

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

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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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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 (Gunnill 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

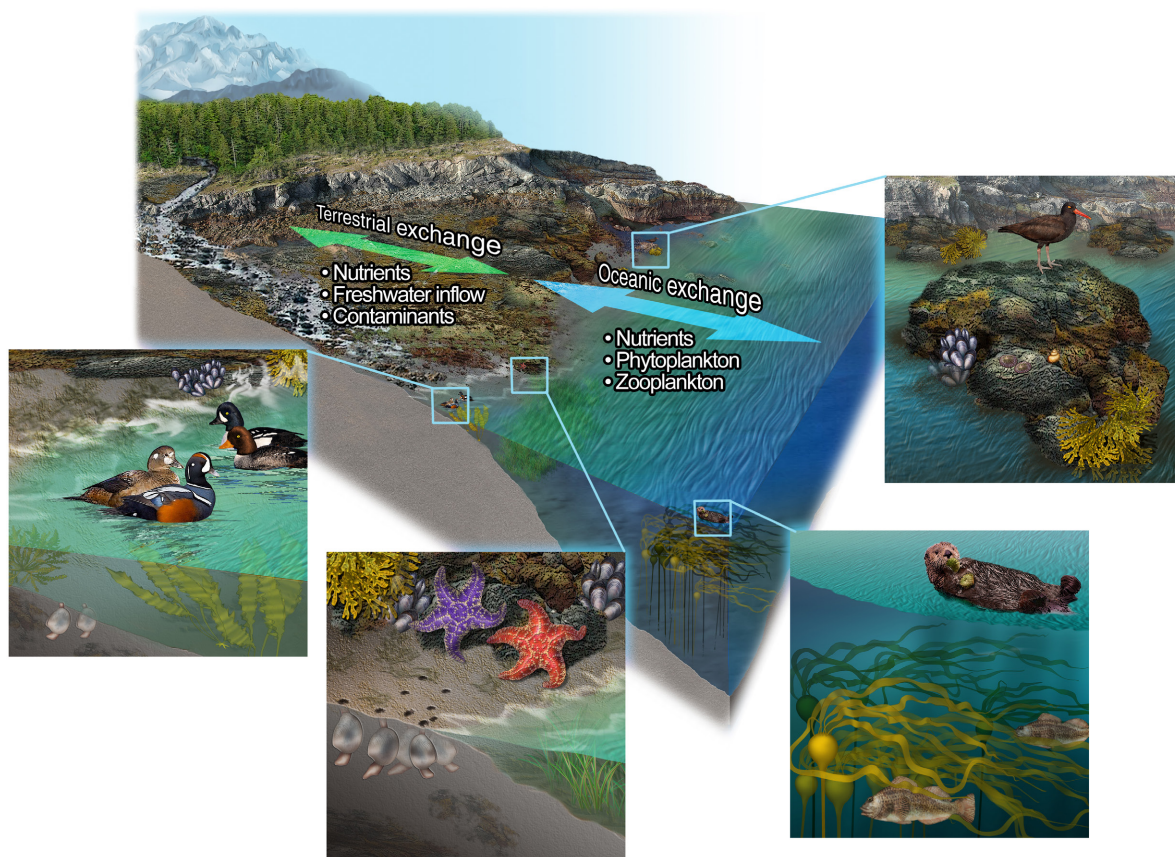


Fig. 1. Conceptual model of the nearshore food web with terrestrial and oceanic influences illustrated. In this model, sea otters, black oystercatchers, sea ducks, and sea stars act as the top-level consumers in a system where primary productivity originates mostly from the macroalgae and seagrass and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

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

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. 2000a, 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

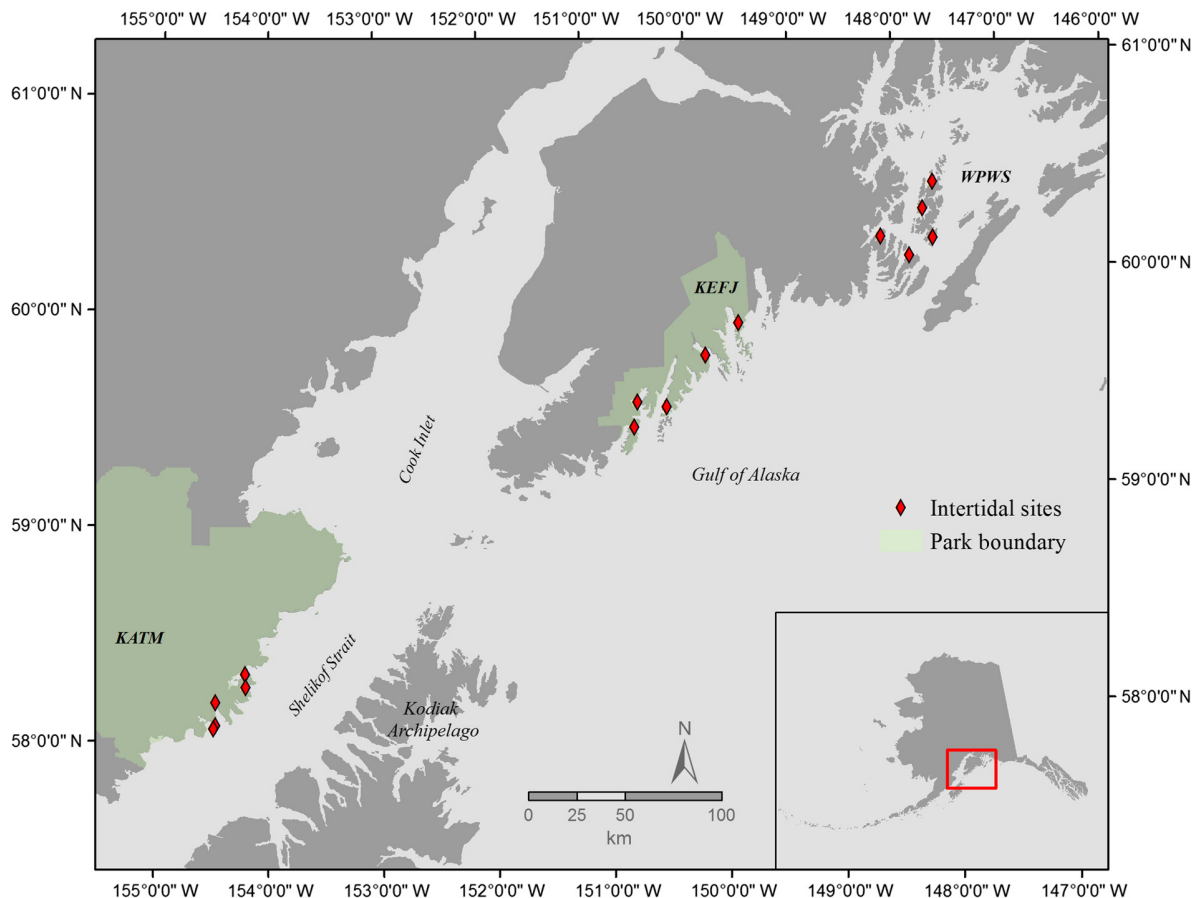


Fig. 2. Map showing study sites within Katmai National Park and Preserve (KATM), Kenai Fjords National Park (KEFJ), and western Prince William Sound (WPWS). The red diamonds represent rocky intertidal sites that act as a central point to establish monitoring sites or transects of several other marine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

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 (<i>Nucella</i> spp.) and chiton (<i>Katharina tunicata</i>) 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 (<i>Lottia persona</i>) 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.

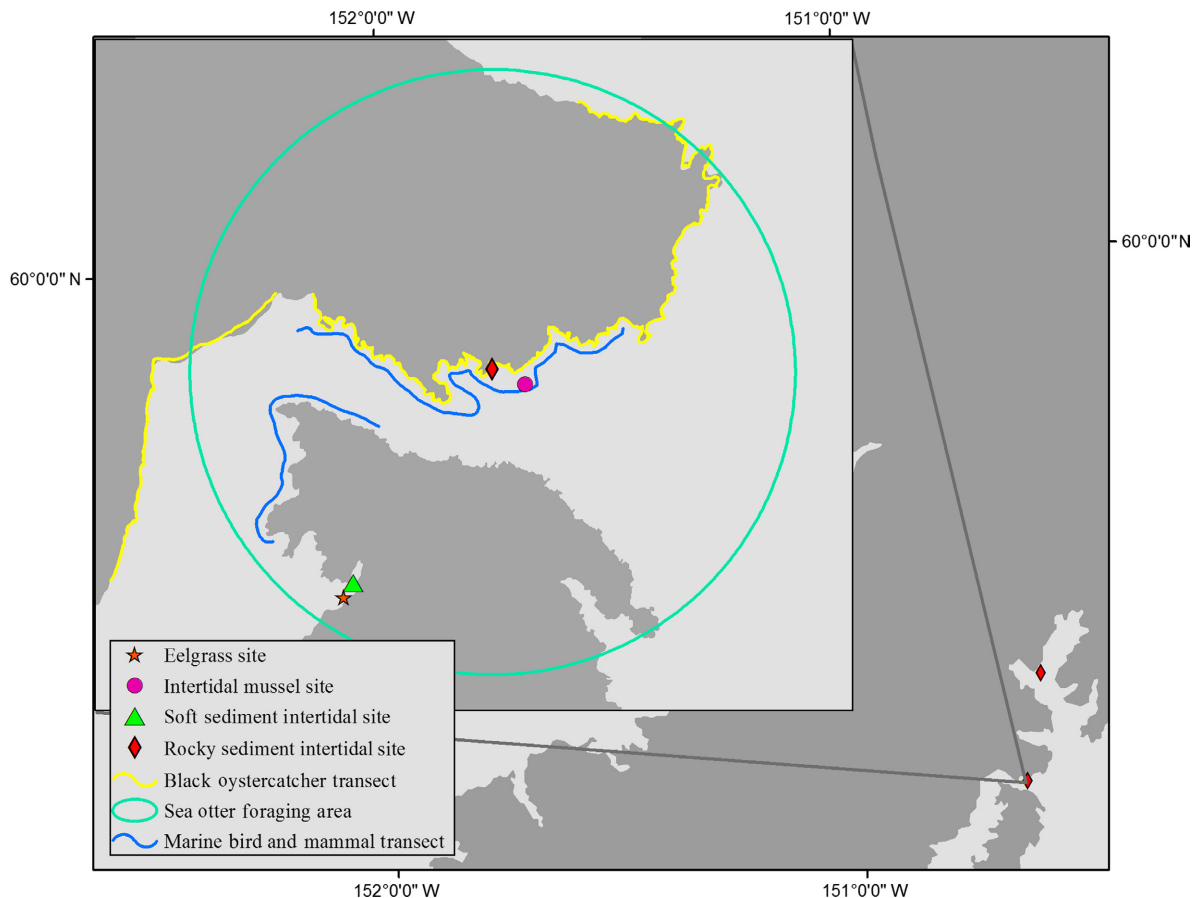


Fig. 3. A hypothetical example of the nested spatial design of the nearshore monitoring program.

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

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 km² in the two NPS units and more than 2000 km² 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)

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. 2000a, 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 ($1 - q_x$) was conservatively adjusted by setting it equal to an assumed preweaning survival rate (Monson et al. 2000b) 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).

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

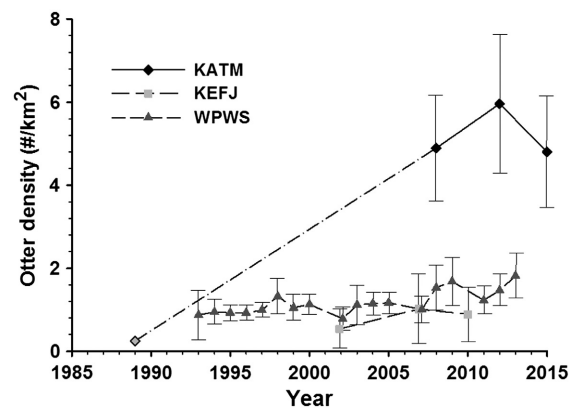


Fig. 4. Density (estimated abundance/available suitable habitat) of sea otters living in the Katmai National Park and Preserve (KATM), Kenai Fjords National Park (KEFJ), and western Prince William Sound (WPWS) study blocks. Available habitat = 1450, 1485, and 2360 km² for KATM, KEFJ, and WPWS, respectively. 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.

(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. 2000a, 2011), population growth was slow although significant ($P < 0.001$), averaging 3% per

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/km² of identified sea otter habitat, which was 6.4× and 3.6× the average density of 0.81/km² and 1.45/km² 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

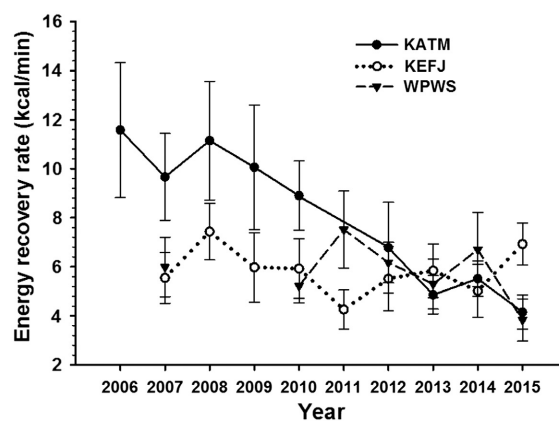


Fig. 5. Energy recovery rates (kcal/min) for sea otters foraging in western Prince William Sound (WPWS), Kenai Fjords National Park (KEFJ), and Katmai National Park and Preserve (KATM). Error bars represent Monte Carlo simulation-based 95% confidence intervals.

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.

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

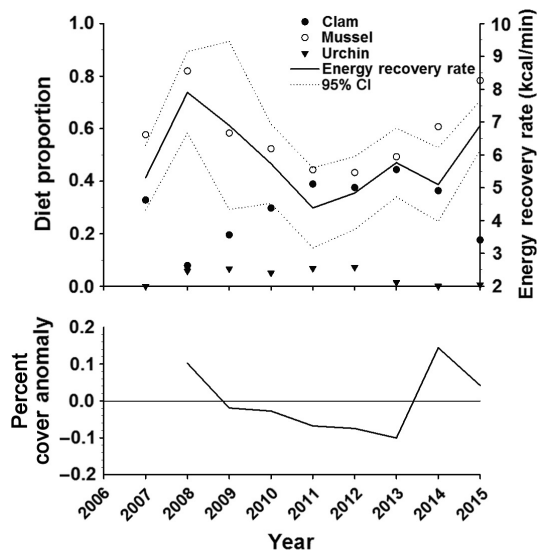


Fig. 6. Proportion of mussels in sea otter diets in Kenai Fjords National Park (KEFJ), 2007–2015 (upper graph), and percent cover anomaly of mussels in KEFJ, 2008–2015 (lower graph).

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

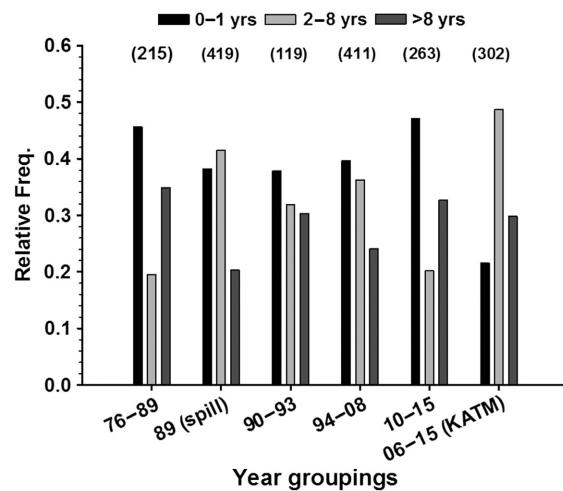


Fig. 7. Age-class structure of sea otters found dead on beaches in Western Prince William Sound prior to and after the *Exxon Valdez* oil spill (1976–2015, first five groupings; Monson 2014) and on beaches in Katmai National Park (2006–2015, last grouping). Note the number of carcasses in each grouping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

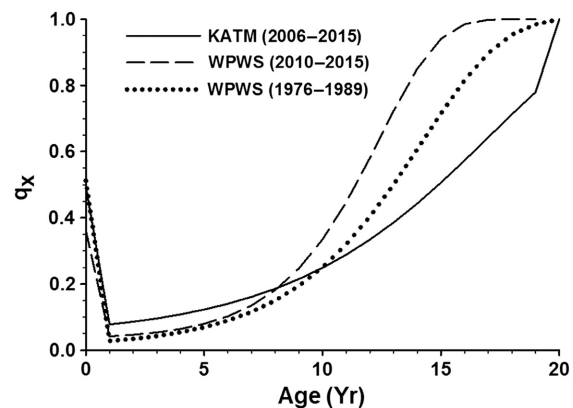


Fig. 8. Estimated mortality rates of sea otters at Katmai National Park and Preserve (KATM) 2006–2015, at western Prince William Sound (WPWS) 2010–2015, and at WPWS pre-*Exxon Valdez* oil spill (1976–1989) based on the age-at-death distributions from beach-cast carcasses.

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

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. 2000b, 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. 2000b). 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

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. 2000a, 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

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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