size of the mussel bed, the density of mussels ≥ 20 mm in length, and the density of all mussels ≥ 2 mm. We distinguished larger (≥ 20 mm) mussels because black oystercatchers and sea otters generally consume mussels of larger size (Cayford and Goss-Custard, 1990; Dean et al., 2002; Hartwick, 1976; VanBlaricom, 1988; Webster, 1941).

3.3. *Bed size*

At each mussel bed site, we established a fixed horizontal 50-m transect near the upper elevation of the mussel distribution. We then established ten systematically placed vertical transects along the horizontal transect using a random start point uniquely selected each year. Vertical transects extended from the top of the mussel bed (i.e. could extend above the horizontal transect) to MLLW. Along each vertical transect, we estimated the upper and lower boundaries of the bed by noting the presence or absence of mussels under the vertical transect tape (i.e. ~15 mm width). Lower mussel bed boundaries were defined by the last mussel under the tape or by a gap of > 1 m in which no mussels were found (i.e. mussels occurring below any 1 m gap were not considered in the bed). Bed size is represented by the average of the lengths (in m) of the 10 vertical transects. We used the product of the average transect length and the 50 m horizontal transect length to estimate bed area (in m^2) annually for each site. Bed area was then used to estimate mussel abundance (see 3.5 below).

3.4. *Mussel density within selected mussel beds*

We estimated mussel density from ten quadrats, with one placed along each of the ten vertical transects. The position of each quadrat was randomly selected as a proportional distance from the upper to the lower boundary of the mussel band, as defined above, for each vertical transect. The density of larger (≥ 20 mm length) mussels was estimated in each quadrat, with quadrat size ranging between 0.004 and 1 m^2 to accommodate the wide range in mussel densities observed (i.e. at the time of sampling, quadrat size was selected to contain about 20 or more mussels of ≥ 20 mm per quadrat). Once quadrat size was determined, all mussels ≥ 20 mm within the quadrat were collected and counted to determine density (expressed as number·m^{-2}). In addition, we collected and counted all mussels ≥ 2 mm from within smaller "cores", using a 51-mm interior diameter section of pipe (to give area sampled of 0.002 m^2) placed just outside the upper left margin of each quadrat used for sampling larger mussels. The cores extracted from mussel beds provide an estimate of density of mussels of all size classes, including newly settled mussels, and help to identify spatial and temporal variability in mussel recruitment events. However, initial settlement often occurs very low in the intertidal, often on algae and below the mussel bed (Seed and Suchanek, 1992), thus densities obtained from cores likely reflect mussel abundance after secondary settlement has occurred.

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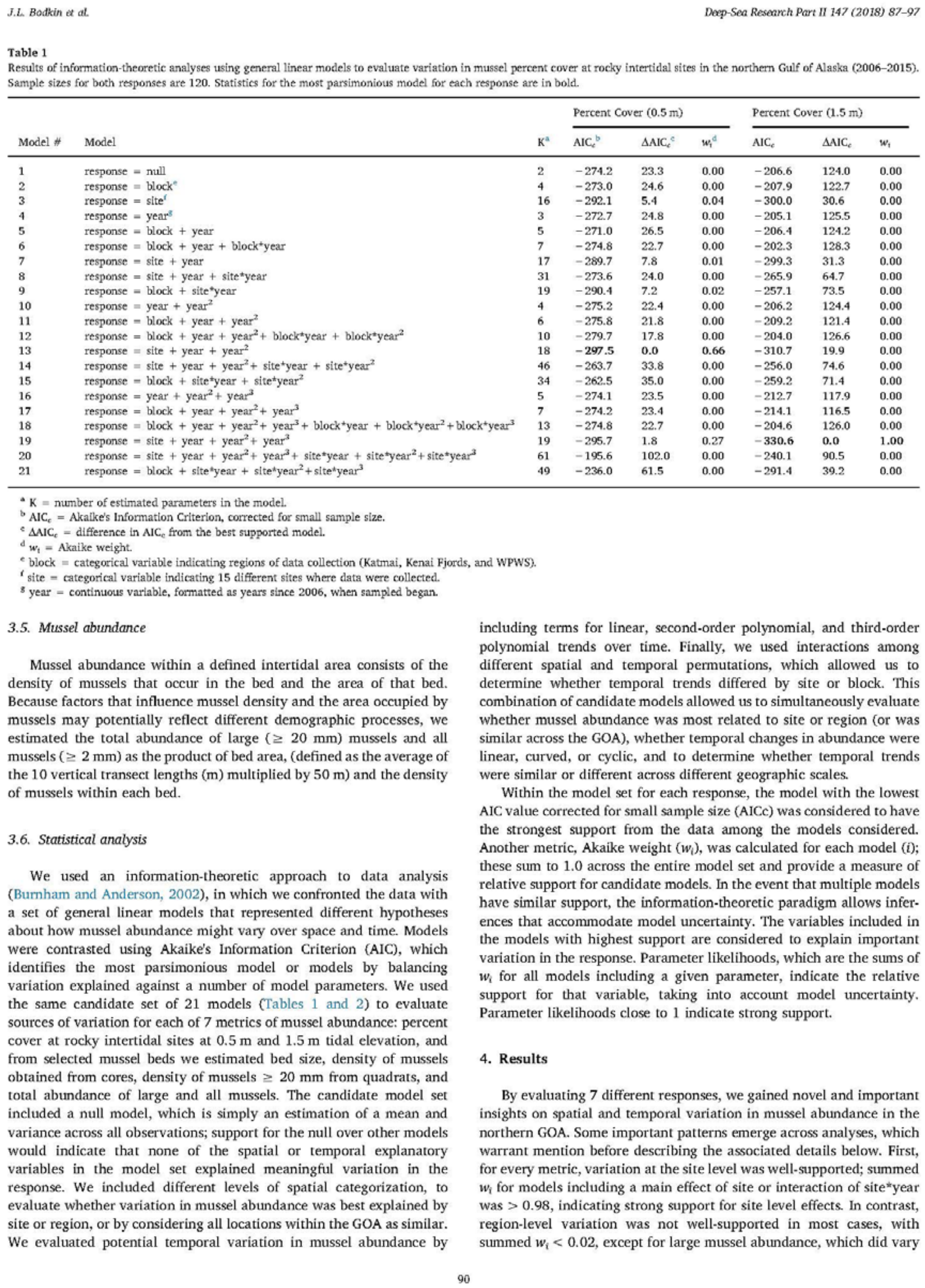

Table 1
Results of information-theoretic analyses using general linear models to evaluate variation in mussel percent cover at rocky intertidal sites in the northern Gulf of Alaska (2006–2015). Sample sizes for both responses are 120. Statistics for the most parsimonious model for each response are in bold.

			Percent Cover (0.5 m)			Percent Cover (1.5 m)		
Model #	Model	K[a]	AIC$_c$[b]	ΔAIC$_c$[c]	w_i[d]	AIC$_c$	ΔAIC$_c$	w_i
1	response = null	2	−274.2	23.3	0.00	−206.6	124.0	0.00
2	response = block[e]	4	−273.0	24.6	0.00	−207.9	122.7	0.00
3	response = site[f]	16	−292.1	5.4	0.04	−300.0	30.6	0.00
4	response = year[g]	3	−272.7	24.8	0.00	−205.1	125.5	0.00
5	response = block + year	5	−271.0	26.5	0.00	−206.4	124.2	0.00
6	response = block + year + block*year	7	−274.8	22.7	0.00	−202.3	128.3	0.00
7	response = site + year	17	−289.7	7.8	0.01	−299.3	31.3	0.00
8	response = site + year + site*year	31	−273.6	24.0	0.00	−265.9	64.7	0.00
9	response = block + site*year	19	−290.4	7.2	0.02	−257.1	73.5	0.00
10	response = year + year^2	4	−275.2	22.4	0.00	−206.2	124.4	0.00
11	response = block + year + year^2	6	−275.8	21.8	0.00	−209.2	121.4	0.00
12	response = block + year + year^2 + block*year + block*year^2	10	−279.7	17.8	0.00	−204.0	126.6	0.00
13	response = site + year + year^2	18	**−297.5**	**0.0**	**0.66**	−310.7	19.9	0.00
14	response = site + year + year^2 + site*year + site*year^2	46	−263.7	33.8	0.00	−256.0	74.6	0.00
15	response = block + site*year + site*year^2	34	−262.5	35.0	0.00	−259.2	71.4	0.00
16	response = year + year^2 + year^3	5	−274.1	23.5	0.00	−212.7	117.9	0.00
17	response = block + year + year^2 + year^3	7	−274.2	23.4	0.00	−214.1	116.5	0.00
18	response = block + year + year^2 + year^3 + block*year + block*year^2 + block*year^3	13	−274.8	22.7	0.00	−204.6	126.0	0.00
19	response = site + year + year^2 + year^3	19	−295.7	1.8	0.27	**−330.6**	**0.0**	**1.00**
20	response = site + year + year^2 + year^3 + site*year + site*year^2 + site*year^3	61	−195.6	102.0	0.00	−240.1	90.5	0.00
21	response = block + site*year + site*year^2 + site*year^3	49	−236.0	61.5	0.00	−291.4	39.2	0.00

[a] K = number of estimated parameters in the model.
[b] AIC$_c$ = Akaike's Information Criterion, corrected for small sample size.
[c] ΔAIC$_c$ = difference in AIC$_c$ from the best supported model.
[d] w_i = Akaike weight.
[e] block = categorical variable indicating regions of data collection (Katmai, Kenai Fjords, and WPWS).
[f] site = categorical variable indicating 15 different sites where data were collected.
[g] year = continuous variable, formatted as years since 2006, when sampled began.

3.5. Mussel abundance

Mussel abundance within a defined intertidal area consists of the density of mussels that occur in the bed and the area of that bed. Because factors that influence mussel density and the area occupied by mussels may potentially reflect different demographic processes, we estimated the total abundance of large (≥ 20 mm) mussels and all mussels (≥ 2 mm) as the product of bed area, (defined as the average of the 10 vertical transect lengths (m) multiplied by 50 m) and the density of mussels within each bed.

3.6. Statistical analysis

We used an information-theoretic approach to data analysis (Burnham and Anderson, 2002), in which we confronted the data with a set of general linear models that represented different hypotheses about how mussel abundance might vary over space and time. Models were contrasted using Akaike's Information Criterion (AIC), which identifies the most parsimonious model or models by balancing variation explained against a number of model parameters. We used the same candidate set of 21 models (Tables 1 and 2) to evaluate sources of variation for each of 7 metrics of mussel abundance: percent cover at rocky intertidal sites at 0.5 m and 1.5 m tidal elevation, and from selected mussel beds we estimated bed size, density of mussels obtained from cores, density of mussels ≥ 20 mm from quadrats, and total abundance of large and all mussels. The candidate model set included a null model, which is simply an estimation of a mean and variance across all observations; support for the null over other models would indicate that none of the spatial or temporal explanatory variables in the model set explained meaningful variation in the response. We included different levels of spatial categorization, to evaluate whether variation in mussel abundance was best explained by site or region, or by considering all locations within the GOA as similar. We evaluated potential temporal variation in mussel abundance by including terms for linear, second-order polynomial, and third-order polynomial trends over time. Finally, we used interactions among different spatial and temporal permutations, which allowed us to determine whether temporal trends differed by site or block. This combination of candidate models allowed us to simultaneously evaluate whether mussel abundance was most related to site or region (or was similar across the GOA), whether temporal changes in abundance were linear, curved, or cyclic, and to determine whether temporal trends were similar or different across different geographic scales.

Within the model set for each response, the model with the lowest AIC value corrected for small sample size (AICc) was considered to have the strongest support from the data among the models considered. Another metric, Akaike weight (w_i), was calculated for each model (i); these sum to 1.0 across the entire model set and provide a measure of relative support for candidate models. In the event that multiple models have similar support, the information-theoretic paradigm allows inferences that accommodate model uncertainty. The variables included in the models with highest support are considered to explain important variation in the response. Parameter likelihoods, which are the sums of w_i for all models including a given parameter, indicate the relative support for that variable, taking into account model uncertainty. Parameter likelihoods close to 1 indicate strong support.

4. Results

By evaluating 7 different responses, we gained novel and important insights on spatial and temporal variation in mussel abundance in the northern GOA. Some important patterns emerge across analyses, which warrant mention before describing the associated details below. First, for every metric, variation at the site level was well-supported; summed w_i for models including a main effect of site or interaction of site*year was > 0.98, indicating strong support for site level effects. In contrast, region-level variation was not well-supported in most cases, with summed w_i < 0.02, except for large mussel abundance, which did vary

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Table 2

Results of information-theoretic analyses using general linear models to evaluate variation in mussel density, contiguous mussel bed width, and mussel abundance at mussel bed sites in the northern Gulf of Alaska (2008–2015). Model numbers correspond to model descriptions in Table 1. Abbreviations and definitions also correspond to Table 1, with the exception of year, which is formatted as years since 2008, when mussel bed sampling was initiated. Sample sizes for all responses are 105, with the exceptions of core density and abundance, which are 104. Statistics for the most parsimonious model for each response are in bold.

		Large Mussel Density			Mussel Core Density			Contiguous Bed Size			Large Mussel Abundance			Mussel Core Abundance		
Model #	K	AIC_c	ΔAIC_c	w_i	AIC_c	ΔAIC_c	w_i	AIC_c	ΔAIC_c	w_i	AIC_c	ΔAIC_c	w_i	AIC_c	ΔAIC_c	w_i
1	2	1586.2	155.2	0.00	2089.0	217.7	0.00	443.0	76.2	0.00	−241.5	49.8	0.00	−54.7	97.3	0.00
2	4	1557.8	126.9	0.00	2068.5	197.2	0.00	425.9	59.1	0.00	−268.6	22.7	0.00	−84.8	67.2	0.00
3	16	1435.9	4.9	0.04	**1871.3**	**0.0**	**0.59**	382.3	15.5	0.00	−280.9	10.4	0.00	−145.6	6.4	0.03
4	3	1586.9	156.0	0.00	2091.0	219.7	0.00	436.1	69.3	0.00	−245.2	46.1	0.00	−53.6	98.4	0.00
5	5	1559.8	128.8	0.00	2070.5	199.2	0.00	420.7	53.9	0.00	−269.9	21.4	0.00	−82.7	69.3	0.00
6	7	1563.9	132.9	0.00	2074.8	203.5	0.00	419.4	52.6	0.00	−271.8	19.5	0.00	−80.0	72.0	0.00
7	17	1437.8	6.9	0.02	1872.7	1.4	0.29	369.7	2.9	0.16	−283.6	7.7	0.02	−142.9	9.1	0.01
8	31	1464.5	33.5	0.00	1887.8	16.5	0.00	**366.8**	**0.0**	**0.68**	−265.0	26.3	0.00	−122.2	29.8	0.00
9	19	1491.5	60.5	0.00	1968.4	97.1	0.00	404.1	37.3	0.00	−271.1	20.2	0.00	−130.7	21.3	0.00
10	4	1586.2	155.2	0.00	2092.9	221.6	0.00	437.1	70.3	0.00	−246.6	44.7	0.00	−55.7	96.3	0.00
11	6	1559.9	128.9	0.00	2072.8	201.4	0.00	421.9	55.1	0.00	−270.4	20.9	0.00	−83.6	68.4	0.00
12	10	1567.6	136.6	0.00	2081.9	210.6	0.00	424.1	57.3	0.00	−268.3	23.0	0.00	−78.2	73.8	0.00
13	18	**1431.0**	**0.0**	**0.51**	1875.6	4.3	0.07	370.3	3.5	0.12	−284.9	6.4	0.04	−149.6	2.4	0.22
14	46	1506.1	75.1	0.00	1953.6	82.3	0.00	405.3	38.5	0.00	−252.5	38.8	0.00	−73.2	78.8	0.00
15	34	1511.1	80.2	0.00	1970.4	99.1	0.00	412.3	45.5	0.00	**−291.3**	**0.0**	**0.92**	−97.2	54.8	0.00
16	5	1588.1	157.1	0.00	2094.7	223.4	0.00	438.9	72.1	0.00	−244.9	46.4	0.00	−55.1	96.9	0.00
17	7	1561.6	130.6	0.00	2074.8	203.5	0.00	454.0	87.2	0.00	−269.0	22.3	0.00	−83.0	69.0	0.00
18	13	1574.6	143.6	0.00	2088.7	217.4	0.00	430.9	64.1	0.00	−262.1	29.2	0.00	−72.9	79.1	0.00
19	19	1431.3	0.3	0.43	1876.2	4.9	0.05	372.2	5.4	0.05	−283.3	8.0	0.02	**−152.0**	**0.0**	**0.74**
20	61	1611.5	180.5	0.00	2064.0	192.7	0.00	525.9	159.1	0.00	−184.6	106.7	0.00	45.1	197.1	0.00
21	49	1581.2	150.2	0.00	2045.1	173.8	0.00	470.3	103.5	0.00	−252.2	39.1	0.00	−22.4	129.6	0.00

by region (summed w_i = 0.92). This pattern indicates that conditions specific to relatively small spatial scales have important influences on mussel abundance. However, after accounting for site-specific variation in abundance levels, we found evidence of consistent temporal patterns of variation across most metrics, with higher abundance at the beginning and end of our sampling period and lower abundance during middle years (Fig. 2). This temporal pattern is indicative of Gulf-wide similarities in trends in abundance, suggestive of processes that are expressed across broad spatial scales. Notably, the response for which this pattern was not observed was mussel density obtained from cores, which measured variation primarily of smaller size classes; suggesting that recruitment, while highly site-specific, may not be responding to broad-scale events.

4.1. *Percent cover at rocky intertidal sites*

At the 0.5 m tidal elevation at randomly selected rocky intertidal sites, variation in percent cover was best described by model 13 (Table 1), in which percent cover varied by site and changed over time similarly across all sites following a second-order polynomial. Averaged across all years, percent cover ranged from 0.1 to 19.5%. The most parsimonious model described highest values of percent cover at the beginning and end of our study period (Fig. 3), with lowest values during 2010, 2011, and 2012. This model was well supported (w_i = 0.66), explaining a moderate amount of the variation in the data (R^2 = 0.40). Model 19, which allowed a second curve via a third-order polynomial, was the next best model (ΔAICc = 1.8, w_i = 0.27). However, the overall shape and fit of the second-best model was very similar to that of the best-supported model, and gave strong support for synchronous temporal trends across the GOA (cumulative w_i = 0.93). Models that combined data at region or GOA geographic scales were not well supported ($w_i \leq 0.02$), indicating that site effects were strong and important, irrespective of region. Also, models that allowed percent cover to vary independently through time among sites (i.e. space by time interaction terms) were not well-supported (cumulative $w_i < 0.03$).

Similar patterns were seen at the 1.5 m tidal elevation at the same rocky intertidal sites, where mussels tend to be more abundant, with averages across all years for percent cover ranging from 2–38% among sites. In this case, the most parsimonious model (model 19: Table 1) received essentially all the support relative to the other models (w_i = 1.00) and provided a good fit to the data (R^2 = 0.75). This model indicated variation in percent cover by site with consistent, third-order polynomial variation through time at all sites, with highest values in 2007, 2008 and 2015, and lowest values during 2012 and 2013 (Fig. 4).

4.2. *Contiguous bed size at mussel bed sites*

Bed size (defined here as the mean length of 10 vertical transects) varied by site, from 3.52 m to 24.02 m averaged over all years. Model 8, which allowed independent linear trends by site (Fig. 5) was the best supported model of changes through time (w_i = 0.68), and had more than 4 times the support of any other candidate model (Table 2), and fit the data well (R^2 = 0.79). The best model suggested trends in bed size ranged from steep declines to slight increases, although the overall pattern in bed width indicated declines through time (12 of 15 sites declined; Fig. 5).

4.3. *Density at mussel bed sites*

Variation in density estimates of large (≥ 20 mm) mussels at established mussel bed sites averaged from 164-5,619 m^{-2} over all years, and was best explained by model 13 (w_i = 0.51), although model 19 had similar support (w_i = 0.43; Table 2); both models explained much of the variation in the data (R^2 = 0.84 and 0.85, respectively). Each of these models included the main effect of site, indicating that density varied across sites. These models also indicated temporal trends that were consistent across all sites (cumulative w_i = 0.94). In the case of model 13, trends were described by a second-order polynomial, with high points early and late in our sampling period (Fig. 6). A similar pattern resulted from model 19, with all sites having highest densities in 2008, 2009, and 2015 and lowest densities in 2012 and 2013. In examination of the data, it is clear that 3 sites differ from the others; in particular, two sites at Kenai Fjords have much higher densities of large mussels and do not show obvious trends over time. A third site at Kenai Fjords also has higher than average densities, and a temporal pattern

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Fig. 2. Photo images of one mussel bed site (Kaflia at Katmai National Park) illustrating the magnitude and temporal trend in mussel abundance (2.a 2008), decline (2.b 2012) and recovery (2.c 2014) that was evident across the northern Gulf of Alaska.

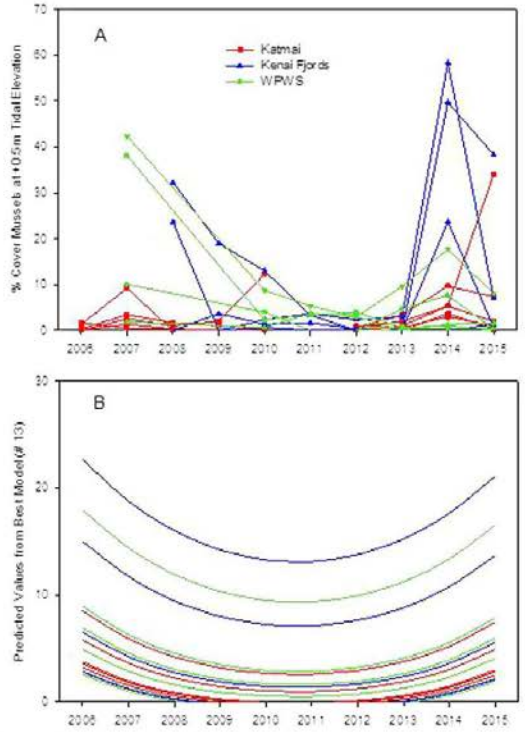

Fig. 3. Estimated (A) and modeled (B) percent cover of mussels at random sheltered rocky intertidal sites within three regions in the northern Gulf of Alaska 2006–2015 at the +0.5 m tidal elevation. Red, blue and green represent Katmai, Kenai Fjords and Western Prince William Sound, respectively.

with a peak at 2010 and subsequent declines to low densities (Fig. 6). The other 12 sites are most consistent with the general pattern described by the best-supported models.

Densities of mussels of all size classes, sampled through coring, were strongly related to site, averaging from 493-78,484 m^{-2} by site across all years, with only site as a main effect in model 3 receiving more than twice the support of any other model ($w_i = 0.59$; Table 2). This model included no variation over time (Fig. 7), and fit the data well ($R^2 = 0.91$). The next best model ($\Delta AICc = 1.4$, $w_i = 0.29$; model 7) included a linear term for year and had a slight positive slope over time at all sites, although the absolute change in density was small. Because we consider densities of smaller size classes of mussels to be an index of recruitment, we conclude that patterns observed did not display consistent trends over time, despite large differences across sites. However, in review of the data, it is apparent that in 2014 relatively high core densities occurred at multiple sites, consistent with the idea that broad-scale pulses of recruitment may occur intermittently (Fig. 7).

4.4. *Abundance at mussel bed sites*

Abundance of mussels at mussel bed sites, defined as the product of estimated density and contiguous bed area, was analyzed for both large mussels (≥ 20 mm) and all size classes (≥ 2 mm). Estimated large mussel abundance averaged from 60,226 to 2,219,456 per bed across all years. Model 15, which constrains intercepts to be the same for all sites within a region and allows trends in abundance to vary by site in a second-order curvilinear fashion, was most parsimonious (Table 2). This model was strongly supported ($w_i = 0.92$) and fit the data well ($R^2 = 0.75$). The parameter estimates from the best-supported model (Fig. 8) indicate that large mussel abundance declined at almost all sites after 2008, with subsequent increases later in the sampling period, a pattern that is consistent with large mussel density results. Averaged across regions, we estimated an 84% decline in abundance from 1,474,980 large mussels per bed in 2008 to 234,587 in 2013, subsequently increasing to 41% of 2008 values, or 608,722 large mussels per bed. A notable exception to this pattern is evident at one site in Kenai Fjords, which shows dramatic increases in abundance during the middle of our sampling period and a subsequent decline at the end of the sampling period.

Abundance of mussels based on core samples also varied by site,

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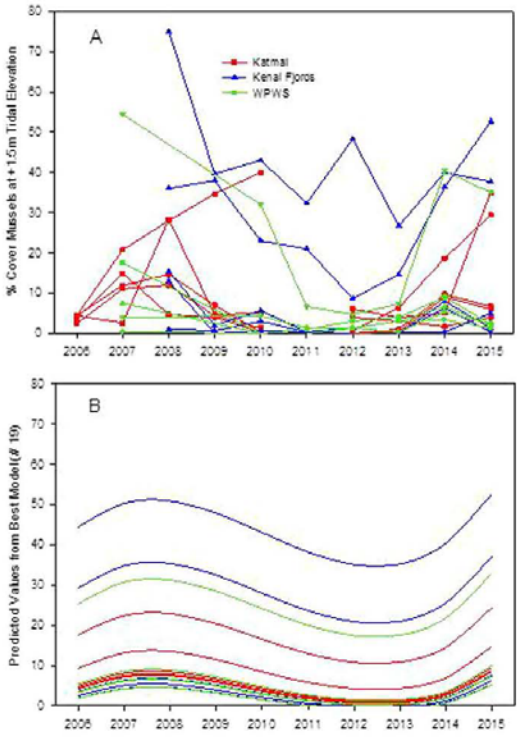

Fig. 4. Estimated (A) and modeled (B) percent cover of mussels at random sheltered rocky intertidal sites within three regions in the northern Gulf of Alaska 2006–2015 at the +1.5 m tidal elevation. Red, blue and green represent Katmai, Kenai Fjords and Western Prince William Sound, respectively.

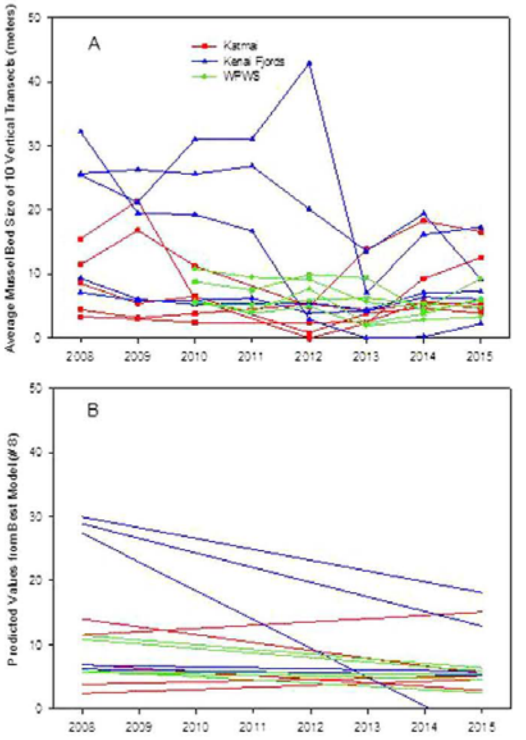

Fig. 5. Estimated (A) and modeled (B) bed size (defined as the mean of 10 vertical transect lengths across a 50 m horizontal transect) at selected sheltered intertidal sites within three regions in the northern Gulf of Alaska 2008–2015. Red, blue and green represent Katmai, Kenai Fjords and Western Prince William Sound, respectively.

with averages across all years ranging from 119,949 to 22,284,764 per bed. The best supported model (Table 2; model 19) suggested consistent third-order polynomial changes over time across all sites. This model was strongly supported ($w_i = 0.74$) and fit the data well ($R^2 = 0.74$). Based on this model, abundance was highest in 2008, at the onset of sampling, with another period of high abundance at the end of the sampling period (Fig. 9). A qualitatively similar model (model 13) was second best ($w_i = 0.22$), strengthening support for early and late peaks in total core abundance over our sampling period (cumulative $w_i = 0.96$), similar to large mussel abundance. Based on examination of the data, this is likely driven by high abundance at many sites in 2008 and 2014. Averaged across regions we estimated an 81% decline in core mussel abundance from 14,432,054 per bed in 2008 to 2,762,621 in 2013, subsequently increasing to 7,533,361, or 52% of 2008 values in 2014.

5. Discussion

A primary finding was that the abundance of mussels varied significantly among sites and we discuss various factors recognized as important to that spatial variation below. We further describe broad scale change in abundance of mussels across the Gulf of Alaska that occurred over rather short periods of time (4–8 years). Vermeij (2001) suggested that at the basin scale of the North Pacific, nearshore benthic community composition and population dynamics are driven by both the "bottom-up" processes that govern the transport of water, nutrients, productivity and larvae, and the "top-down" process of predation, that affects survival at each trophic level. Witman et al. (2003) demonstrated the role of these two processes in the Gulf of Maine, tracking a large mussel recruitment event with subsequent increases in predators and predation that eventually acted to eliminate mussels. In subsequent sections we discuss our findings in the context of these two processes, and the implication of temporal variation of the first to the second.

5.1. Spatial variation

Physical attributes such as substrate and wave exposure are widely recognized as important factors influencing species composition and abundance of organisms in benthic nearshore marine communities (Denny and Wethey, 2001; Menge and Branch, 2001; Cockrell et al., 2015), and while they can vary at relatively small spatial scales, they generally can be considered as static, varying little from year to year (Konar et al., 2016). Mussels largely rely on intertidal habitats in the GOA, and their abundance is directly influenced by substrate type and slope, which define the areal extent of potential mussel habitat (Seed and Suchanek, 1992; Hunt and Scheibling, 1996). Thus, intertidal habitats with steeper slopes will generally provide less mussel habitat, and lower mussel abundance, than areas with less slope. Exposure to wave energy is also reported as an important physical attribute contributing to variation in mussel abundance and species composition (Seed and Suchanek, 1992; O'Clair and O'Clair, 1998). Although our mussel site selection was based on proximity to sheltered rocky shorelines, variation in the degree of exposure, slope and substrate was evident and likely contributed to the high variation in mussel

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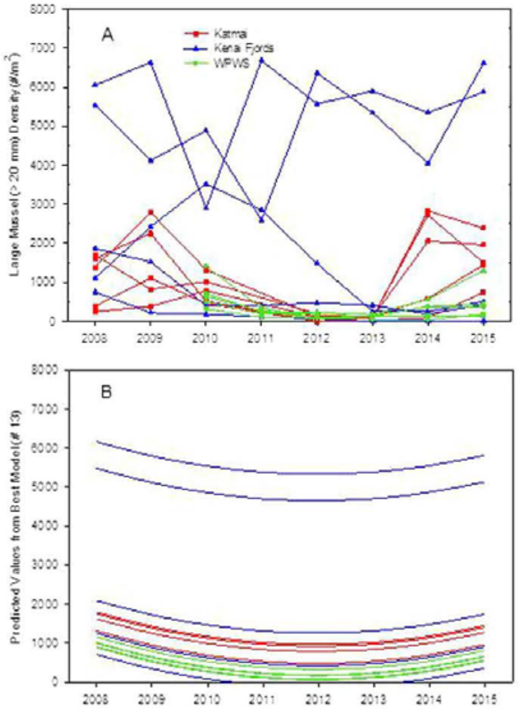

Fig. 6. Estimated (A) and modeled (B) large (≥ 20mm) mussel density at selected sheltered intertidal sites within three regions in the northern Gulf of Alaska 2008–2015. Red, blue and green represent Katmai, Kenai Fjords and Western Prince William Sound, respectively.

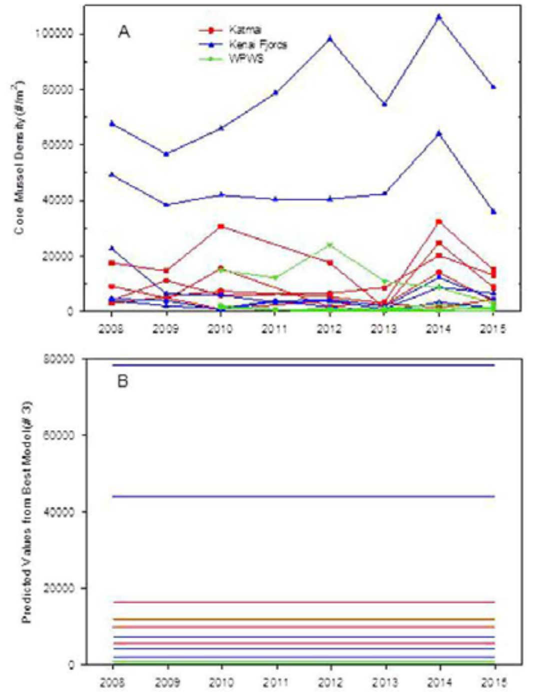

Fig. 7. Estimated (A) and modeled (B) mussel density from cores (51mm interior diameter) obtained at selected sheltered intertidal sites within three regions in the northern Gulf of Alaska 2008–2015. Red, blue and green represent Katmai, Kenai Fjords and Western Prince William Sound, respectively.

abundance across sites.

In contrast to static attributes that remain fairly constant over time, a broad suite of environmental factors (some related to tidal elevation, and including temperature, salinity, desiccation, and disturbance) are well documented as potentially important in the composition of intertidal communities, including mussels (Dayton, 1971; Seed and Suchanek, 1992; Hunt and Scheibling. 1996). The spatial variation in the density, bed size and total abundance of mussels that we observed across the northern GOA likely reflects, at least in part, both the physical and local environmental characteristics of individual sites.

Larger scale basin or regional processes, often related to ocean conditions driven by winds and currents and affecting nutrients and productivity, also will affect benthic marine communities (Blanchette and Gaines, 2007; Broitman et al., 2008; Menge et al., 2009), including the presence and abundance of mussels in intertidal habitats (Seed and Suchanek, 1992; Blanchette and Gaines, 2007; Navarrete et al., 2005). In addition to the widespread differences across individual sites for most of our estimates of mussel abundance, we also detected significant differences in the estimated abundance of large mussels at the regional level, where mussels were most abundant (and most variable) at Kenai Fjords, and least abundant (and least variable) in WPWS (Fig. 8). The reasons for the regional differences we observed are not clear but may be related to larger scale physical and environmental attributes, such as bathymetry, temperature and salinity extremes and coastal ocean transport processes that vary over both large spatial and temporal time scales (Weingartner, 2007).

5.2. Temporal variation

We found significant support in models for a consistent temporal pattern across several estimates of mussel abundance across the northern GOA (Figs. 3, 4, 6 and 8). This pattern consisted of relatively high densities and abundances of larger mussels at the time of initial sampling, a subsequent decline, to values approaching zero in some cases, with return to near initial abundances by 2015 at many sites. While we have little direct evidence of factors driving these trends, the fact that they occurred over large spatial scales suggests the potential influence of large-scale oceanographic or climatic factors, perhaps related to post settlement survival. The consistency in temporal patterns of abundance over such a large spatial scale (> 500 km) contrasts with patterns observed elsewhere, where very different temporal patterns in abundance can occur over much smaller spatial scales, often 200 km or less (Menge et al., 2003; Navarrete et al., 2005; Blanchette and Gaines, 2007). We hypothesize that the large-scale pattern in mussel abundance we observed may relate to the northern GOA being largely a downwelling system (Mundy, 2005; Weingartner, 2005) where larval retention may be enhanced, in contrast to more spatially variable upwelling systems (Navarrete et al., 2005; Blanchette and Gaines, 2007). The declines and increases we observed likely reflect high post settlement mortality during the decline and high survival as mussel abundance increased, possibly related to increases in food availability or quality (Bustamante and Branch, 1995; Bracken et al., 2012).

In contrast to the temporal pattern of decline and recovery we observed for most estimates of mussel abundance, we found little support in models for variation in densities of mussels estimated from cores over time (Fig. 7). A variety of mechanisms may be contributing

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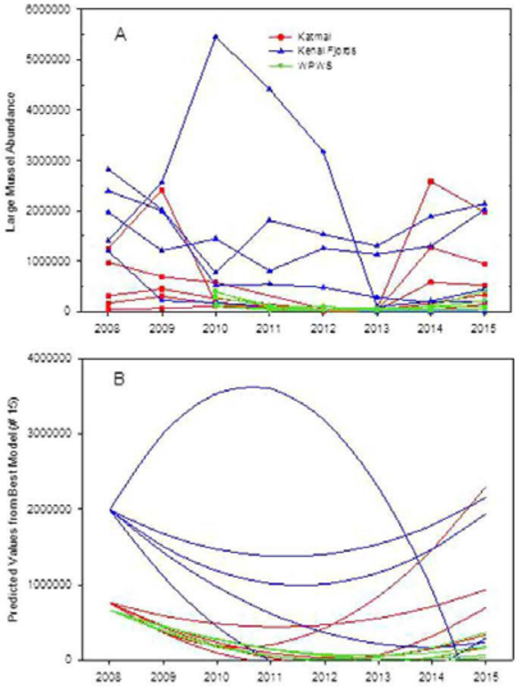

Fig. 8. Estimated (A) and modeled (B) large (≥ 20mm) mussel abundance (density x bed size) at selected sheltered intertidal sites within three regions in the northern Gulf of Alaska 2008–2015. Red, blue and green represent Katmai, Kenai Fjords and Western Prince William Sound, respectively.

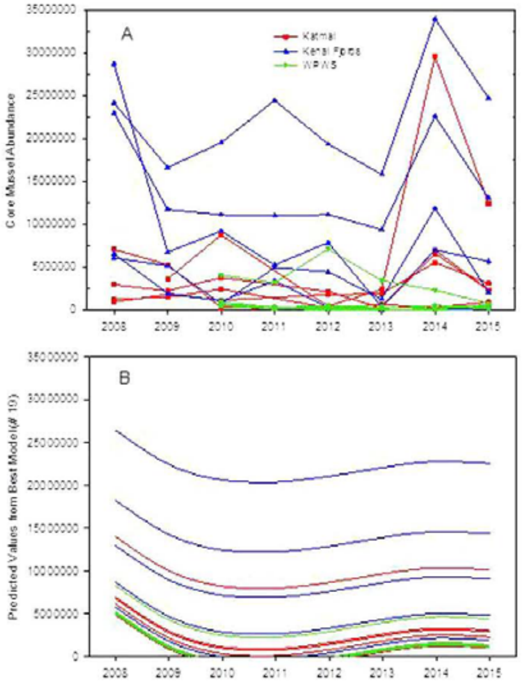

Fig. 9. Estimated (A) and modeled (B) mussel abundance (core density x bed size) from cores (51mm interior diameter, 0.002 m^2) obtained at selected sheltered intertidal sites within three regions in the northern Gulf of Alaska 2008–2015. Red, blue and green represent Katmai, Kenai Fjords and Western Prince William Sound, respectively.

to consistent recruitment of young mussels, including widespread distribution of reproductive adults, and high retention and survival of planktonic larvae and newly settled plantigrades. While we have no estimates of larval supply or settlement, the magnitude of recruitment represented by core densities was sufficient to produce the abundance of mussels observed across sites and times (Figs. 3, 4, 6 and 8). This is consistent with observations of Navarrete et al. (2005) who suggested that in regions not affected by consistent upwelling (such as the GOA) larval supply may be less important than mortality influences in determining mussel abundance.

A broad suite of aquatic and terrestrial consumers, across a range of sizes from small snails to sea otters and bears, prey upon mussels following settlement from the water column and recruitment into suitable adult intertidal habitats (Seed and Suchanek, 1992; O'Clair and O'Clair, 1998). Predation occurs across all post-settlement sizes and while not all predators consume all sizes, it is unlikely that any mussel achieves refuge in size or age from all predators, with larger mussels preferred by larger predators, including some sea stars, black oystercatchers, and sea otters. Thus the pattern we observed of decline and recovery of mussel abundance over a time span of 4–8 years might be best explained by a combination of predictable annual recruitment of young mussels, annual variation in juvenile mortality and relatively persistent predation related mortality among larger mussels across the GOA.

5.3. *Biological controls*

In addition to physical and environmental attributes, ecological processes are widely recognized as fundamental in structuring mussel populations (Dayton, 1971; Paine, 1974; Seed and Suchanek, 1992; Navarrete et al., 2005). Predation on mussels was initially documented by sea stars, defining their lower distribution in the intertidal on the west coast of North America (Connell, 1972; Paine, 1974). Various species of crab, including species of *Cancer, Caurinus and Pachygrapsus*, prey on mussels and prefer smaller size classes (Seed and Suchanek, 1992). Harger (1972) concluded that settlement densities of mussels below 10,000 m^{-2} may be insufficient to overcome crab predation in the two-month period post-settlement. Various species of *Nucella* and other predatory snails are known to limit mussel abundance (Seed and Suchanek, 1992) and Suchanek (1978) found from 61–95% of mussel shells showed evidence of snail predation. Avian predators on mussels in Alaska include black oystercatchers, Barrow's goldeneye, harlequin ducks (*Histrionicus histrionicus*), common eiders (*Somateria mollissima*), several species of scoters (*Melanitta sp.*), glaucous wing gulls (*Larus glaucescens*), surfbirds (*Aphriza virgate*), and black turnstones (*Arenaria melanocephala*) (O'Clair and O'Clair, 1998). In Holland, Meire and Ervynck (1986) concluded that 40% of annual mussel production could be consumed by Eurasian oystercatchers (*Haematopus ostralegus*). The sea otter likely represents the main mammalian predator on mussels, which can represent up to 58% of the otter's diet (VanBlaricom, 1988; Coletti et al., 2016), although mussel use by sea otters will vary spatially (Doroff and Bodkin, 1994; Coletti et al., 2016). Given the abundance and diversity of mussel consumers in the northern GOA (O'Clair and O'Clair, 1998), it seems likely they exert influence on mussel populations that vary both spatially and temporally, contributing to the patterns described in our data.

Biological controls, primarily related to larval supply and recruitment, and various sources of mortality are now recognized to regulate mussel populations across the globe and both spatial and temporal

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variation in these processes can contribute to variation in mussel abundance (McGrorty et al., 1990; Menge, 2000; Menge et al., 2003; Navarrete et al., 2005; Beukema and Dekker, 2007; Blanchette and Gaines, 2007; Menge et al., 2009; Cockrell et al., 2015).

In addition to the complimentary perspectives of "bottom up" and "top down" processes that drive mussel populations discussed above, below we consider the comparatively unexplored role that variation in mussel abundance may play in the performance of consumer populations. From the predators' perspective, energy in the form of prey resources is widely recognized as important in driving trends in consumer populations (Keith, 1983; Hilderbrand et al., 1999; Monson et al., 2000). Among the array of mussel consumers in the GOA are several species of conservation concern, including the sea otter, the black oystercatcher, and Barrow's goldeneye being monitored under the Gulf Watch Alaska Program (Dean et al., 2014). Recent work presented by Coletti et al. (2016) interprets variation in trends in sea otter abundance among our Katmai, Kenai Fjords and WPWS study areas relative to prey availability and otter energy intake rates. Consistent with our finding of high mussel abundance at Kenai Fjords, Coletti et al. (2016) report mussels providing a large (58%) proportion of the caloric content consumed by sea otters at Kenai Fjords. Coletti et al. (2016) also describe a temporal pattern of declining energy obtained by sea otters foraging on mussels at Kenai Fjords over time that tracks the decline and recovery of mussel abundance we describe across the Gulf. While relations between prey and predator can be complex, the sea otter/mussel example at Kenai Fjords supports the concept that monitoring prey populations can provide valuable inference to understanding trends in consumer populations that should aid management and conservation efforts. We suggest that the relations described between sea otters and mussels may be extended to the black oystercatcher, Barrow's goldeneye, and other species whose diet may be dominated by mussels. It appears likely that population level performance metrics of consumers, such as reproduction and survival, may be linked to trends in prey populations. Defining those functional relations between production and predators would benefit from high resolution data on larval supply, transport, settlement, survival and growth of primary and secondary producers that fuel nearshore food webs.

6. Conclusion

We draw several generalizations from our monitoring of intertidal Pacific blue mussel abundance in the northern GOA. First, mussel abundance varies dramatically across sites, in some cases by orders of magnitude. We also detected differences in abundance of large mussels at the region level within the GOA. It is likely that site and region specific physical attributes and ecological processes are related to this variation. Second, we detected relatively consistent densities of small mussels (generally ≤ 10 mm) from core samples across years, after accounting for effects of site, suggesting that recruitment occurred on a regular basis, at levels adequate to accommodate subsequent increases in adult mussel abundance. Third, we detected Gulf-wide temporal patterns in abundance of large mussels and mussels from cores that occurred over relatively brief time scales, where the average of large and core estimates of mussel abundance across all sites declined by 83% between 2008 and 2013, and in most cases rapidly recovered much of that loss by 2014 or 2015. The rate and magnitude of change we observed in mussel abundance in the GOA suggests high rates of annual recruitment of juveniles into mussel beds and widespread temporal variability in post-recruitment mortality. These findings suggest potentially important consequences of mussel population dynamics to the array of consumers that depend on intertidal mussels.

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Appendix B

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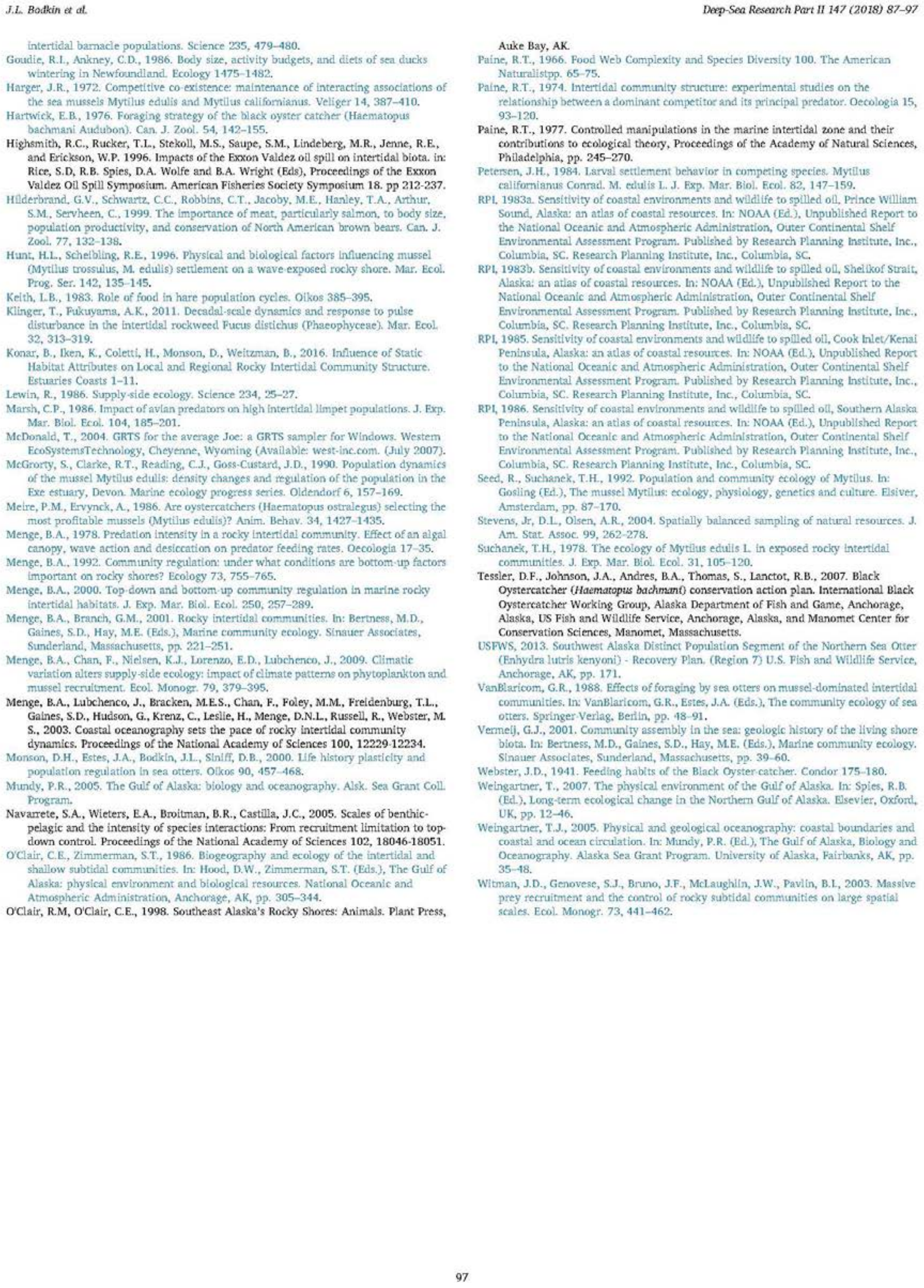

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