

Sea otter population collapse in southwest Alaska: assessing ecological covariates, consequences, and causal factors

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Citation: Tinker, M. T., J. L. Bodkin, L. Bowen, B. Ballachey, G. Bentall, A. Burdin, H. Coletti, G. Esslinger, B. B. Hatfield, M. C. Kenner, K. Kloecker, B. Konar, A. K. Miles, D. H. Monson, M. J. Murray, B. Weitzman, and J. A. Estes. 2021. Sea otter population collapse in southwest Alaska: assessing ecological covariates, consequences, and causal factors. *Ecological Monographs* 00(00):e01472. 10.1002/ecm.1472

Abstract. Sea otter (*Enhydra lutris*) populations in southwest Alaska declined substantially between about 1990 and the most recent set of surveys in 2015. Here we report changes in the distribution and abundance of sea otters, and covarying patterns in reproduction, mortality, body size and condition, diet and foraging behavior, food availability, health profiles, and exposure to environmental contaminants over this 25-yr period. The population decline, which resulted in densities on the order of 5% of environmental carrying capacity, ranged from Attu Island in the west to about Castle Cape (on the south side of the Alaska Peninsula) in the east. Remaining sea otters moved closer to shore and into shallow, protected habitats. Reproductive rates appeared unchanged with the decline. Although the demographic cause of the decline was clearly elevated mortality, stranded carcasses were rare or absent. The net rate of energy gain by foraging sea otters, body length and condition, and prey biomass density, all increased after the decline and varied inversely with sea otter population density beyond the area of decline. Sea otters within the area of decline showed no increases in health anomalies, disease, contaminant exposure, or abnormal gene transcription patterns as compared to animals outside the area of decline. These collective findings are inconsistent with nutritional limitation, disease, or environmental contaminants, and consistent with predation (or possibly some other density-independent factor) as the reason for the sea otter population decline. Our approach and analyses provide a broad conceptual template for thinking about and assessing the causes of wildlife population declines.

Key words: body condition; carcass recovery; contaminants; disease; distribution; *Enhydra lutris*; foraging success; gene transcription; population decline; predation; sea otter; southwest Alaska.

INTRODUCTION

Once-abundant populations of harbor seals (*Phoca vitulina*), Steller sea lions (*Eumetopias jubata*), and sea otters (*Enhydra lutris*) collapsed across southwest Alaska during the mid to late 20th century (Pitcher 1990, Doroff et al. 2003, National Research Council [NRC] 2003, Small et al. 2008). Due in large part to the surprising nature of this collapse and the remote region within which it occurred, neither the detailed patterns of the declines nor their specific cause or causes have been well

Manuscript received 7 September 2020; revised 11 December 2020; accepted 15 January 2021; final version received 21 May 2021. Corresponding Editor: Nicholas J. Gotelli.

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understood. The collapse began with harbor seals in the 1970s and ended with sea otters in the 1990s (Springer et al. 2003, Estes et al. 2009). The sea otter decline has been the most closely observed and is arguably the best understood of these declines. This decline, which began in about 1990 (Estes et al. 1998, Burn et al. 2003, Doroff et al. 2003), approached two orders of magnitude in some areas by the early 2000s (Estes et al. 2005), thereby leading to concern over the possibility of localized or even larger-scale extinctions of sea otters in a region where the species previously abounded and appeared to be thriving (Bodkin 2015). Consequently, in 2005 the U.S. Fish and Wildlife Service (USFWS) listed the southwest Alaska stock of sea otters, which extends from eastern Kodiak to Attu Island, as “Threatened” under the Endangered Species Act (USFWS 2013).

The cause (or causes) of the sea otter decline have been inferred from field studies in the central and western Aleutian Islands. Post hoc analyses and interpretations of these data initially suggested killer whale (*Orcinus orca*) predation as the cause of the decline (Estes et al. 1998, Williams et al. 2004, Estes et al. 2005, USFWS 2013). This conclusion was based on the following evidence: (1) increased killer whale sightings in nearshore habitats occupied by sea otters; (2) a significant increase in the observed killer whale attack rate on sea otters; (3) persistent high densities of otters in habitats that afforded refuge to sea otters from killer whale predation (Stewart et al. 2015); (4) demographic and energetic analyses indicating that the observed number of attacks by killer whales on sea otters was similar to that expected based on elevated mortality from killer whale predation, and all the deaths could be accounted for by a small change in transient killer whale foraging behavior; and (5) patterns of variation in the ecology and natural history of sea otters and their coastal ecosystem that were consistent with predation and inconsistent with other potential explanations. However, there are outstanding points of uncertainty or debate (Kuker & Barrett-Lennard 2010, USFWS 2013). One point of uncertainty is the geographical extent of the decline, especially in the east where data on distribution and abundance of sea otters were either limited or nonexistent. Information on the spatial and temporal dimensions of the decline are needed to determine if it is stable or spreading, and if the rate of decline is spatially consistent or heterogeneous. Moreover, Kuker and Barrett-Lennard (2010) argued that either new information or reanalyses of the older data weakened the evidence for killer whale predation and cast doubt on the claims that disease, nutritional limitation, or various natural or anthropogenic toxic compounds were not responsible for the decline. The cause of the sea otter decline probably will always be surrounded by some degree of uncertainty. This is because the scales of pattern and process are large, causal hypotheses are retrospective and thus cannot be put to rigorous experimental tests, and the evidence for or against each of the potential drivers of population change is imperfect and subject to differing interpretations. It

seems reasonable to infer increased mortality (as opposed to redistribution or reduced fecundity) as a general cause of the decline (USFWS 2013), but the specific causes of mortality remain uncertain.

Most compelling inferences about the rate and importance of different sources of mortality in wildlife populations are based on the analysis of death assemblages, not on direct observations or records of mortality (Monson et al. 2000a, Sinclair et al. 2003, Hoppe 2004, Terry 2008). However, few remains of sea otters have been recovered from the beaches of southwest Alaska since the onset of the decline. Thus, it would be imprudent to mount a field program with the a priori intent of directly measuring predation rates. Similarly, the demographic consequences of diseases are often difficult to infer in host populations (Tompkins et al. 2011). Evidence for disease exposure, by itself, means little, as parasites and microbes are ubiquitous in nature (Dobson et al. 2008), and individual organisms can be exposed to diseases without significant impacts on their health. Even unequivocal evidence for disease-induced mortality in large numbers of dead or dying animals does not necessarily indicate an epidemic or a disease-induced population decline, because deteriorating health and the elevated frequency of disease are common manifestations of high population density and resource limitation in many wildlife species (Wobeser 2013).

These difficulties notwithstanding, differing potential causes of the sea otter population decline lead to differing expectations of pattern in the morphology, behavior, physiology, and life history of sea otters themselves, and in various features of their associated ecosystem. Therefore, we thought a comprehensive analysis of these kinds of data, obtained and analyzed over the appropriate scales of space and time, would be revealing. We reasoned that it should be a relatively straightforward undertaking to establish the eastern extent of the decline, to assess whether the sea otter declines in different areas of southwest Alaska have similar or differing associated patterns, and thus to infer whether they likely resulted from a common or differing causes. Beyond that, our general approach was to establish an exhaustive list of reasonable hypotheses for the cause of the sea otter population decline and then formulate a suite of measurable response variables in the sea otters and their coastal ecosystems that we expected to vary in predictable ways under each hypothesis (Table 1). We then evaluated the degree of support for each of these hypothesized causes by measuring the pattern of variation in these response variables at locations throughout and beyond the range of the decline, and comparing these patterns with the a priori predictions. We expected that the best-supported hypotheses would be the ones with fewest inconsistencies between predictions and empirical data.

Bering Island, Russia, and Prince William Sound, Alaska, were known to lie beyond the western and eastern extremes of the decline (USFWS 2013). This knowledge, combined with the fact that sea otter populations are thought to be at or near environmental carrying capacity

TABLE 1. Prediction matrix for alternative hypotheses of sea otter decline.

Data type	Alternative hypothesized causes of sea otter decline					
	Nutritional limitation	Reproductive failure	Disease	Contaminants	Fisheries or harvest	Large-scale redistribution
Abundance trends	Variable decline rate, dependent on local food resources and population density	Slow and continuous rate of decline (if driven by low birth rates)	NA (could be variable or consistent, depending on scale of disease exposure)	Variable, dependent on distribution of contaminant exposure	Variable, dependent on distribution of fisheries bycatch and/or harvest	Trends vary spatially, dependent on balance between immigration and emigration
Habitat selection	NA	NA	NA	NA	Shift to areas protected from human harvest	Otters abundant at some islands, rare at others
Pup production	Reduced pup ratios	Reduced pup ratios	NA	Reduced pup ratios	NA	NA
Carcass production	Increase in carcasses	NA	Increase in carcasses	Increase in carcasses	NA (increase or decrease possible)	NA
Body size and condition	Decrease in size and condition	NA (decrease possible depending on cause)	Decrease in size and condition	NA	Possible increase in size and condition	Possible increase in size and condition
Diet and foraging success	Increased diet diversity and decreased energy recovery rate	NA (decrease possible depending on cause)	NA	NA	Possible increase in energy recovery rate	Possible increase in energy recovery rate
Food availability	Reduction in prey abundance	NA (decrease possible depending on cause)	NA	NA	Possible Increase in prey abundance	Possible Increase in prey abundance
Serum chemistry and hematology	Patterns in decline area similar and resemble other food-limited populations	Differences in area of decline vs. nondecline	Differences in area of decline vs. nondecline	Differences in area of decline vs. nondecline	NA	NA
Gene transcription	Patterns in decline area similar and resemble other food-limited populations	Differences in area of decline vs. nondecline	Differences in area of decline vs. nondecline	Differences in area of decline vs. nondecline	NA	NA
Contaminant exposure	NA	NA (increase possible depending on cause)	NA	Consistently higher levels in area of decline vs. non-decline	NA	NA
Documented observations of deaths	NA	NA	Higher observed incidence of causal factor inside vs. outside area of decline	NA	Higher observed incidence of causal factor inside vs. outside area of decline	Higher observed incidence of causal factor inside vs. outside area of decline

Note: For each combination of hypothesized cause (columns) and data type (rows), the predicted response is listed. NA indicates the lack of a clear prediction for a given data type under a particular hypothesis.

at both places (Bodkin et al. 2000, Bodkin et al. 2002, Bodkin 2015), made these specific locations important points of comparison. Signals from the cause of the decline in either the sea otters or their associated ecosystem might appear in a contrast between the areas that have declined and those that have not. Moreover, if the sea otter decline had a common cause across its geographic range, we expected to see this manifested as common signaling patterns across that range. Similarly, if there was indeed a common cause, we expected the temporal patterns in each metric over the course of the decline to match the spatial patterns between areas that had or had not experienced a decline. The predicted responses for each variable or data type, under each alternative hypothesis, are summarized in Table 1. In addition to predicted responses with respect to data sets collected as part of this study, we also include in Table 1 predictions for previously documented or published reports of observed deaths associated with the hypothesized causal agent (e.g., Hatfield et al. 1998). In general, we would predict a higher incidence of such reports during the period of decline as compared to periods before the decline, and for populations within vs. outside the area of decline.

Using standard and well-tested protocols, we collected and compared data over two spatial and temporal scales. One set of contrasts, made over a large spatial scale but smaller temporal scale, used data collected from 42 locations across and beyond the range of the decline, sampled during field seasons conducted between 2007 and 2010 (Table 2). The other set of contrasts involved a smaller spatial scale but broader temporal scale and utilized data from a limited number of sites (mostly within the area of decline) collected over several decades spanning the periods before, during, and after the decline had occurred. Data for both sets of contrasts include: (1) sea otter population density; (2) habitat use patterns (distance from shore); (3) reproductive rates; (4) stranded carcass encounter rates; (5) size and body condition of live-captured sea otters; (6) diet diversity and net rate of energy gain by foraging sea otters; (7) food availability (from scuba surveys); (8) broad spectrum analyses of hematology and blood serum chemistry; (9) gene transcription as an indicator of immune response to toxins, disease, or infection; and (10) concentrations of persistent organic compounds in blue mussels (*Mytilus trossulus*) from the rocky intertidal zone and in sea otter blood samples. Because of logistical constraints, not all of the data types were obtained from each island/location. However, all data types were obtained from at least some islands/locations within and beyond the range of the decline, and most of the data types are broadly represented from multiple islands/locations across the region and from multiple time periods (Table 2).

Our overall purpose in this monograph is to provide a detailed overview and discussion of data obtained from field studies of sea otters and their coastal ecosystems in south-central and southwest Alaska over the past several decades, and to analyze these data to evaluate support for

alternative hypotheses about the cause of decline. We have four specific objectives. First, we describe the patterns of sea otter population density at a reasonably high spatial resolution across the region bounded by Alaska's Prince William Sound in the east and Russia's Commander Islands in the west, from which we infer the geographic extent of the decline. Second, we report covarying patterns of sea otter habitat use, reproduction, mortality, growth and body condition, diet and energy acquisition, food availability, individual health indices, and environmental contaminants over this same area. Many of these contrasts focus on comparisons of data collected at Amchitka and Adak (and nearby Islands) in the early 1990s before or during the early stages of the decline, with data collected from 2007 to 2012 (a time period after which the preponderance of the decline had occurred). Third, we summarize time-series changes in the distribution and abundance of sea otters and their prey resources from a subset of locations at which we have obtained data from well before the decline to 2015. Finally, based on the spatial and temporal patterns in these data sets and their degree of consistency or inconsistency with a priori predictions (Table 1), we provide a weight of evidence analysis for the various possible causes of the sea otter decline.

METHODS

Spatial terminology

Our study was conducted over a vast region ranging from southeast Alaska to Russia (Fig. 1), within which samples were obtained and analyses conducted at different spatial scales. We have therefore attempted to use consistent terminology to describe various nested spatial scales in our study design and analyses (Table 3). We use "site" in reference to points on a map with specific GPS coordinates; "island" to denote large areas of land surrounded by ocean in the Aleutian archipelago; "location" to denote stretches of coastline from the west end of the Alaska Peninsula through southeast Alaska that are of roughly similar coastal length to average Aleutian Islands; "area" to denote one of three larger spatial extents (encompassing multiple islands/locations), that is, the area within which sea otter populations have declined (Castle Cape to Attu Island), and those areas to the west and to the east in which sea otter populations have not declined; "region" to denote large spatial extents (of sometimes differing boundaries) encompassing multiple islands/locations but that do not coincide with the boundaries of the area of the sea otter population decline; and "population" to denote collective animals at particular islands or locations.

Temporal trends in abundance

Sea otter populations in Alaska were monitored by two general methods: boat-based counts and aerial surveys (Kenyon 1969, Estes 1990b, Doroff et al. 2003).

TABLE 2. Matrix of data types by location across the range of sampling locations, arranged west to east from Bering Island (Russia) to southeast Alaska.

Location	Population density (no./km)	Distribution (distance to shore)	Reproductive rates	Carcass recovery rates	Morphometrics (body size and condition)	Diet and energy recovery	Prey availability	Health metrics (blood chemistry)	Gene transcription for sea otters	Contaminants (mussel and/or sea otter tissue)
Bering Island	×	×	×	×	×	×	×	×	×	
Attu	×	×	×			×	×			×
Agattu	×	×	×			×	×			
Alaid/Nizki/Shemya	×	×	×				×			×
Buldir										×
Kiska/Little Kiska	×	×	×			×	×	×		×
Rat (Hawada)	×	×	×			×	×			×
Anchitka	×	×	×	×	×	×	×	×	×	
Semisopochnoi	×	×	×				×			
Kavalga/Ogliuga/Skagul	×	×	×				×			×
Tanaga/Kanaga							×			×
Adak/Clam Lagoon	×	×	×	×	×	×	×	×	×	×
Kagalaska	×	×	×							×
Great Sitkin										×
Seguam							×			×
Yunaska										×
Umnak/Unalaska										×
Akutun	×	×	×			×	×			×
Akun	×	×	×			×	×			
Sanak	×	×	×	×		×	×			
Pavlov	×	×	×	×	×	×	×	×	×	
Unga	×	×	×	×	×	×	×	×	×	
Kupreanof	×	×	×				×			
Mitrofanof	×	×	×	×			×			
Castle Cape	×	×	×				×			
Semidi	×	×	×				×			
Aniakchak	×	×	×	×			×			
Katmai	×	×	×	×	×	×	×	×	×	
Kodiak/NE Kodiak Archipelago	×				×	×	×	×	×	
Kachemak Bay					×	×	×			
Kenai Peninsula					×		×			
Prince William Sound (PWS)	×	×	×	×	×	×	×	×	×	
Southeast Alaska (SEAK)							×			×

Note: Sites and place names are ordered east to west (see Fig. 1). Location names in bold font represent locations where one or more data types were obtained at multiple time periods (including prior to, during, and after decline).

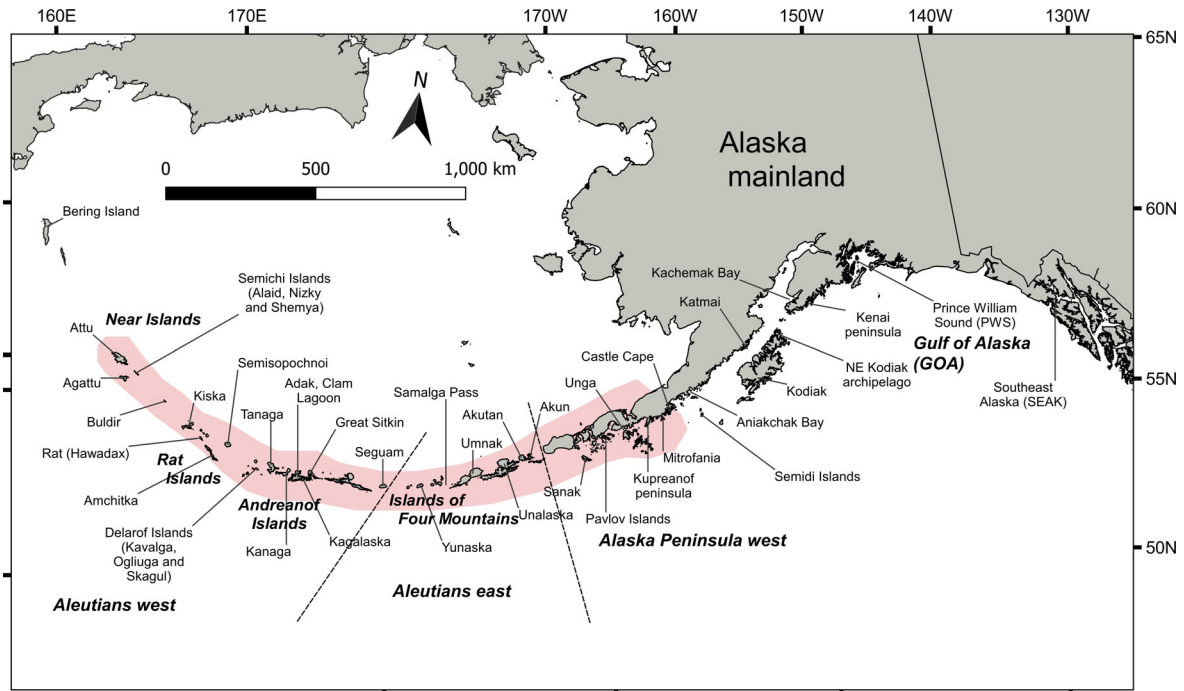


FIG. 1. Map of southwest Alaska showing study area and sampling locations for the various data sets included in the study. The red-shaded ellipse indicates the approximate spatial extent of the sea otter population decline. Dashed lines separate the regions of Aleutians west, Aleutians east, and Alaska Peninsula west.

Each method has distinct advantages and disadvantages. Aerial surveys provide broad geographical coverage over relatively short time periods. However, they are expensive and potentially dangerous, and thus were conducted only infrequently in the Aleutian Islands and along the Alaska Peninsula. Furthermore, surveys from twin engine aircraft that could access and work safely in the remote Aleutian Islands provided comparatively imprecise and inaccurate data, in part because of high speed and lack of maneuverability and in part because of the vagaries of weather and viewing conditions, both of which resulted in relatively low and variable detection probabilities (Doroff et al. 2003).

Information obtained from twin engine aerial surveys established that a population decline in sea otter density occurred during the last several decades of the 20th century (Doroff et al. 2003). However, these data were insufficient to estimate the geographic extent of the decline, the magnitude of the decline, and any smaller-scale spatial patterns that may exist across the area of the decline. We therefore supplemented the aerial survey data with survey counts made from small boats (skiffs). Skiff counts can be conducted more easily and cheaply than aerial surveys, and although they cannot provide true abundance estimates at large scales, they can provide more precise data on relative abundance at smaller scales. Detection probability during skiff counts, although not routinely estimated, is generally high under good survey conditions (Udevitz et al. 1995). It is also

possible to map the precise locations of animals and record more detailed aspects of their behavior, habitat associations and life history during skiff counts.

Skiff counts were conducted over recent decades at numerous islands in the central and western Aleutian Islands, several of which provide detailed time series dating back to the 1960's (Rasher et al. 2020). Although the data from these earlier surveys provide reasonably detailed assessments of (1) trends in sea otter abundance and distribution at several index islands (Fig. 2), (2) the extent to which current density varies among locations, and (3) spatial and temporal patterns in female reproductive output and distance from shore, they were insufficient to assess the geographic extent of the sea otter population decline. For that purpose, from 2007 to 2010 we expanded the geographic range of the skiff survey database to locations throughout and beyond the range of the sea otter population decline (Table 4).

Surveys were conducted from a small open skiff containing three people, following methods described in Udevitz et al. (1995). We attempted to count all sea otters between the skiff and shore as well as offshore of the skiff transect along transects approximately 100 km in length at each specific island/location. We used entire islands as the sample units in the Commander Islands, the Aleutian archipelago, and at several locations along the Alaska Peninsula. Elsewhere, when islands of a suitable size were not available in the general areas we intended to sample, we surveyed predetermined lengths

TABLE 3. Definitions for spatial terminology used in this monograph.

Spatial term	Number	Description	Geographic extent
Site	100s	Specific geographical location	10s to 100 m
Island	10s	Island or island complex	10s to 100 km
Location	10s	Stretch of continuous coast	10s to 100 km
Area	3	Island or location groups (defined by extent of decline). Bering Island = “west of decline,” Attu to Castle Cape = “decline area,” east of Castle Cape = “east of decline”)	100s to 1,000 km
Region	3	Island or location groups (defined by geophysical processes). Bering Island to Seguam = “west,” Eastern Aleutians and Alaska Peninsula = “east,” Kodiak and Prince William Sound = “Gulf of Alaska” (GOA)	100s to 1,000 km
Population	10s	Sea otter population associated with an island or island complex or location	10s to 100 km

of shoreline. Starting points and survey directions were selected arbitrarily, and precise lengths of survey transects were determined a posteriori from GPS track lines (Table 4). For each sea otter sighting on a transect (single otter or group), we recorded the numbers of independent animals and dependent pups, and their distance from shore. Distances to shore data were used to assess patterns of habitat use by sea otters: We calculated the mean and standard deviation in the distance from shore of observed sea otters for each skiff survey, as well as the proportion of otters occurring within 20 m of the shore (where shore is defined as the coastline or any emergent offshore islet or rock at low tide). We used either a map-based GPS or a weatherproof laptop computer to record sighting coordinates.

To assess the timing and magnitude of the decline, we evaluated temporal trends in sea otter populations over four decades at six islands: Bering, Attu, Kiska, Amchitka, Kagalaska, and Adak (Figs. 1, 2). In the case of Adak Island, we separated the time series by the outer coast and Clam Lagoon (a shallow, sandy bottom estuary inaccessible to killer whales) and treated these as distinct locations, based on previous analyses that indicated that Clam Lagoon represented a semidistinct subpopulation that exhibited differing dynamics than the outer coast population (Estes et al. 1998). Clam Lagoon was surveyed by shore-based observers scanning with binoculars and 50× telescopes from access points around the lagoon. For each survey at each island/location, an index of population density was calculated as the total number of animals counted divided by track line length (or by total area in the case of Clam Lagoon). We used a linear (one-dimensional) index of relative population density for all outer coast areas, as opposed to more conventional density in two dimensions, for two reasons: (1) consistency with previously reported skiff-based index counts for this region (Estes et al. 1998, Doroff et al. 2003, Estes et al. 2005); and (2) because converting encounter rate to density in two dimensions would require a reliable and consistent estimate of strip width, which was not possible because nearshore bathymetry varied greatly across the region (and thus effective strip width of skiff surveys widened or narrowed

corresponding to the width of sea otter habitat) and because a nearshore concentration of sea otter distribution that occurred concurrent with the decline (discussed below) meant that effective strip width was confounded with population status.

At Bering Island, skiff surveys began in the early 1980s, shortly after the Island was recolonized by sea otters, and continued through 2007, thus providing a time series showing population growth and equilibrium at an Island believed to be outside the area of decline. At Attu Island, the skiff counts began soon after otters recolonized the island in the late 1960s (Jones 1965, Kenyon 1969), continued opportunistically through 2015, and thus describe both a partial recovery of the population following the Pacific maritime fur trade and its subsequent collapse. At the remaining islands, skiff surveys were conducted opportunistically from 1990 to 2015; however, sea otters at these islands were already present at high densities (presumably at or near carrying capacity) by the early 1960s (Kenyon 1969), during which period skiff surveys were not available. Consequently, we used available aerial survey data (Kenyon 1969, Doroff et al. 2003) to provide indices of abundance for these islands prior to 1990 and, following Doroff et al. (2003), we multiplied aerial densities by a correction factor of 3.6 to obtain values that were comparable to linear densities estimated from skiff surveys.

Analysis of temporal trends in abundance

A previous analysis of the timing and magnitude of the sea otter decline in the western Aleutians (Estes et al. 1998) was based on only four islands (Amchitka, Adak, Kagalaska, and Kiska) and required restrictive assumptions such as a constant exponential rate of decline and homogenous predecline densities. With our more extensive data set for seven index islands/locations ($n = 106$ island/location-by-year combinations; Fig. 2), we were able to relax these assumptions in order to infer better (1) processes of density-dependent population growth and regulation, (2) additional unexplained or “residual” variation in vital rates (deviations from expected density-dependent variation in survival), and (3) how

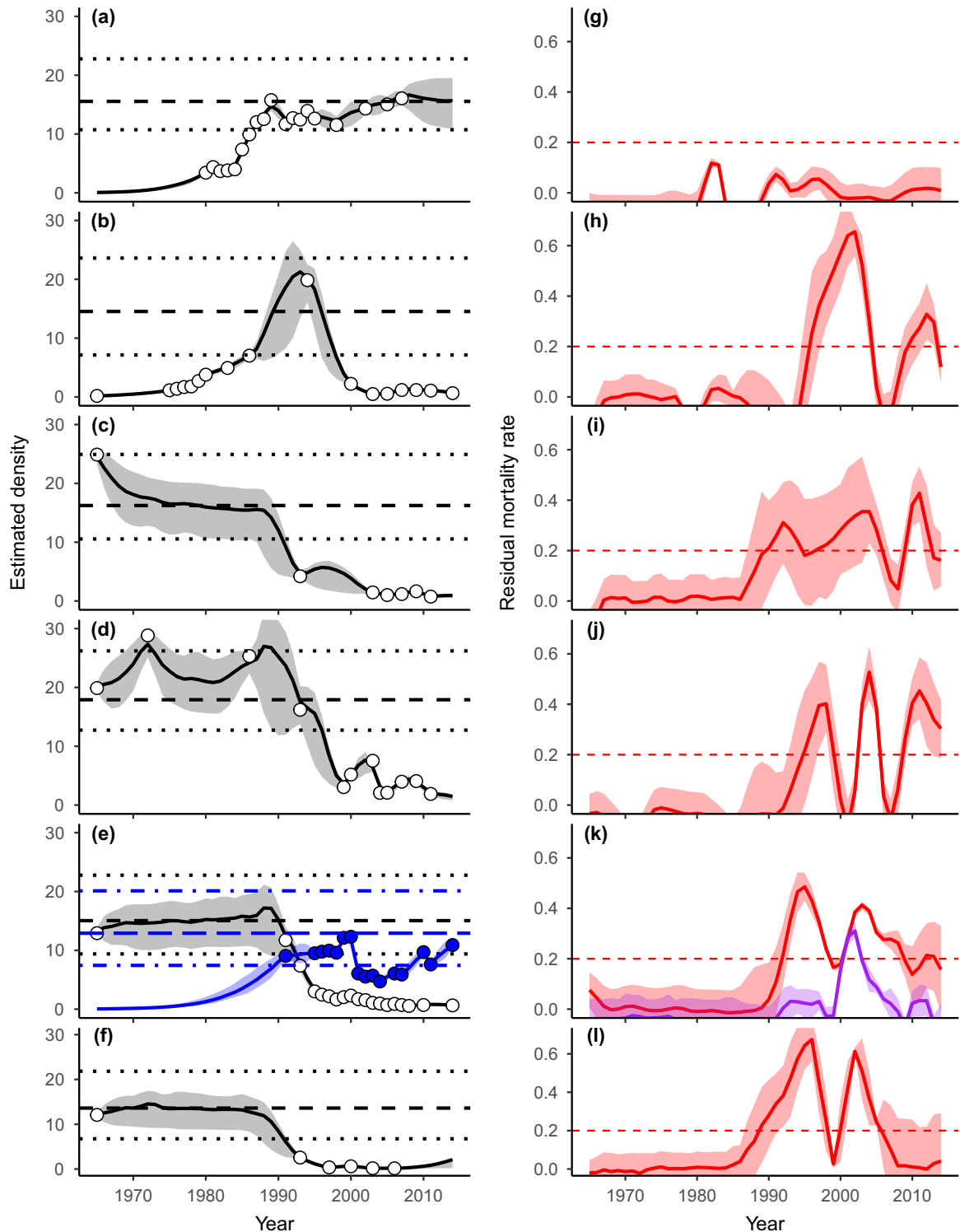


FIG. 2. Temporal trends in relative density plots (a)–(f) and time-averaged residual mortality rate $\delta_{i,t}$ plots (g)–(l) for sea otter populations at six index islands, ordered west to east: Bering (a), (g); Attu (b), (h); Kiska (c), (i); Amchitka (d), (j); Adak (e), (k); and Kagalaska (f), (l). Observed data from aerial and skiff surveys are shown as open points, mean estimated trends as solid lines, and 80% credible intervals (CI) as shaded bands. For Adak Island, separate trend lines are shown for the outer coast [black line in (a), red line in (g)] and Clam Lagoon [blue line in (a), purple line in (g)]. Estimated values of K for each Island are shown as dashed lines (95% CI as dotted lines) in plots (a)–(f), and the critical mortality rate (0.2) as a red dashed line in plots (g)–(l) (values above this threshold cause a decline).

TABLE 4. Results of skiff surveys and distribution of sea otters relative to shore during the 2007–2010 field seasons.

Island/location	Time period	Track length (km)	No. of Adults	No. of Pups	Total no.	Pup ratio	Linear density	Mean distance to shore (km)	Proportion observations <20 m shore
Bering Island	2007	263	3,222	996	4,218	0.31	16.1	0.74	0.02
Attu	2007 and 2009	372	256	86	342	0.34	0.9	0.03	0.59
Agattu	2009	38	42	12	54	0.29	1.4	0.03	0.52
Alaid	2007 and 2009	22	21	4	25	0.19	1.1	0.04	0.39
Nizki	2009	26	2	1	3	0.50	0.1	0.03	0.67
Kiska	2009	206	173	55	228	0.32	1.1	0.03	0.84
Little Kiska	2009	21	20	5	25	0.25	1.2	0.02	0.76
Rat (Hawadax)	2009	50	10	1	11	0.10	0.2	0.05	0.18
Amchitka	2007 and 2009	163	8	3	11	0.38	0.1	0.03	0.62
Semisopochnoi	2009	77	12	4	16	0.33	0.2	0.03	0.88
Kavalga	2009	37	9	1	10	0.11	0.3	0.04	0.70
Ogliuga	2009	36	47	16	63	0.34	1.8	0.17	0.24
Skagul	2009	32	5	2	7	0.40	0.2	0.08	0.71
Adak	2008 and 2010	522	292	68	360	0.23	0.7	0.04	0.73
Akutan	2008	41	27	10	37	0.37	0.9	0.06	0.31
Akun	2008	122	355	85	440	0.24	3.6	0.14	0.41
Sanak	2008	173	86	27	113	0.31	0.7	0.47	0.56
Pavlov	2008 and 2009	187	88	27	115	0.31	0.6	0.25	0.55
Unga	2008	178	175	46	221	0.26	1.2	0.21	0.27
Kupreanof	2009	245	4	2	6	0.50	0.0	0.09	0.83
Mitrofanina	2008	187	54	18	72	0.33	0.4	0.08	0.85
Castle Cape	2009	126	77	12	89	0.16	0.7	0.10	0.18
Semidi	2008	55	16	7	23	0.44	0.4	0.02	1.00
Aniakchak	2009	368	1,053	198	1,251	0.19	3.4	0.93	0.02
Katmai	2008	236	1,339	298	1,637	0.22	6.9	0.36	0.10
Prince William Sound	2009	1,792	365	89	454	0.24	5.2	0.68	0.00

these processes varied over time and among islands/locations. We used a Bayesian state-space framework to fit a process-based model to the time series, estimating parameters of a function describing density-dependent dynamics (Dennis et al. 2006) as well as residual variation in mortality, after removing the effects of variation in the data attributable to observer error (de Valpine & Hastings 2002, Moore & Barlow 2011).

The relative abundance (N , otters per km) of sea otters at island/location i and year t was calculated using the recursive growth function:

$$N_{i,t+1} = N_{i,t} \cdot \exp\left(r\left(1 - \frac{N_{i,t}}{K_i}\right) - \epsilon_{i,t}\right), \quad (1)$$

where r is the maximum intrinsic rate of population growth at low densities, K_i is the carrying capacity for island/location i , and $\epsilon_{i,t}$ represents unexplained residual variation in vital rates at island/location i in year t (i.e., variation in mortality not explained by average density-dependent variation). We recognize that the simple logistic function in Eq. 1 is unable to capture many of the complex features of population dynamics (nonlinearities in the strength of density dependence, Allee effects, etc.); however, the limited sample sizes available for some islands precluded the parameterization of a more

complex growth function. Moreover, our elaboration of the residual variation term (explained in next paragraph) allowed for additional flexibility in the model fit. Based on previous analyses of data collected from multiple sea otter populations (Estes 1990a, Monson et al. 2000b, Gerber et al. 2004, Lafferty & Tinker 2014, Tinker et al. 2019b), we used a constant value for maximum intrinsic growth rate ($r = 0.2$), which reflected the consistency of sea otter growth potential at low population densities. The carrying capacity K_i was allowed to vary across islands/locations, which we achieved by treating K_i as a hierarchical variable, normally distributed with mean $\bar{K}$ and standard deviation σ_K (where $\bar{K}$ and σ_K were parameters to be fit).

The residual variation term $\epsilon_{i,t}$ in Eq. 1 is a random normal variable with mean 0 and standard deviation σ_p (a parameter to be fit), and accounts for the effects of both “typical” environmental stochasticity (reflecting year-to-year variation in food abundance, severe weather events, disease prevalence, and other factors that affect survival of pups and adults) as well as more extreme density-independent mortality factor(s) such as that responsible for the 1990s population decline (USFWS 2013). Recognizing that the 1990s decline represented an atypical phenomenon (i.e., one that had not been observed in the previous 50 yr of survey data, or in other

sea otter populations), we can infer that the mortality factor responsible for the decline falls outside the typical range of stochastic variation. We therefore relaxed the assumption of a single value of σ_p , and instead consider two possible values, σ_{p1} and σ_{p2} , corresponding to typical stochastic variation and elevated variation in mortality, respectively. Both σ_{p1} and σ_{p2} represent parameters to be fit, and we used an information-theoretic approach (leave-one-out cross validation information criteria [LooIC], described later in this section) to determine which island/location-by-year combinations were subjected to elevated variation in mortality (i.e., σ_{p2} vs. σ_{p1}).

To estimate process model parameter values, we related predicted abundance ($N_{i,t}$, as calculated using Eq. 1) to observed survey data. Specifically, the observed density from skiff survey counts ($O_{i,t}$) can be modeled as a gamma distribution (Dick 2004) with a mean value equal to $N_{i,t}$:

$$O_{i,t} \sim \text{Gamma} \left(\text{shape} = \frac{(N_{i,t})^2}{(N_{i,t} \cdot \text{CV})^2}, \text{inverse scale} = \frac{N_{i,t}}{(N_{i,t} \cdot \text{CV})^2} \right), \quad (2)$$

where CV represents the coefficient of variation for observer error in skiff surveys and is treated as a fitted parameter.

We used Markov-chain Monte Carlo (MCMC) methods to estimate values of model parameters that maximize the likelihood of Eq. 2, implemented using STAN software (Carpenter et al. 2017) in the R programming environment (R Development Core Team 2014). We used vague Cauchy or half-Cauchy priors for all model parameters, and after a burn-in period of 5,000 iterations we saved 1,000 samples for each of 20 chains, for a total of 20,000 posterior samples. We evaluated model convergence by graphical examination of trace plots from 20 independent chains and by ensuring that the Gelman-Rubin convergence diagnostic (r-hat) was ≤ 1.1 for all fitted model parameters (Gelman et al. 2013). We conducted posterior predictive checking (PPC) to evaluate model goodness of fit, using the χ^2 statistic (sum of squared Pearson residuals of annual survey counts and grid cell cumulative counts vs. expected values) to compare fit of observed data and “new” data generated from the same distributions (Gelman et al. 2000). We examined scatter plots of the posterior distribution of χ^2 scores for new vs. observed data (in the case of well-fitting models, points in such a plot should be distributed around a line with slope 1) and we computed the associated Bayesian- P value (the proportion of new observations more extreme than existing observations; Gelman 2005, Ghosh et al. 2007), which should fall within the range $0.2 < \text{Bayesian-}P < 0.8$ for a well-fit model.

To determine the island/location-by-year combinations for which residual mortality values ($\epsilon_{i,t}$) were described by typical (σ_{p1}) vs. elevated (σ_{p2}) variation, we

compared alternative models in which various combinations of islands and year ranges were assigned σ_{p2} , and all others were assigned σ_{p1} . We also evaluated a null model having constant magnitude of variance (σ_p). We then used LooIC (Vehtari et al. 2017), to identify the best-supported model. For all fitted parameter estimates we report means and 95% credible intervals (CI₉₅) calculated from sampled posterior distributions. We plotted estimated trends in $N_{i,t}$ for each island/location. To examine how density-independent mortality varied over time and space we plotted time-averaged residual mortality estimates, $\delta_{i,t}$, which were computed as 3-yr running averages of $\epsilon_{i,t}$ at each island/location. By focusing on $\delta_{i,t}$ we minimized the influence of “typical” environmental stochasticity (which averages out to 0) and were thereby able to identify prolonged periods of elevated mortality. Because population declines will necessarily occur when residual mortality consistently exceeds the intrinsic growth potential r we identified the time ranges for each island when $\delta_{i,t}$ exceeded 0.2, and graphically assessed the temporal consistency of these periods of elevated mortality and decline. For subsequent analyses involving contrasts of various indices with respect to the status of populations, we defined the initiation of decline as the year that $\delta_{i,t}$ first exceeded 0.2, and we defined the end of the intensive period of decline as the year that relative abundance dropped below 10% of the predecline value. The years bounding the intensive decline period were averaged across all index sites for which a decline was determined to have occurred.

Spatial trends in abundance, distance to shore, and reproduction

We compared abundance of “current” (post-2005) sea otter populations at 26 sites, ranging from Bering Island in the west to Prince William Sound in the east (Fig. 1, Table 4), in order to determine if there were clear transitions in relative abundance and distribution that would demarcate the spatial extent of the decline. We excluded Clam Lagoon from this analysis because we were specifically interested in distributional shifts within outer coast habitats, and because the nature of Clam Lagoon survey data precluded a linear density estimate. Two previously reported characteristics of postdecline sea otter populations in the Aleutians include very low abundance (Doroff et al. 2003) and a shift in habitat selection by the remaining otters, such that individuals spend more time in protected waters very near shore (Stewart et al. 2015). We therefore incorporated two variables from the skiff survey data collected at each island/location—linear density (otters per kilometer surveyed) and proportion of observed otters within 20 m of the shore—into a k-means cluster analysis (Hartigan & Wong 1979). Our a priori expectation (assuming that a change in density and distribution was ubiquitous within the area of decline but rare or nonexistent outside the area of decline) was that islands/locations should cluster into

two groups: areas that had experienced decline (low density and higher proportion of sightings <20 m from shore) and areas that had not declined (higher abundance and lower proportion of sightings <20 m from shore). In addition, we examined pup:independent ratios (Bodkin et al. 2002) with the logic that if the decline were the result of poor reproductive output or success, we should see low pup:independent ratios in areas of decline and higher ratios in nondecline areas.

We log-transformed linear density data (otters per kilometer surveyed) and proportion of otters within 20 m of shore prior to analysis to achieve normality and used the silhouette method (Kaufman & Rousseeuw 2009) to select the optimal number of spatial clusters. We then used multiple analysis of variance (MANOVA) to test for significant differences between islands/locations assigned to each cluster with respect to (1) mean density, (2) mean distance to shore, and (3) ratio of pups to adults (as a measure of reproductive output). Finally, we created a plot of linear density at each island/location vs. longitude in order to see if cluster assignments resulted in clear breaks on an east–west spatial axis (i.e., separating the area of decline from areas that had not declined to the east and west). Spatial transitions in cluster assignments were used to identify the east–west spatial extent of the decline. All further analyses used these three “area” boundaries (Table 3) to classify islands/locations spatially into decline or east vs. west nondecline categories. We examined pup:independent ratios by contrasting mean pup ratios within each area.

Stranded carcass recoveries

The determination of rates and causes of mortality is notoriously challenging for most wildlife species (Caughley 1966). This is especially true in the marine realm, where populations are difficult to survey and the remains of individuals following their death commonly sink or are rapidly consumed by scavengers. Because of their nearshore distribution, sea otters commonly haul out to die or their carcasses drift ashore following death (Kenyon 1969, Bodkin et al. 2000, Estes et al. 2003). Although these stranded carcasses do not include all the deaths in their source population and do not necessarily provide a representative sample of mortality (Estes et al. 2003), they are useful in assessing certain causes of mortality and, especially, as indices of population status and local conditions. For example, many of the sea otters that perish from health-related difficulties, such as starvation or disease, apparently haul out as they become moribund (Kenyon 1969), thus greatly increasing the chance of recovery during beach surveys. Animals that die from acute trauma, such as oil spills, shooting, boat strikes, and shark bites may also become beach cast, representing other mortality sources (Monson et al. 2000a, Kreuder et al. 2003, Monson et al. 2011, Tinker et al. 2016). Mortality rates tend to be higher in populations that exist at or near carrying capacity, reflected in beach

cast carcasses (Bodkin & Ballachey 1996, Tinker et al. 2006). Conversely, even large but still growing populations may produce lower numbers of stranded carcasses, consistent with lower mortality rates (Kenyon 1969), although strandings of some segments of such growing populations (such as males) may occur following acute disease exposure events (Carrasco et al. 2014). For these reasons, comparative information on the occurrence of stranded carcasses or remains through time or among islands/locations can be a useful adjunct in assessing the status of populations.

We sought to obtain information on the relative abundance of sea otter carcasses across and beyond the range of the decline. We reasoned that if the decline or current failure of the sea otter populations to recover were the result of nutritional limitation, disease, environmental contaminants, or other health-related factors, we should find evidence for this in the form of a high frequency of carcass detection (given that per capita mortality rates would be high; Table 1). Conversely, a low detection rate of carcasses (consistent with observations at Adak and Amchitka and in the Semichi Islands (Konar 2000)) would suggest a common cause for the decline that was associated with reduced numbers of beach cast carcasses.

At each location, one or two people searched stretches of shoreline, recording beginning and end points and the location of any sea otter carcasses or remains that were found. The condition of the remains was noted as (1) fresh, (2) old but with flesh still remaining, (3) intact skeleton with no flesh, (4) disarticulated skeleton, or (5) scattered bones. The length of shoreline searched was determined from the GPS coordinates using a geographic information system (GIS). We augmented the 2008–2009 data with earlier unpublished carcass data collected at three additional locations: Amchitka Island, Adak Island outer coast, and Clam Lagoon on Adak Island (Table 5). Carcass surveys at Amchitka were conducted prior to the decline (1970–1971) and during the decline (1992–1994 and 1997). Carcass surveys at Adak and Clam Lagoon were conducted during the decline in 1995–1996.

For each data point (representing a survey or cumulative set of surveys conducted at a given location and time period), we tabulated the total number of carcasses (filtered to those cases for which a skull was present, to avoid duplicate records), total distance surveyed (km), and the estimated population density at the time of the survey (see “Methods/Analysis of temporal trends in abundance”). We computed per capita carcass recovery rate as the number of carcasses divided by the product of survey length (km) and population density (otters/km). We also classified the sea otter population status associated with each data point as (1) “stable or growing” for islands/locations that did not experience a decline or if the data were collected prior to the onset of decline, (2) “declining” for islands/locations that had declined and where data were collected during the intensive period of decline (between 1989 and 2001, which correspond, respectively, to the

TABLE 5. Beach cast sea otter carcass (skull) recovery rates.

Island/location	Year	Status	Population density (otters/km)	Region	Survey length (km)	Skulls (no.)	Skulls/km	Per capita recovery rate
Bering	2008	Stable/growing	16.1	West	644	704	1.09	0.07
Amchitka	1971	Stable/growing	26.0	West	30	47	1.57	0.06
Amchitka	1994	Declining	16.5	West	340	174	0.51	0.03
Amchitka	1997	Declining	8.4	West	155	20	0.13	0.02
Clam Lagoon	1995	Stable/growing	9.6	West	11	26	2.36	0.25
Adak	1995	Declining	3.3	West	19	1	0.05	0.02
Akutan	2008	Postdecline	0.91	East	10.4	0	0.00	0.00
Sanak	2008	Postdecline	0.65	East	31.5	2	0.06	0.10
Pavlof	2008	Postdecline	0.61	East	3.2	0	0.00	0.00
Dolgoi	2008	Postdecline	0.61	East	17.5	0	0.00	0.00
Unga	2008	Postdecline	1.24	East	20.1	0	0.00	0.00
Unga	2009	Postdecline	1.24	East	12.6	2	0.16	0.13
Chiachi	2008	Postdecline	0.38	East	3.5	0	0.00	0.00
Mitrofanina	2008	Postdecline	0.38	East	3.7	0	0.00	0.00
Katmai	2009	Stable/growing	6.93	East	73	133	1.82	0.26
Prince William Sound	2000	Stable/growing	5.20	GoA	550	149	0.27	0.05

initiation of elevated mortality and the average time at which populations at index sites dropped below 10% of their predecline abundance; see trend analysis, above), or (3) “postdecline” for islands/locations that had declined but where data were collected after 2001.

We used a GLMM to test for an effect of population status (with respect to the decline) on the per capita carcass recovery rate. Because per capita carcass recovery rates correspond to proportions of population size, our GLMM assumed a binomial distribution (with a logit link function), and we used survey length (km) as a weighting variable for each data point. We also included population density as a covariate (to allow for the possibility that per capita rates of carcass deposition varied as a function of population density), and we included “region” as a random effect to allow for geographic differences in ocean currents and bathymetry that might affect carcass retention on beaches. We identified three broad oceanographic regions: (1) “West,” spanning the Aleutian archipelago from Bering Island to Seguam Island; (2) “East,” including both the Eastern Aleutian Islands and Alaska Peninsula; and (3) Gulf of Alaska (“GoA”), including Kodiak Island to Prince William Sound (Fig. 1, Table 3). We tested for differences in carcass recovery rates for declining and postdecline populations relative to stable/growing populations (the reference level in the GLMM).

Morphometrics

Numerous studies of various species of terrestrial and aquatic mammals have found correlations between body size and population density or productivity of the environment (Bryden 1968, Innes et al. 1981, Skogland 1990, Trites & Bigg 1992, McLaren 1993, Bester & Jaarsveld 1994, Etnier 2004, Laidre et al. 2006, Rode et al. 2010).

All else being equal, changes in body size over time or between areas may reflect differences in resource availability (Laidre et al. 2006). It was primarily for this reason that we contrasted body size and condition indices of sea otters across and beyond the range of the population decline in southwest Alaska. Our hypothesis was that density-dependent mechanisms of population regulation (such as food limitation) would lead to reduced body size, whereas density-independent drivers of population decline would lead to greater body size, mediated through increasing prey abundance.

There are two general approaches to assessing body size and condition: measurements of relative structural size (generally reflecting skeletal length), and measurements of body condition (soft tissue stores, including muscle mass and body fat reserves). In sea otters, structural body size is phenotypically plastic, meaning the abundance of prey available to juveniles as they develop influences their eventual adult body size (Monson & Bowen 2015). Like all mammals, sea otters are characterized by deterministic growth, so that structural size does not change after the onset of adulthood, regardless of short-term fluctuations in food abundance, and thus cohort-specific adult size reflects conditions during development. In contrast, body condition reflects resource availability and individual feeding efficiency over shorter time scales, that is, months, weeks, or even days, because sea otters have the capacity to gain or lose body mass rapidly due to their high metabolic rate and reliance on fur instead of blubber for thermoregulation in the cold marine environment (Costa & Kooyman 1982, Yeates et al. 2007). However, the absolute amount of muscle and fat that an individual can store is dependent on its structural size, as larger individuals can accrue more body tissue than smaller individuals (Monson & Bowen 2015). Consequently, assessments of

dynamic body condition should also account for absolute size of individuals.

Sea otters were captured and sampled for standardized morphometric and biomedical data (Murray 2015) at nine islands/locations ranging from Bering Island to Prince William Sound (Table 6). At some locations, including Kodiak Island and the western Aleutians (including Adak and Amchitka islands and Clam Lagoon on Adak), data were available for multiple sampling periods between the late 1980s (predecline) and 2012 (postdecline), for a total of 15 location/year combinations (Table 6). Sea otters were captured using tangle nets and diver-operated Wilson traps (Ames et al. 1983). Captured sea otters were immobilized with intramuscularly administered fentanyl citrate and midazolam hydrochloride (Monson et al. 2001). We recorded body mass to the nearest 0.5 lb, standard length as the straight-line distance from tip of nose to tip of tail bone (with the animal lying flat on its back), and tail length using a PVC pipe slid over the tail (Monson 2009). Because the ratio of tail length to total body length was found to vary slightly among islands/locations (Monson & Bowen 2015), we subtracted tail length from standard length to obtain the “adjusted body length,” which we used as a measure of structural size. For samples prior to 2000, when tail length was rarely measured, we adjusted body length by subtracting “expected tail length,” computed from a linear regression of known tail length vs. total body length for the local population (Monson 2009). Age of each animal was determined by counting growth rings in premolar

cementum annuli (Bodkin et al. 1997). After tagging and sampling, the fentanyl was reversed with naltrexone hydrochloride (Monson et al. 2001) and the animals were released near the capture site.

To determine how resource abundance has varied over both long term and shorter time scales, we utilized three distinct indices: (1) a structural size index (SSI), which measured relative length at age and was calculated as residuals from a length-age growth function; (2) a dynamic condition index (DCI), representing the deviation in body mass from what is expected for an “average otter” of a given age and length; and (3) a body mass index (BMI), which measured relative mass at age and was calculated as residuals from a mass-age growth function. Because BMI integrates both structural size and muscle and fat reserves, it reflects combined effects of both long-term and short-term food abundance. All these indices were calculated separately for males and females, in order to account for sexual dimorphism as well as the differing physiological demands of reproduction between the sexes (Thometz et al. 2014).

To compute SSI, we fit von Bertalanffy growth functions to male and female data on body length (i.e., excluding tail length) vs. age:

$$f(\text{Age}) = \theta_1(1 - \exp(-\theta_2[\text{age} - \theta_3])), \quad (3)$$

where θ_1 , θ_2 , and θ_3 are parameters estimated by nonlinear least squares. To account for differing sample sizes among study groups, we used bootstrap resampling

TABLE 6. Summary of morphometric indices for sea otters at 15 island/location–time groupings (study groups) nested within three regions.

Region/study group	Status	No. of otters	No. of Females	No. of Males	BMI (mean)	BMI (sd)	SSI (mean)	SSI (sd)	Morphometric Indices	
									DCI (mean)	DCI (sd)
West										
West Aleutians (pre-1970)	Stable	1,413	993	420	5.47	3.66	−5.24	5.54	−0.79	2.80
Bering Island (2004–2006)	Stable	103	42	61	−2.28	3.74	0.12	5.38	−0.76	2.52
Amchitka (1992–1993)	Declining	115	77	38	−1.81	3.27	−2.73	7.55	1.29	3.00
Adak (1995)	Declining	37	28	9	−1.05	2.58	−3.52	3.12	2.48	2.27
Clam Lagoon (1995)	Stable	17	11	6	−4.76	2.83	−7.69	3.09	1.08	1.97
Clam Lagoon (2012)	Stable	24	12	12	0.10	2.89	1.66	4.73	0.76	1.22
West Aleutians (1997)	Declining	71	42	29	−0.58	3.28	−0.90	3.85	1.50	2.30
West Aleutians (2004)	Postdecline	11	9	2	3.28	2.56	2.82	2.96	3.30	2.71
East										
AK_Peninsula W (2009)	Postdecline	37	19	18	2.47	3.44	4.09	5.25	1.79	1.63
Katmai (2009)	Growing	30	18	12	1.62	3.53	0.45	3.26	2.95	2.34
GOA										
Neastern Kodiak (1986–1988)	Growing	54	32	22	2.17	2.93	3.88	3.99	1.60	2.60
Kodiak Island (2004–2005)	Growing	30	14	16	2.68	3.18	4.80	3.52	1.61	2.27
Northeastern Kodiak (2004–2005)	Stable	54	33	21	1.42	3.35	2.40	4.88	1.68	1.77
Kachemak (2007)	Growing	44	12	32	3.24	3.47	3.71	4.09	2.77	2.18
PWS (2007–2012)	Stable	151	113	38	−0.78	2.51	−0.79	3.76	1.24	1.84

Note: BMI = body mass index; SSI = structural size index; DCI = dynamic condition index (see text for details).

methods to draw random samples (with replacement) from each group ($n = 50$ for each sex), fit the growth functions to the bootstrap samples, and repeated this process 1,000 times to obtain a sample-size adjusted average growth curve (Table 7). We then computed SSI as the residual values from this average curve. Positive SSI values thus indicated animals that were longer than expected for their age while negative values indicated otters that were shorter than expected. To compute BMI, we repeated the above process for body mass vs. age growth curves (Table 7). Positive BMI values thus indicated animals that were heavier than expected for their age, and negative values indicated that the animals were lighter than expected.

To compute DCI, we first fit a robust, iteratively reweighted least-squares regression (Hampel et al. 2011) to individual estimates of BMI vs. SSI. The resulting linear fit indicated the expected deviation from the average mass at age curve after accounting for deviation from average length at age (i.e., accounting for the fact that longer animals will also be heavier by reason of allometry). We calculated DCI as the residuals from this linear model: positive DCI values indicated animals that were heavier than expected after accounting for the effects of both age and structural size, and negative values indicated otters that were lighter than expected after accounting for the effects of age and structural size.

For each index—SSI, BMI, and DCI—and for each sex, we fit a linear mixed effect model (LMM) to test for an effect of population status (with respect to the decline) on body size/condition. Similar to our classification of islands/locations for carcass recovery rate analysis, we assigned each sample group to one of four values of population status based on available survey data: (1) “stable” (no significant positive or negative trend, presumably near K); (2) “growing” (time series indicate positive population growth); (3) “declining” (populations within the area of decline sampled after 1989 but before 2001); or (4) “postdecline” (populations within the area of decline sampled after 2001). We also assigned each island/location to broad oceanographic regions (West,

East, Gulf of Alaska), using the same definitions described for the carcass analysis, and included region as a random effect in the model. We tested for differences in each metric for growing, declining, and postdecline populations relative to stable populations (the reference level in the LMM model).

We calculated and plotted means and 95% CI for SSI, BMI, and DCI by population status. To examine spatial trends in contemporary data (post-2004) visually, we plotted the indices by study group, arranged by longitude. For the western Aleutian Islands where there were multiple sampling periods, we also evaluated temporal trends in morphometric indices, to determine if these were consistent with spatial comparisons. We fit a simple linear model to the index-vs.-time data to test for directional change. In particular, we wanted to know if there were predictable trends in body size/condition at those islands/locations that underwent a population decline.

Diet and energy intake rate (EIR)

Uncertainty about the cause of the recent population decline in southwest Alaska has resulted in questions about nutritional limitation as a potential contributing factor (Kuker & Barrett-Lennard 2010). If limited food resources were a causal factor in the decline or in preventing population recovery, we would expect predictable trends in energy intake rates and diet composition (Table 1). Specifically, we would predict a reduction in energy intake rates and an increase in diet diversity within the area of decline, as compared to non-decline areas to the east and west. Conversely, if the cause of the decline (and impediments to recovery) were independent of prey abundance, then we would expect prey populations to respond to reduced sea otter densities through increased abundance and sizes (Estes & Duggins 1995, Tinker et al. 2008a). Consequently, we would predict an increase in energy intake rates and a decrease in diet diversity in the area of decline, as compared with areas to the east and west that were not in decline. Comparisons of these parameters among study groups allows us to infer whether or not nutritional limitation has been important in causing the decline or preventing recovery in the area of decline.

Sea otters are unique among marine mammals in that they bring all captured prey to the ocean’s surface for consumption (Riedman & Estes 1990). And because feeding generally occurs in proximity to shore, this trait allows for the measurement of diet composition and food intake rates via direct observation (Calkins 1978, Estes et al. 1981, Bodkin & Ballachey 1996, Dean et al. 2002, Tinker et al. 2008a). In particular, because the relative abundance of food resources limits further population increase, sea otter populations at high densities typically exhibit patterns consistent with nutritional limitation—that is, a reduction in the rate of biomass intake and energy intake (Watt et al. 2000, Dean et al. 2002), increased time spent feeding (Estes et al. 1982, Ralls &

TABLE 7. Parameters for von Bertalanffy function fit to data on mass at age and length at age (excluding tail length) for male and female sea otters.

Model	θ [1] mean (sd)	θ [2] mean (sd)	θ [3] mean (sd)
Female mass	24.347 (0.153)	0.930 (0.096)	−0.252 (0.120)
Female length	93.635 (0.206)	1.221 (0.139)	−0.511 (0.134)
Male mass	32.854 (0.251)	0.700 (0.044)	−0.238 (0.062)
Male length	101.522 (0.295)	0.937 (0.083)	−0.851 (0.144)

Note: Refer to Eq. 3 in text for functional form of von Bertalanffy equation.

Siniff 1990, Bodkin et al. 2007) and increased dietary diversity at the population level (Ostfeld 1982, Tinker et al. 2012, Newsome et al. 2015), although the latter pattern may in some cases be caused by diet specialization at the individual level (Tinker et al. 2008a, Newsome et al. 2009). In contrast, sea otter populations at low density typically exhibit the opposite patterns.

We recorded observations of sea otter foraging behavior at 15 locations (Table 8) using focal animal sampling methods (Altmann 1974) adapted for sea otter work in many previous studies (Calkins 1978, Estes et al. 1981, Ostfeld 1982, Doroff & Degange 1994, Ralls et al. 1995, Bodkin & Ballachey 1996, Watt et al. 2000, Dean et al. 2002, Tinker et al. 2008a). We used high power telescopes (Questar Corp., New Hope, Pennsylvania, USA) and 10× binoculars, along with stopwatches to record dive and surface times, capture success, prey type, prey number, and prey size during foraging bouts of focal animals. The length of foraging bouts was limited to 20 dives, or 1 h, after which a new focal animal was chosen.

We identified >50 different types of prey, which were collapsed into 16 prey categories for analysis (Table 9). We assembled information on diameter–biomass relationships and calorific content of each prey type from the literature, relying primarily on a study of sea otter nutrition in California and Southeast Alaska (Oftedal et al. 2007). The species-specific diameter–biomass power functions allowed us to convert the size class estimates of each captured prey item into an estimate of wet-edible biomass (Oftedal et al. 2007, Tinker et al. 2008a, Tinker et al. 2012). By multiplying the estimated biomass of each prey item by the species-specific calorific density (Table 9), we calculated the number of calories contributed by each prey capture. Standard error values were associated with both the biomass and caloric estimates for each prey capture (Oftedal et al. 2007), such that this source of uncertainty could be incorporated into further analyses.

For the data collected in each island/location we quantified diet diversity at the population level using the Shannon diversity index:

$$H' = - \sum_{i=1}^S p_i \ln(p_i), \quad (4)$$

where S is the total number of prey types and p_i is the proportion of all prey captures accounted for by the i th prey type. The Shannon index provides a measure of diet richness and evenness, with higher values indicating a more diverse diet.

We calculated energy intake rates (henceforth EIR) and diet composition using a Monte Carlo, resampling algorithm designed to account for uncertainty and biases inherent in the raw data by using maximum-likelihood methods to identify the most likely outcome of “unidentified” prey within the forage record rather than simply assume the composition of unidentified prey

is the same as that of identified prey types (Dean et al. 2002, Tinker et al. 2008a, Tinker et al. 2012).

We calculated means, standard errors, and 95% CI for EIR and H' metrics for each sample group, and fit linear mixed effect models (LMM) to test for an effect of population status (with respect to the decline) on these metrics. We assigned each sample group to one of four values of population status (stable, growing, declining, postdecline) using the same definitions and criteria described above for morphometric analyses. We included region as a random effect in LMM models (region = west, east, or Gulf of Alaska), as for carcass recovery and morphometric analyses. We tested for differences in each metric for growing, declining and postdecline populations relative to stable populations (the reference level in the LMM models). In the case of significant differences, we examined spatial trends in contemporary data (post-2004) along a latitudinal gradient. For the western Aleutian Islands where there were multiple sampling periods, we also evaluated temporal trends over the past four decades, fitting a linear regression model to the EIR-vs.-time data to test for directional change. Finally, to test whether variation in body condition (see *Morphometrics*) was related to variation in EIR, we combined morphometric data and foraging data for those island/location-by-year combinations where both data types were available, and used linear regression to evaluate potential relationships between body size/condition indices (SSI, BMI, DCI) and EIR while feeding.

Food availability

Sea otter predation has a strong limiting influence on the density, distribution, and size of their benthic and epibenthic invertebrate prey. There is also extensive evidence that the relative abundance of food resources and associated nutritional factors are the primary determinants of carrying capacity in most sea otter populations (Kenyon 1969, Garshelis et al. 1986, Estes et al. 1996, Bodkin et al. 2000, Thometz et al. 2016, Tinker et al. 2019a). One of our objectives was thus to measure food availability across and beyond the range of the sea otter population decline. If food limitation figured prominently in the decline, we would expect the sea otter's invertebrate prey resources, especially urchin biomass densities, to correlate positively with sea otter population trajectory and density. Conversely, if food limitation was not a factor in the decline, we would expect benthic invertebrate prey and biomass densities to correlate negatively with sea otter population abundance because of the sea otter's strong and well-established limiting influence on prey populations.

Our analyses are based exclusively on hard-bottom habitats, in part because the relations between sea otters and their prey are well described in these habitats and in part because of the availability of historic and contemporary data. We assumed that any overall relationship between sea otter population status and prey availability

TABLE 8. Summary of diet composition (% biomass) and foraging metrics for 15 island/location-year groupings (study group), grouped within three regions.

Study group	Status	Bouts (no.)	Diet composition (prey type)											Energy intake rate (se)	
			Urchin	Clam	Mussel	Crab	Cephalopod	Fish	Star	Snail	Worm	Chiton	Other		Diversity
West															
Bering Island 2006–2007	Stable	59	0.54	0.04	0.13	0.19	0.02	0.02	0	0.05	0	0	0.01	1.41	4.04 (0.28)
Amchitka 1992–1994	Declining	610	0.68	0.12	0.01	0.01	0	0.17	0.01	0	0	0	0.00	1.00	6.28 (0.21)
Adak 1995–1996	Declining	184	0.33	0.4	0	0.18	0	0.02	0.01	0	0.05	0	0.01	1.39	9.09 (0.55)
Clam Lagoon 2007–2012	Stable	84	0	0.55	0	0.25	0.01	0	0	0	0.13	0.02	0.02	1.21	6.36 (0.30)
Adak 2005–2008	Postdecline	539	0.52	0.11	0.06	0.04	0	0.2	0	0	0.01	0.03	0.04	1.50	18.10 (0.99)
West Aleutians 2009–2015	Postdecline	101	0.8	0	0	0.01	0	0.18	0	0	0	0.01	0.01	0.60	19.19 (3.06)
East															
East Aleutians 2009	Postdecline	44	0.6	0.02	0	0.23	0.02	0.02	0	0	0.05	0.06	0.01	1.18	15.40 (1.50)
Alaska Peninsula West 2009	Postdecline	106	0.55	0.03	0	0.19	0.07	0	0.01	0.02	0.01	0.03	0.10	1.43	19.08 (1.99)
Katmai 2006–2009	Growing	199	0.15	0.6	0.02	0.02	0	0	0.03	0.13	0	0.05	0.00	1.30	10.98 (0.61)
Katmai 2010–2013	Stable	170	0.09	0.58	0.02	0.04	0	0.01	0.05	0.15	0	0.05	0.00	1.42	6.31 (0.29)
GOA															
Kodiak Island 1988	Growing	62	0.07	0.7	0.05	0.13	0	0	0	0.04	0	0	0.00	1.02	19.26 (1.03)
Northeastern Kodiak 1988	Growing	88	0.04	0.67	0.05	0.22	0	0	0	0	0	0	0.01	0.97	16.39 (1.11)
Kodiak Island 2004–2005	Growing	48	0.01	0.39	0.08	0.45	0	0	0.02	0	0	0.03	0.00	1.23	12.63 (1.56)
Kenai 2007–2013	Stable	324	0.06	0.33	0.49	0.02	0	0	0.01	0	0	0.06	0.03	1.31	6.33 (0.37)
Prince William Sound 2007–2013	Stable	443	0.02	0.46	0.13	0.11	0.03	0.02	0.02	0	0.01	0.02	0.17	1.87	7.10 (0.27)

TABLE 9. Summary of prey types identified in foraging data.

Prey class	Prey description	Number of occurrences	Edible biomass (g) mean	Edible biomass (sd)	Mean energy density (kcal/g)
1. Urchin	Green urchin, <i>Strongylocentrotus droebachiensis</i>	2,848	16.4	37.6	0.24
	Red urchin, <i>Strongylocentrotus franciscanus</i>	2	114.5	41.9	0.39
	Purple urchin, <i>Strongylocentrotus purpuratus</i>	15	83.6	153.6	0.39
	Urchin, unidentified species	28,767	10.3	37.5	0.32
2. Clam	Bivalve, unidentified	3,724	8.0	24.8	0.65
	Clam, unidentified	11,450	9.9	18.1	0.51
	Nuttall's cockle, <i>Clinocardium nuttallii</i>	41	23.8	32.8	0.46
	California sunset clam, <i>Gari californica</i>	11	16.1	10.8	0.51
	<i>Humilaria kennerleyi</i>	1	7.7		0.65
	Rock jingle, <i>Pododesmus macrochisma</i>	960	21.6	17.0	0.53
	Bent nosed clam, <i>Macoma nasuta</i>	9	7.0	5.7	0.32
	<i>Mactromeris polynyma</i>	2	38.7	18.7	0.51
	<i>Macoma</i> spp.	108	12.4	12.0	0.32
	Softshell clam, <i>Mya arenaria</i>	20	11.0	10.8	0.38
	<i>Mya</i> spp., softshell clam	31	14.4	27.1	0.38
	Soft-shell clam, <i>Mya truncata</i>	1,395	5.9	19.4	0.38
	Littleneck clam, <i>Leukoma staminea</i>	24	12.1	18.1	0.54
	Butter clam, <i>Saxidomus giganteus</i>	2,541	32.5	33.9	0.51
	Clam, <i>Serripes groenlandicus</i>	23	15.1	11.7	0.51
3. Mussel	Fat gaper clam, <i>Tresus capax</i>	33	172.1	99.7	0.68
	Discordant mussel, <i>Musculus</i> sp.	140	0.7	1.7	0.33
	Blue mussel, <i>Mytilus trossulus</i>	17,333	2.2	5.4	0.33
	Mussel, unidentified	7,109	3.2	14.9	0.41
4. Modiolus	Horse mussel, <i>Modiolus modiolus</i>	8	36.5	27.2	0.50
5. Crab	Dungeness crab, <i>Cancer magister</i>	54	63.6	51.8	1.22
	Cancer crab, <i>Cancer</i> spp. (usually <i>productus</i>)	6	69.4	54.6	1.22
	Crab, <i>Chinectes bairdi</i>	2	46.4	52.4	0.84
	Crab, unidentified	1,133	38.6	52.0	0.84
	<i>Pacific lyre crab, Hyas lyratus</i>	8	32.3	21.0	0.80
	Red king crab, <i>Paralithodes camtschaticus</i>	5	320.4	117.4	0.84
	Hermit crabs, <i>Pagurid</i> spp.	6	42.1	28.9	1.06
	Kelp Crabs, <i>Pugettia</i> spp.	5	9.8	0.0	1.06
	Helmet crab, <i>Telmesus</i>	556	57.8	46.6	0.80
6. Shrimp	Shrimp, <i>Pandalus</i>	105	37.9	54.3	0.80
7. Cephalopod	Octopus, <i>Enteroctopus dofleini</i>	91	277.2	93.2	0.98
8. Fish	Fish, various species	232	41.0	33.6	1.22
	Flatfish, various species	94	54.3	12.4	1.23
	Greenling, <i>Hexagrammos</i> spp.	57	24.6	16.6	1.38
	Pacific lumpsucker, <i>Aptocyclus ventricosus</i>	279	33.7	6.0	1.38
	Sand lance, <i>Ammodytes hexapterus</i>	907	2.6	3.9	1.17
	Sculpin, Family <i>Cottidae</i>	7	59.4	10.2	1.11
9. Fish egg	Fish egg mass	277	51.1	111.2	1.43
10. Star	Star, <i>Leptasterias</i> spp.	33	66.8	43.1	1.38
	Brittle star, <i>Ophiopsilla</i> spp.	105	1.8	1.4	0.86
	Ochre star, <i>Pisaster ochraceus</i>	37	66.9	31.6	1.38
	Sunflower star, <i>Pycnopodia helianthoides</i>	11	32.8	55.7	0.46
	Sunstar, <i>Solaster</i> spp.	9	56.9	41.3	0.46
	Sea star, various species	205	47.3	31.5	1.01
11. Snail	Moon snail, <i>Neverita lewisii</i> (previously <i>Euspira lewisii</i>)	3	28.9	13.9	1.11
	<i>Fusitriton oregonensis</i>	11	20.8	0.0	1.11
	Lyre whelk, <i>Neptunea</i> spp.	12	36.9	16.0	1.11
	<i>Nucella</i> spp.	130	3.3	6.9	1.11
	Marine snail, various species	1,396	8.2	17.2	1.11

TABLE 9. Continued.

Prey class	Prey description	Number of occurrences	Edible biomass (g) mean	Edible biomass (sd)	Mean energy density (kcal/g)
12. Worm	Fat innkeeper worm, <i>Echiuris</i> spp.	203	17.5	7.2	0.50
	Peanut worm, <i>Phascolosoma agassizi</i> , <i>Golfingia procera</i>	5	10.0	1.1	0.74
	Worm, various species	1,194	11.0	5.7	0.74
	Worm-like prey	98	8.8	3.4	0.50
13. Chiton	Chiton, various species	195	57.7	81.2	0.54
	Gumboot chiton, <i>Cryptochiton stelleri</i>	98	54.0	67.7	0.54
	Black katy chiton, <i>Katharina</i> spp.	200	11.1	13.4	0.54
14. Scallop	Pink scallop, <i>Chlamys rubida</i>	1,112	2.7	10.0	0.53
	Scallop, various species	860	3.5	7.6	0.53
15. Sea cucumber	<i>Parastichopus californicus</i>	137	38.6	45.9	0.11
16. Other	Algae with invertebrate fauna	709	0.9	3.6	0.50
	Barnacle, various species	305	1.8	17.5	0.60
	Sand dollar, <i>Dendraster</i> spp.	20	6.2	6.2	0.21
	Skate egg case	3	639.2	0.0	1.43
	Sea peach, <i>Halocynthia aurantium</i>	3	177.8	107.2	0.34
	Algal holdfast with invertebrate fauna	82	4.3	1.1	0.50
	Limpet, various species	92	1.4	1.6	0.92
	Mollusk, unidentified	301	1.3	4.2	0.70
	Tunicates, various species	18	6.7	3.8	0.34

would be reflected in the hard-bottom system, which, while proportionally more abundant in the oceanic islands of the Aleutian archipelago than along the shores of the continental shelf, was common throughout the areas of our study.

Data on urchin abundance were obtained by scuba divers using an established sampling protocol (Estes & Duggins 1995, Estes et al. 2010, Watson & Estes 2011). Briefly, at each island/location, a large number of sites along the shoreline were selected randomly using a stratified GIS-based method (random points distributed within the desired depth range filtered to rocky substrate). The benthic communities at each site were then sampled by placing 0.5 × 0.5 m quadrats at random intervals along the 20–25-ft. depth contour. All sea urchins were collected from within these quadrats, noting the number of individuals in each quadrat but pooling the samples in a single bag. Sampling was continued at any site until 200 individual urchins or 20 plots had been sampled, whichever occurred first. The urchin samples were brought to the surface where the diameter of each individual was measured. We focused on sea urchins because (1) they are common in shallow rocky habitats throughout much of the North Pacific Ocean, (2) they are a preferred prey item of sea otters throughout the otter’s range, and (3) an inverse relationship between sea otter abundance and sea urchin biomass density has been well documented. We conducted this sampling protocol at 30 islands/locations in the 2005–2009 period (Table 2), with 2–31 sites (mean = 15.6, median = 15.5) sampled at each, depending upon weather and other logistic constraints. We use these data (1) to describe geographic variation in sea urchin biomass density in

the postdecline period, (2) to assess how geographic variation in this parameter corresponds with sea otter population status, and (3) to explore the patterns of sea urchin recruitment based on size-frequency distributions. We augmented this data set with historical data from Bering Island and the Aleutian archipelago collected prior to 2005 (Estes & Duggins 1995, Estes et al. 1998), in order to evaluate temporal trends at index Islands and to contrast mean urchin biomass densities between populations in predecline, declining, and postdecline states. We note that all urchin data included in this analysis have been previously published in a range-wide summary of urchin life history parameters (Ebert et al. 2018).

Sea urchin biomass varies with test diameter in accordance with a log-linear allometric relationship (Estes & Duggins 1995). We used this function to calculate average biomass values for urchin sizes varying from 1 to 165 mm in diameter. For each sample site having >0 urchins, we fit a nonparametric kernel density distribution to the urchin size-frequency data, using a log-spline density algorithm (Kooperberg & Stone 1992). We took the product of the resulting density distributions for each site (a vector of size-specific relative frequency values summing to 1 and the size-specific biomass values, summed these products, and multiplied by the mean urchin density (urchins per quadrat) to obtain the mean estimated urchin biomass density for each site. We also computed the cumulative probability densities associated with a threshold diameter (5 mm) and used this value as a recruitment index (i.e., a sample-size independent estimate of the relative proportion of urchins that recruited recently at a given site).

We fit GLMMs to test for an effect of population status (with respect to the decline) on sea urchin biomass and urchin recruitment (Table 10). We assigned each island/location to one of four values of population status (stable, growing, declining, postdecline) using the same definitions and criteria described above for morphometric analyses. For these models we included both region (west, east, or Gulf of Alaska, using the same definitions as for carcass and morphometric analyses) and island (nested within region) as random effects. We assumed a log-normal distribution for urchin biomass (Gaussian with log-link function) and a gamma distribution (with log-link function) for urchin recruitment, based on visual examination of the data distributions. We tested for differences in each metric for growing, declining, and postdecline populations relative to stable populations (the reference level in the GLMMs).

To explore spatial and temporal trends in prey availability further, we subdivided the data set in two ways. First, we filtered the data to include just those islands/locations sampled during the 2005–2009 field seasons (i.e., the postdecline period) and used these data to examine spatial trends while holding time constant. For this spatial analysis we fit GLMMs to test for differences in urchin biomass and recruitment as a function of population status and region, using island as a random effect (assuming the same data distributions and link functions described above), and we plotted island-specific estimates on a longitudinal axis to visually examine spatial patterns. Next, to examine temporal trends, we filtered the data to include only data for the three most frequently sampled index islands—Attu, Amchitka and Adak—for all years between 1987 and 2015. We fit GLM models to test for differences in urchin biomass and recruitment as a function of island and time period (predecline = 1987–1990, declining = 1990–2000, postdecline = 2001–2015), and allowed for an interaction between these two categorical effects. We then plotted island-specific estimates vs. time period to assess temporal patterns in urchin biomass within the area of decline.

Health and disease assessment

Although the available evidence led Estes et al. (1998) to conclude that health or disease factors were not likely involved in the decline of sea otters in the Aleutian archipelago, it is possible that these factors were important elsewhere in the area of decline, or that they contributed to the lack of recovery. To assess those possibilities further, we looked for evidence of disease, disease exposure, and general health conditions in the animals that were captured for the morphometric analyses (see *Morphometrics*).

During captures (described in *Morphometrics*), animals were examined by a wildlife veterinarian (MM) to obtain a qualitative health profile and scored for presence/absence of seven different types of readily diagnosed infectious and noninfectious diseases (Table 11).

In addition, tissue samples were obtained for subsequent laboratory analyses that included serum chemistry, hematology, and gene transcription. We then contrasted these data among the various sample populations to determine if there were any covarying patterns with sea otter population status.

Blood samples for serum chemistry were collected in anticoagulant free tubes, and the tubes centrifuged to separate the cellular and serum components of the blood. Aliquots of approximately 1.0 mL of serum were harvested and frozen at -20°C until they could be shipped for processing. Serum chemistry was evaluated with a Beckman-Coulter AU640E clinical chemistry analyzer (the Olympus AU640E was used in 2004) by Quest Diagnostics[®] laboratory in Portland, Oregon, USA. We report data for 15 serum variables: glucose (GLU), blood urea nitrogen (BUN), creatinine (CREAT), sodium, potassium, chloride, carbon dioxide (CO_2), calcium, total protein, albumin, globulin, albumin:globulin ratio (A:G), aspartate transaminase (AST), and alanine transaminase (ALT; Tables 12 and 13).

Evaluation of the hemogram is often problematic in field research settings where laboratory resources are not available. In the traditional clinical setting, whole blood samples with an anticoagulant are evaluated within 24 h of collection. Over time, the cellular components of the blood deteriorate, negatively impacting both the quantitative and qualitative aspects of the hemogram. For that reason, we elected to analyze only those components of the complete blood count (CBC) that could either be performed in the field (hematocrit and hemoglobin level) or tolerate a protracted storage period before analysis (e.g., peripheral smear evaluation to provide a differential cell count). We report data for eight hematology variables (Tables 12 and 14): total estimated white blood cell count (WBC), packed cell volume (PCV), hemoglobin (Hgb), and the differential white blood cell count consisting of neutrophils (Neut%), lymphocytes (Lymph%), monocytes (Mono%), eosinophils (Eos%), and basophils (Baso%).

We compared the results of physical examinations of animals in populations within and outside the area of decline. Specifically, for each of seven disease types, we created a contingency table of cases scored by disease presence/absence and decline status (yes/no) and used Barnard's exact test (Barnard 1945) to determine whether observed frequencies of disease incidence differed as a function of population status. We next used linear models to analyze the influence of location on blood-based health parameters, visually comparing the means and 95% CI for each parameter across locations. However, examination of differences in individual parameters in the serum and hematology data sets are of limited use because of strong correlations between metrics and the inflated type-I error rates associated with a large number of comparisons. We therefore employed nonparametric multidimensional scaling analysis (NMDS) to evaluate variation in serum and hematology

TABLE 10. Summary of subtidal sampling and resulting estimates of urchin biomass and recruitment index.

Region and island/location	Status	Latitude	Longitude	First year sampled	Last year sampled	No. of years sampled	No. of urchin sites sampled	Mean urchin biomass (g/0.25 m ²)	Urchin recruitment index
West									
Bering	Stable	55.252	166.042	2006	2006	1	25	28.64	0.004
Attu	Growing	52.800	173.184	1987	1990	2	24	187.98	0.008
Attu	Declining	52.810	173.187	1993	2000	3	43	91.11	0.004
Attu	Postdecline	52.832	173.203	2008	2015	3	31	594.75	0.003
Agattu	Declining	52.396	173.592	1993	1993	1	6	114.25	0.077
Agattu	Postdecline	52.396	173.592	2008	2015	2	10	681.65	0.012
Alaid	Growing	52.767	173.900	1987	1987	1	10	373.79	0.036
Alaid	Declining	52.767	173.900	1994	1997	2	19	357.87	0.013
Alaid	Post-Decline	52.765	173.906	2008	2015	3	14	390.06	0.003
Nizki	Growing	52.744	173.981	1987	1987	1	8	412.55	0.024
Nizki	Declining	52.744	173.982	1993	1997	3	15	247.89	0.005
Nizki	Postdecline	52.744	173.981	2008	2015	3	11	618.85	0.000
Shemya	Growing	52.730	174.110	1987	1987	1	16	408.36	0.036
Shemya	Declining	52.731	174.106	1993	1997	3	31	331.51	0.009
Shemya	Postdecline	52.731	174.105	2008	2015	3	20	425.62	0.002
Kiska	Declining	51.930	177.586	1993	2000	2	40	333.64	0.015
Kiska	Postdecline	51.931	177.592	2008	2015	4	36	505.52	0.015
Rat	Declining	51.801	178.292	1994	1994	1	13	637.95	0.010
Rat	Postdecline	51.800	178.304	2008	2015	3	24	582.30	0.004
Amchitka	Stable	51.424	179.271	1987	1987	1	29	46.78	0.029
Amchitka	Declining	51.427	179.260	1999	2000	2	42	438.13	0.060
Amchitka	Postdecline	51.427	179.259	2008	2015	3	42	371.08	0.027
Ogliuga	Declining	51.598	-178.658	1994	1994	1	4	309.16	0.015
Ogliuga	Postdecline	51.598	-178.663	2008	2015	3	20	771.38	0.009
Skagul	Declining	51.583	-178.584	1994	1994	1	2	348.31	0.020
Skagul	Postdecline	51.588	-178.581	2008	2008	1	6	984.86	0.008
Tanaga	Declining	51.767	-177.936	1994	1994	1	13	104.44	0.023
Tanaga	Postdecline	51.775	-177.891	2008	2014	3	25	380.12	0.011
Adak	Stable	51.846	-176.545	1987	1987	1	29	42.86	0.027
Adak	Declining	51.847	-176.544	1997	2000	3	88	268.69	0.008
Adak	Postdecline	51.847	-176.546	2008	2015	4	42	280.93	0.015
Atka	Postdecline	52.135	-174.628	2008	2008	1	10	377.34	0.007
Seguam	Declining	52.304	-172.605	1994	1994	1	10	560.44	0.035
Seguam	Post-Decline	52.268	-172.606	2009	2010	2	7	309.86	0.008
East									
Yunaska	Declining	52.678	-170.715	1994	1994	1	12	562.73	0.033
Yunaska	Postdecline	52.657	-170.769	2009	2009	1	8	603.14	0.010
Chuginadak	Declining	52.882	-169.825	1994	1994	1	12	480.75	0.087
Chuginadak	Postdecline	52.882	-169.823	2008	2009	2	13	268.06	0.018
Anangula	Declining	53.003	-168.903	1994	1994	1	4	1.53	0.000
Anangula	Postdecline	53.003	-168.907	2009	2009	1	10	0.35	0.000
Umnak	Declining	52.936	-168.943	1994	1994	1	4	3.93	0.000
Umnak	Postdecline	52.936	-168.943	2009	2009	1	4	2.51	0.000
Unalaska	Declining	53.389	-167.648	1994	1994	1	12	4.74	0.036
Unalaska	Postdecline	53.389	-167.650	2009	2010	2	14	1.11	0.000
Akutan	Declining	54.185	-165.820	1994	1994	1	12	61.07	0.052
Akutan	Postdecline	54.176	-165.801	2008	2008	1	27	59.61	0.003
Sanak	Postdecline	54.399	-162.751	2008	2008	1	27	8.08	0.000
Pavlof Bay	Postdecline	55.080	-161.858	2008	2008	1	16	2.80	0.000
Unga	Postdecline	55.169	-160.588	2008	2008	1	29	11.28	0.000
Chiacha	Postdecline	55.844	-159.107	2008	2008	1	16	6.09	0.004
Mitrofanina	Postdecline	55.838	-158.811	2008	2008	1	17	2.33	0.006
Semidi	Postdecline	56.047	-156.702	2008	2008	1	19	0.29	0.000

TABLE 10. Continued.

Region and island/location	Status	Latitude	Longitude	First year sampled	Last year sampled	No. of years sampled	No. of urchin sites sampled	Mean urchin biomass (g/0.25 m ²)	Urchin recruitment index
Amalik Bay	Growing	58.065	−154.444	2008	2008	1	16	0.92	0.000
Kodiak	Growing	56.916	−154.069	2008	2008	1	7	5.02	0.004
Kukak Bay	Growing	58.335	−154.071	2008	2008	1	15	0.10	0.000
Sitkalidak	Growing	57.063	−153.372	2008	2008	1	13	138.35	0.000
GOA									
Kachemak Bay	Growing	59.430	−151.803	2008	2008	1	3	1.16	0.000
SEAK									
Sitka	Growing	57.006	−135.332	2009	2009	1	29	2.46	0.004

TABLE 11. Summary of disease incidence based on physical examinations of captured sea otters.

Inside region of decline?		Capture site and year					
		Bering Island	Aleutian Island	Clam Lagoon	Alaskan Peninsula	Katmai	PWS
		2008 N	West 2004 Y	2012 N	2009 Y	2009 N	2008–2010 N
Total captured	No.	42	11	24	31	28	45
Males	No.	8	2	12	15	11	8
Females	No.	34	9	12	16	17	37
Dental disease	No.	11	2	4	1	0	6
	%	26.2%	18.2%	16.7%	3.2%	0.0%	13.3%
Wounds	No.	5	3	2	5	2	1
	%	11.9%	27.3%	8.3%	16.1%	7.1%	2.2%
Papilloma	No.	0	0	1	1	0	1
	%	0.0%	0.0%	4.2%	3.2%	0.0%	2.2%
Neoplasia I	No.	0	0	0	0	0	1
	%	0.0%	0.0%	0.0%	0.0%	0.0%	2.2%
Cardiac disease	No.	1	0	0	0	0	1
	%	2.4%	0.0%	0.0%	0.0%	0.0%	2.2%
Abscess	No.	0	1	0	0	0	1
	%	0.0%	9.1%	0.0%	0.0%	0.0%	2.2%
Lymphadenopathy	No.	0	0	1	0	0	0
	%	0.0%	0.0%	4.2%	0.0%	0.0%	0.0%
SUM otters	No.	17	6	8	7	2	11
MEAN	%	5.8%	7.8%	4.8%	3.2%	1.0%	3.5%

parameters in multivariate space. We used a Bray–Curtis dissimilarity metric, and assuming successful model convergence, we saved NMDS scores for three dimensions and used these within a k-means cluster analysis (Hartigan & Wong 1979) to assess whether there were natural groupings in the transformed data. We used the silhouette method combined with examination of elbow plots (Kaufman & Rousseeuw 2009) to determine the optimal number of clusters. We then plotted an ordination of NMDS scores, color-coded by location. If the k-means cluster analysis showed support for multiple distinct clusters, we overlaid the scatter plot with 95% confidence ellipses corresponding to each cluster, and visually assessed whether the clusters separated samples from populations within vs. outside the area of decline. If the k-means cluster analysis failed to show support for

multiple clusters, we overlaid the scatter plot with 95% confidence ellipses around data collected within vs. outside the area of decline, to assess whether the distribution of data in NMDS space reflected differences between decline and nondecline populations. We then statistically compared NMDS scores across locations using multiple analysis of variance (MANOVA) followed by post hoc pairwise comparisons using Tukey adjustments for multiple comparisons (implemented using the “emmeans” package in R).

Gene transcription

Molecular technology to amplify and simultaneously quantify a targeted DNA molecule have provided important information on the physiological mechanisms that

TABLE 12. Summary and interpretation of serum and hematology variables.

Parameter					
Analyte	Acronym	Primary	Secondary	Minor use	Comments
Glucose	GLU	Energy intake, mobilization	Catecholamine response (fight or flight)	Endocrine function	Labile parameter in whole blood
Blood urea nitrogen	BUN	Kidney	Hydration	Postprandial, high-protein meal	
Creatinine	CREAT	Kidney	Hydration		
BUN:creatinine ratio	BUN:CR	GI hemorrhage			Not very useful in vet medicine
Sodium	Na	Hydration, water intake	Kidney	Endocrine function	
Potassium	K	RBC hemolysis	Acid/Base balance	Endocrine function	Artifact of sample handling >> increase
Chloride	Cl	Hydration, water intake	Kidney	Acid/Base balance	
Carbon dioxide	CO ₂	Acid/base balance	Kidney	Respiratory, GI tract	Proxy for HCO ₃ buffering
Calcium	Ca	Vitamin D metabolism	Dietary	Systemic neoplasia	
Total protein	TP	Hydration	Protein loss (blood loss, renal loss)	Nutrition, GI tract	
Albumin	ALB	Hydration	Liver	Kidney	
Globulin	GLOB	Hydration	Inflammatory disease		Calculated value (TP – Alb = Glob)
Albumin:globulin ratio	A:G	Systemic inflammatory disease	Immune status		The ratio and globulin fractions are typically calculated
Alkaline Phosphatase	AP	Liver, biliary stasis	Bone	Hormone induction	Higher values with growing skeleton
Aspartate transferase	AST	Liver inflammation	Muscle (skeletal, cardiac)	GI tract, RBC hemolysis	Not considered liver-specific in carnivores
Alanine transferase	ALT	Liver inflammation	Muscle (skeletal, cardiac)	RBC hemolysis	Most liver-specific enzyme in most chemistry panels
White blood cell count	WBC	Increase = infection	Decrease = immunosuppression	Increase due to catecholamine release	Estimated counts less accurate than automated or hemocytometer counts
Packed cell volume	PCV	Decrease = anemia	Increase = dehydration		Differentiating regenerative vs. non-regenerative anemia important
Hemoglobin	Hgb	Decrease = anemia	Increase uncommon	Decrease may be associated with red cell destruction	Differentiating regenerative vs. non-regenerative anemia important
Neutrophils	Neut%	Increase = infection	Decrease = chronic, overwhelming infection	Increase due to catecholamine release	See Note
Lymphocytes	Lymph%	Increase = chronic inflammation	Decrease = acute inflammation	Chronic stress may decrease	See Note
Monocytes	Mono%	Increase = chronic inflammation	Increase may be associated with tissue necrosis	Stress may elevate numbers	See Note
Eosinophils	Eos%	Increase = parasitism	Increase = allergic disorders	Function in sea otters not well described. Often elevated without causation ID	See Note

TABLE 12. Continued.

Parameter					
Analyte	Acronym	Primary	Secondary	Minor use	Comments
Basophils	Baso%	Increase = allergic reactions	Increase may be associated with some parasitic sensitivities	Function in sea otters not well described.	See Note

Note: Interpretation of the leukogram (white blood cell [WBC] count and its various cell types) must be done in consideration all WBC parameters, including WBC count and the differential count, both percentage of cell types and absolute numbers. Microscopic appearance of various cell types is also an important component of leukogram evaluation.

orchestrate an organism's integrated response to external stressors (Acevedo-Whitehouse & Duffus 2009). Gene transcription, which provides the transcriptional messages important in mediating toxicological and immunological reactions, can be measured to identify an organism's genomic stress response to environmental contaminants, disease, or other forms of biological or physical injury (Bartosiewicz et al. 2001, Bowen et al. 2007, Bowen et al. 2012, Miles et al. 2012). We used this technique to aid in identification of genes expressed among sea otter populations in southwest Alaska that could subsequently provide insight into external factors, such as various contaminants and diseases, potentially affecting these populations. Because this is a relatively new and developing method, it was only applied to samples obtained following the decline.

Between 2008 and 2012 we assayed gene transcription from 193 free-ranging sea otters from Clam Lagoon ($n = 24$), the western Alaska Peninsula ($n = 25$), Katmai National Park and Preserve (Katmai; $n = 32$), Kodiak Island ($n = 25$), and Prince William Sound ($n = 87$), and 17 healthy captive otters from California (Table 15). Sea otter blood was drawn into a tube containing RNA preservative, and RNA was subsequently isolated according to manufacturer's protocols (Qiagen Corp, Valencia, California, USA). A standard cDNA synthesis was performed on extracted RNA from each animal. Quantitative real-time polymerase chain reaction (qPCR) systems for individual, sea otter-specific reference gene and genes of interest were run in separate wells (Bowen et al. 2007). Amplifications were conducted on a 7300 Real-time Thermal Cycler (Applied Biosystems™, Foster City, California, USA) with reaction conditions identical to those in Bowen et al. (2007, 2012) and Miles et al. (2012). Analysis of real-time PCR data was conducted using normalized values, that is, housekeeping gene (computational) cycle threshold (C_T) crossing subtracted from the gene of interest threshold crossing. We analyze data from 10 genes of interest (Table 15): translationally controlled tumor protein HDCMB21P (HDC), arylhydrocarbon receptor (AHR; immune response, hydrocarbon exposure), thyroid hormone receptor (THRβ; response to contaminants); cyclooxygenase 2 (COX2; immune response, tumor), heat shock protein 70 (HSP70; response to stress); interleukin

18 (IL-18; immune response, interferon production), major histocompatibility complex DRB (DRB; immune response, pathogens), Mx1 (response to pathogens); complement cytolysis inhibitor (CYT; associated with cell and tissue death); and interleukin 10 (IL-10; anti-inflammatory associated with chronic disease).

We used linear models to analyze the influence of sex and location on each gene transcription level. The results of these univariate linear models were employed to inspect for differences in individual genes and identify those genes contributing the most variation. We then compared the marginal means and 95% CI for each gene by location. However, recognizing that univariate tests were complicated by covariation across suites of genes, as well as inflated type-I error rates associated with a large number of comparisons, we also conducted nonparametric multi-dimensional scaling analysis (NMDS) to evaluate variation in gene transcription profiles in multivariate space. We used a Bray–Curtis dissimilarity metric, and assuming successful model convergence, we saved NMDS scores for three dimensions and used these within a k-means cluster analysis (Hartigan & Wong 1979) to assess whether there were natural groupings in the gene transcription data. We used the silhouette method combined with examination of elbow plots (Kaufman & Rousseeuw 2009) to determine the optimal number of clusters. Having assigned each sample to its appropriate cluster membership, we plotted an ordination of NMDS scores (color coded by location) and 95% cluster confidence ellipses, to assess whether the clustering of samples tended to reflect differences between populations within vs. outside the area of decline. We statistically compared NMDS scores across locations using MANOVA, followed by post hoc pairwise comparisons (using Tukey adjustments for multiple comparisons).

Contaminants

Adverse influences of anthropogenic, biogenic, and naturally occurring chemical compounds on wildlife are widely known (Corvalan et al. 2005). These compounds are divisible into three broad classes—persistent organic compounds (POCs), inorganic compounds, and biotoxins. Our focus here is on POCs, in large measure because data on inorganics and biotoxins are unavailable.

TABLE 13. Summary of sea otter serum chemistry data from 11 island/location-by-year sampling events.

Location (Year)	Decline	No. of otters	Average parameter values by location/year															
			GLU	BUN	CR	BUN:CR	Na	K	Cl	CO2	Ca	TP	ALB	GLOB	A:G	AP	AST	ALT
Bering (2004)	N	32	109.5	64.2	0.7	109.0	151.0	4.2	112.6	20.7	8.5	6.2	2.6	3.6	0.73	95	200	153
Bering (2005)	N	26	146.3	66.7	0.5	131.7	150.2	4.1	115.1	26.0	8.4	6.3	2.6	3.7	0.72	95	267	189
Clam Lagoon (2012)	N	24	132.8	51.2	0.4	142.0	152.7	4.2	116.0	22.6	8.8	6.2	2.8	3.4	0.84	96	148	146
Aleutians West (2004)	Y	11	149.5	58.0	0.4	161.0	150.3	4.4	112.8	26.8	9.0	6.6	2.8	3.8	0.75	129	115	120
Aleutians East (2004)	Y	4	121.0	55.3	0.3	184.3	151.8	4.5	114.5	21.3	8.9	6.5	2.8	3.7	0.75	147	116	132
Alaska Peninsula W (2009)	Y	34	128.0	48.4	0.4	147.9	154.3	4.2	115.0	21.4	9.0	6.5	2.9	3.7	1.64	147	166	150
Katmai (2009)	N	25	132.1	51.8	0.4	124.9	153.9	4.2	113.9	22.5	8.9	6.9	3.0	3.9	0.76	113	151	127
Kodiak (2004)	N	44	125.5	43.7	0.4	146.3	153.1	4.3	115.5	22.2	8.7	6.6	2.8	3.8	0.78	183	310	186
Kodiak (2005)	N	28	125.2	46.5	0.4	135.8	152.1	3.9	117.2	23.4	8.7	6.6	2.7	3.8	0.73	113	192	142
Prince William Sound (2008)	N	46	155.0	47.0	0.4	131.4	151.8	3.9	114.9	21.1	8.7	6.6	2.7	3.8	0.73	98	179	186
Prince William Sound (2010)	N	27	137.3	55.7	0.4	162.0	150.7	3.9	116.5	26.8	8.8	6.5	2.8	3.7	0.77	84	188	183

Note: Glu, glucose; BUN, blood urea nitrogen; CR, creatinine; TP, total protein; ALB, albumin; GLOB, globulin; ALB:GLOB, albumin:globulin; AP, alkaline phosphatase; AST, aspartate transferase; ALT, alanine transferase.

Assessments are based on POC concentrations in blue mussels (*M. trossulus*), a widely used surrogate for measures of contaminants in coastal marine ecosystems (Lauenstein 1995), and in liver and blood of sea otters. In this case, our assessment of potential contaminant effects is based on contrasts between various islands in the Aleutian archipelago and southeast Alaska, where sea otters occur at high densities and their population has increased steadily since being reintroduced to this region in the late 1960s (Esslinger & Bodkin 2009, Bodkin 2015, Tinker et al. 2019b). We chose southeast Alaska over Prince William Sound for the contaminant comparisons because of concerns over confounding effects from the *Exxon Valdez* oil spill in 1989 and subsequent clean-up efforts.

Between 1996 and 2001 mussel samples (*M. trossulus*) were obtained and analyzed from 39 sites in the Aleutian archipelago (ranging from Attu Island in the west to Akutan Island in the east) and five sites in southeast Alaska (all from the Cross Sound/Port Althorp locations; Table 16). We calculated mean values (μg/kg, dry wt) for each of five contaminant types—total polychlorinated biphenyls (PCBs), dichlorodiphenyltrichloroethanes (DDTs), hexachlorocyclohexanes (HCHs), hexachlorobenzenes (HCBs), and chlordane—at each location and fit a locally weighted regression model (LOESS) describing variation in each contaminant as a function of longitude. We plotted the data for each contaminant type, along with LOESS smoothed trend and associated 95% confidence interval, to inspect trends and determine whether there were elevated levels of contaminants in the Aleutian archipelago (area of decline) as compared to southeast Alaska (nondecline area). A secondary question was whether elevated contaminant levels were associated with the sites of past or present military activity, as previous analyses have indicated that these sites may have elevated levels of certain chemical compounds (Estes et al. 1997, Bacon et al. 1999, Miles et al. 2009, Jessup et al. 2010, Reese et al. 2012).

We also sampled sea otter tissues at a subset of locations (Table 17) to determine whether patterns of variation in sea otter blood contaminant levels corresponded to the spatial patterns observed for mussels (using the same five contaminant types). Sea otter blood samples were obtained from wild-caught animals in the Aleutian Islands (Kiska, *n* = 7; Amchitka, *n* = 8; Kanaga, *n* = 7; Adak, *n* = 29), and southeast Alaska (Cross Sound/Port Althorp, *n* = 20). We plotted mean values (μg/kg, lipid wt) by capture island/location, with error bars denoting the ranges of measured values, and we compared values from Aleutian Islands locations to those from southeast Alaska. We also compared contaminant levels in otters captured near the sites of military bases with contaminant levels in otters captured at more pristine locations.

We note that previous analyses of these data have been presented elsewhere (Bacon et al. 1999, Jessup et al. 2010, Reese et al. 2012) and further details on methods of sample collection, preservation, and laboratory analyses are provided in these papers.

TABLE 14. Summary of sea otter hematology parameters from 11 island/location-by-year sampling events.

Location (year)	Decline	No. of otters	WBC	Average parameter values by location/year						
				Neut%	Lymph%	Mono%	Eos%	Baso%	PCV	Hgb
Bering (2004)	N	32	7.000	58.83	23.00	5.93	12.20	0.03	54.2	18.5
Bering (2005)	N	26		68.08	16.15	8.08	7.54	0.15	50.8	10.5
Clam Lagoon (2012)	N	24	8.075	52.88	38.08	6.71	1.79	0.33	.	.
Aleutians West (2004)	Y	11	6.514	40.55	38.64	4.36	16.45	0.00	51.7	.
Aleutians East (2004)	Y	0		.	.	.	.	.	.	.
Alaska Peninsula West (2009)	Y	34	9.088	63.12	33.06	3.32	0.03	0.15	51.5	18.2
Katmai (2009)	N	25	10.264	54.20	41.04	4.00	0.04	0.08	51.8	18.1
Kodiak (2004)	N	0	.	.	.	.	.	.	.	.
Kodiak (2005)	N	0	.	.	.	.	.	.	.	.
Prince William Sound (2008)	N	46	6.053	54.04	37.00	8.18	0.02	0.56	.	.
Prince William Sound (2010)	N	27	9.630	49.00	44.33	5.41	0.22	0.41	54.7	18.1

Note: WBC = Total white blood cell count (1000/ μ l); Neut%, neutrophils; Lymph%, lymphocytes; Mono%, monocytes; Eos%, eosinophils; Baso%, basophils; PCV, packed cell volume; Hgb, hemoglobin. “.” indicates no data.

TABLE 15. Gene transcription results (cycle threshold, or CT) on sea otters captured at 5 island/locations and from captive sea otters at aquaria, sampled between 2008 and 2012

			Genes									
Location	Decline	No. of otters	AHR	COX2	CYT	DRB	HDC	HSP70	IL10	IL18	MX1	THRβ
Alaska Peninsula West	Y	27	30.58	26.71	22.26	19.07	26.33	28.61	33.20	22.38	32.73	33.25
Clam Lagoon	N	24	32.80	29.51	21.65	20.44	30.31	34.16	42.18	22.70	37.11	36.95
Katmai	N	30	30.59	27.92	22.21	19.37	24.73	28.46	33.72	23.09	32.69	32.77
Kodiak	N	25	27.24	25.62	20.35	20.36	18.13	25.65	26.22	25.36	28.35	29.65
Prince William Sound	N	87	32.14	29.42	21.73	19.91	29.12	33.80	40.54	22.43	35.11	36.25
Captive otters	N	17	31.03	26.91	22.63	19.65	26.11	29.73	33.75	21.68	31.12	33.36

Note: AHR, arylhydrocarbon receptor; COX2, cyclo-oxygenase 2; CYT, complement cytolysis inhibitor; DRB, major histocompatibility complex; HDC, translationally controlled tumor protein HDCMB21P; HSP70, heat shock protein 70; IL10, interleukin 10; IL18, interleukin 18; THR β , thyroid hormone receptor.

Comparing support for alternative hypotheses

For each of the data types and associated analyses described above, we evaluated the results with respect to the hypothesis-specific predictions listed in Table 1 and made a binary assessment of support (scored as 1) or lack of support (scored as 0). The result was a consistency–inconsistency matrix (Table 18), with columns corresponding to alternative hypotheses, rows corresponding to data types, and cell values indicating consistency (1) or inconsistency (0) between each data type and the relevant predictions. In cases where predictions were undescribed or nondefinitive with respect to a given data type, the cell value was listed as NA. We summarized the consistency matrix in two ways: first, we simply tabulated the number of data sets that were inconsistent with the predictions associated with each hypothesis, reasoning that hypotheses with fewer inconsistencies were better supported. Second, we used a Bayesian-based, information-theoretic approach to evaluate how the combined results of all analyses should affect our belief about the degree of support for each hypothesis. To achieve this, we considered the nonnull cell values for

each column of the consistency matrix as the observed outcomes of a series of independent Bernoulli trials. For focal hypothesis h and data type d , the probability of obtaining an outcome of 1 (vs. 0) is thus described as

$$\text{outcome}_{d,h} \sim \text{Bernoulli}(\theta_h), \quad (5)$$

where θ_h represents the underlying degree of consistency of all possible data types with the predictions of hypothesis h . Moreover, if we assume that hypotheses are mutually exclusive, then any consistencies between a given data type and the predictions of hypotheses other than the focal hypothesis would be expected to occur with probability $1 - \theta_h$:

$$\max(\text{outcome}_{d,i \neq h}) \sim \text{Bernoulli}(1 - \theta_h). \quad (6)$$

Eq. 6 reflects the fact that the implied degree of support for hypothesis h is more affected by consistency with data type d if that same data type is inconsistent with all other hypotheses.

We used Bayesian MCMC methods to find the values of θ_h that maximized the likelihood of equations given

TABLE 16. Mussel tissue contaminant data ($\mu\text{g/kg}$, dry wt.) collected from 1996 to 2001.

Location	Decline	Longitude	Latitude	% Lipid	% Water	Contaminant				
						Σ PCB	Σ DDT	Σ HCH	Σ Chlordane	HCB
Attu	Y	-172.770	52.860	2.0	80.4	12	6.6	7.0	3.5	1.1
Attu	Y	-173.180	52.816	1.4	83.5	27	5.5	4.7	2.1	0.9
Attu	Y	-173.273	52.948	1.1	85.0	13	6.5	5.9	2.1	0.9
Alaid	Y	-173.864	52.773	1.2	84.9	32	13.0	5.5	3.9	0.9
Nizki	Y	-174.002	52.741	0.8	84.2	14	7.7	4.1	3.2	0.6
Shemya	Y	-174.079	52.730	0.9	87.0	18	5.7	4.3	2.6	0.9
Shemya	Y	-174.140	52.730	0.8	87.9	21	7.9	4.9	3.1	0.7
Buldir	Y	-175.947	52.369	1.3	85.0	39	26.0	6.5	18.0	1.2
Kiska	Y	-177.539	51.977	3.6	78.0	8	8.8	9.3	5.2	0.8
Kiska	Y	-177.561	51.923	1.4	81.6	24	8.5	6.5	4.2	1.1
Kiska	Y	-177.584	51.925	1.6	83.8	21	16.0	7.9	6.9	1.1
Kiska	Y	-177.599	52.022	1.5	83.5	21	14.0	6.9	4.2	1.1
Amchitka	Y	-178.992	51.583	1.5	82.9	16	18.0	8.1	8.6	1.0
Amchitka	Y	-179.301	51.418	1.2	82.8	83	15.0	14.0	11.0	1.3
Ogliuga	Y	-178.644	51.586	1.0	80.9	12	7.8	5.3	5.1	1.6
Tanaga	Y	-178.179	51.844	1.3	84.4	12	8.1	5.6	4.4	0.8
Tanaga	Y	-178.057	51.780	1.5	81.5	14	4.7	8.3	6.4	1.1
Tanaga	Y	-177.807	51.783	1.3	86.7	13	7.9	5.6	4.5	0.7
Adak	Y	-176.809	51.817	1.7	84.2	12	4.2	8.5	4.1	1.0
Adak	Y	-176.650	51.958	0.6	88.9	7	2.3	3.2	2.2	0.4
Adak	Y	-176.646	51.858	1.8	81.9	430	10.0	7.5	4.5	0.9
Adak	Y	-176.632	51.862	2.0	81.9	280	8.3	5.8	4.5	0.7
Adak	Y	-176.626	51.832	3.0	79.4	110	12.0	9.8	6.3	1.1
Adak	Y	-176.606	51.840	2.0	79.4	62	7.5	6.2	3.9	0.9
Adak	N	-176.577	51.930	1.4	82.2	19	5.6	4.6	4.1	0.5
Adak	Y	-176.478	51.730	1.1	84.8	10	2.9	3.4	2.2	0.5
Kagalaska	Y	-176.295	51.824	1.1	86.3	7	7.7	4.5	1.9	0.5
Great Sitkin	Y	-176.192	51.999	1.2	86.9	15	9.8	7.4	6.3	1.2
Great Sitkin	Y	-176.086	51.971	0.7	85.7	12	6.5	4.6	4.1	0.7
Seguam	Y	-172.302	52.330	1.0	83.3	12	5.3	4.7	6.8	0.4
Yunaska	Y	-170.744	52.666	1.9	81.8	19	18.0	13.0	10.0	1.0
Umnak	Y	-168.910	52.998	0.8	85.1	8	2.4	4.3	3.2	0.3
Umnak	Y	-168.882	52.946	1.3	83.8	12	5.1	7.1	4.9	0.9
Unalaska	Y	-167.695	53.391	1.2	84.3	7	4.7	7.6	3.4	0.6
Unalaska	Y	-167.642	53.394	1.3	83.0	9	3.4	6.1	2.9	0.5
Unalaska	Y	-167.482	53.441	1.0	83.9	8	4.2	5.1	3.0	0.5
Unalaska	Y	-166.503	53.913	1.6	86.4	2,800	19.0	5.8	6.9	0.5
Akutan	Y	-165.866	54.216	1.2	85.6	24	8.2	5.9	5.5	0.6
Akutan	Y	-165.785	54.129	1.3	84.2	14	4.7	6.9	3.5	0.7
SEAK	N	-136.521	58.096	0.4	90.1	51	4.6	3.3	3.2	0.3
SEAK	N	-136.360	58.251	0.7	88.1	33	4.7	3.7	2.9	0.4
SEAK	N	-136.230	58.192	0.4	91.5	39	5.3	4.4	2.9	0.4
SEAK	N	-136.147	58.778	0.4	88.9	23	3.8	3.4	1.4	0.3
SEAK	N	-135.987	58.464	0.6	87.2	21	2.4	3.1	1.5	0.2

Note: See text for abbreviations and units of contaminants.

Data are shown for each of five contaminant types: total polychlorinated biphenyls (PCB), dichlorodiphenyltrichloroethanes (DDT), hexachlorocyclohexanes (HCH), hexachlorobenzenes (HCB) and chlordane.

the observed consistency matrix and our prior beliefs about the degree of support for each hypothesis. We made the simplifying and conservative assumption of equivalency in terms of our a priori support for five of the seven alternative hypotheses, defining vague priors for θ_h as Beta distributions with parameters $a = b = 1$. For the remaining two hypotheses, “fisheries/harvest”

and “redistribution,” previous assessments concluded that these hypotheses had very low feasibility (USFWS 2013), so we adjusted the priors for these hypotheses to be weakly informative such that the mean prior probability was 1/10 that of the other hypotheses (Beta parameters $a = 0.2$, $b = 3.5$). We used R and STAN software to code and solve the model, running 1,000 iterations for

TABLE 17. Sea otter tissue contaminant data ($\mu\text{g/kg}$, lipid wt.) collected between 2004 and 2010.

Location	N	DoD site	Contaminant					
			ΣPCB (range)	ΣDDT (range)	ΣHCH (range)	$\Sigma\text{Chlordane}$ (range)	HCb (range)	Dieldrin (range)
Kiska	14	N	445 (170–1,900)	91 (21–730)	70 (5–120)	80 (19–390)	58 (21–130)	15 (6.5–54)
Amchitka	8	Y	1,095 (270–8,000)	150 (34–690)	205 (150–350)	165 (81–310)	74 (39–98)	23 (0–50)
Kanaga	7	N	220 (170–680)	110 (57–710)	11 (3.8–39)	62 (23–130)	24 (16–45)	11 (6.5–19)
Adak-BOI	20	N	400 (140–1,100)	58 (4.7–270)	62 (3.7–470)	60 (4.2–290)	41 (11–81)	27 (6.2–95)
Adak-Kuluk	9	Y	2,200 (740–8,600)	97 (40–730)	270 (60–480)	220 (30–410)	85 (33–160)	18 (0–45)
SEAK	20	N	530 (150–4,900)	115 (33–340)	180 (60–770)	155 (32–290)	84 (54–140)	17 (0–60)

Note: See text for abbreviations and units of contaminants. Sites are classified as to whether they occur near to a current or former Department of Defense (DoD) military base.

TABLE 18. Consistency matrix for alternative hypotheses for sea otter decline.

Data type	Alternative hypothesized causes of sea otter decline						
	Nutritional limitation	Reproductive failure	Disease	Contaminants	Fisheries or harvest	Large-scale redistribution	Predation
Abundance trends	0	0	NA	0	0	0	1
Habitat selection	NA	NA	NA	NA	0	0	1
Pup production	0	0	NA	0	NA	NA	NA
Carcass production	0	NA	0	0	NA	NA	1
Body size and condition	0	NA	0	NA	1	NA	1
Diet and foraging success	0	NA	NA	NA	1	NA	1
Food availability	0	NA	NA	NA	1	NA	1
Serum chemistry and hematology	0	0	0	0	NA	NA	NA
Gene transcription	0	0	0	0	NA	NA	NA
Contaminant exposure	NA	NA	NA	0	NA	NA	NA
Documented observations of deaths	NA	NA	0	NA	0	NA	1
Number of inconsistent data types	8 of 8	4 of 4	5 of 5	6 of 6	3 of 6	2 of 2	0 of 7
Posterior estimate	0.24	0.29	0.28	0.26	0.34	0.25	0.80
of relative support (q)	(± 0.09)	(± 0.11)	(± 0.10)	(± 0.10)	(± 0.10)	(± 0.10)	(± 0.09)
Relative support (qualitative)	Low	Low	Low	Low	Low	Low	High

Note: For each combination of hypothesized cause (columns) and data type (rows), “1” indicates consistency between the hypothesis and data type, “0” indicates inconsistency, and “NA” indicates nonapplicable data or an ambiguous result.

burn in and then saving 20,000 samples from the posterior distributions. We present the means and 95% CI for our estimates of θ_h , which represent our a posteriori beliefs about the relative degree of support for each hypothesis.

RESULTS

Temporal trends in abundance

The state-space model converged well and provided an excellent fit to the survey data (Fig. 2a–f), with $\hat{r}$ values for all parameters < 1.1 (Appendix S1: Table S1) and a Bayesian- P value of 0.488 (Appendix S1: Fig. S1). Of the 20 model forms evaluated, the best-supported model (based on comparison of LooIC values; see Appendix

S1: Table S2) included a temporal break point in residual mortality values ($\epsilon_{i,t}$) for some islands/locations but not others. Specifically, there was increased variation in residual mortality after 1989 at the five outer coast islands in the Aleutians (Attu, Kiska, Amchitka, Adak, and Kagalaska Island) but not at Bering Island or Clam Lagoon (Appendix S1: Table S2). At the five Aleutian outer coast locations, time-averaged residual mortality rates ($\delta_{i,t}$) increased above 0.2 around or soon after 1989 and then fluctuated dramatically after that (Fig. 2h–l), exceeding 0.2 in most years. In contrast, $\delta_{i,t}$ remained below 0.2 for all years at Bering Island (Fig. 2g) and all but two years at Clam Lagoon (Fig. 2k). As a result of these divergent mortality patterns, the Aleutian outer coast islands experienced a sharp decline in otter abundance through the 1990s (Fig. 2b–f), dropping below

10% of their predecline abundance by 2001 (on average), while the Bering Island and Clam Lagoon populations showed no consistent pattern of decline (Fig. 2a, e). The estimated timing of increased mortality (the first year $\delta_{i,t}$ exceeded 0.2) varied slightly across the five Aleutian outer coast islands (Fig. 3a), ranging from 1987 (Kagalaska Island) to 1994 (Attu Island), but in all cases there was a sustained increase in the magnitude of $\delta_{i,t}$ after 1989, with average values of approximately 0 (or less) in the former period and approximately 0.2 (or greater) in the latter period (Fig. 3b). In contrast, at Bering Island and Clam Lagoon the average value of $\delta_{i,t}$ in the periods before and after 1989 was not significantly different from 0 (Fig. 3b).

The state-space model also provided insights into carrying capacity (K) and variation in status with respect to K at each island/location. The average estimated number of otters per kilometer of coastline at K for all index islands was 15.1 (CI₉₅ = 10.7–20.8), with island/location-specific values ranging from 12.9 to 17.9 (Appendix S1: Table S1). Prior to 1989, trends in population status with respect to K fell into one of two

patterns: (1) at Kiska, Amchitka, Adak (outer coast), and Kagalaska islands, estimated abundance was generally stable and fluctuated around K for several decades (Fig. 2c–f); (2) at Bering Island, Attu Island, and Clam Lagoon, populations were increasing through the 1970s and 1980s, and were just approaching K by 1989 (Fig. 2a, b, e). One decade later, in 1999, populations at the five Aleutian outer coast islands had declined to densities representing 18% of K on average (range = 4–29%), and by 2015 had further declined to just 8% of K (range = 4–15%). In contrast, at Bering Island and Clam Lagoon, estimated densities in 1999 corresponded to 83% and 98% of K (respectively), and estimated densities in 2015 represented 101% and 90% of K .

Spatial trends in abundance, distance to shore, and reproduction

We surveyed 5,576 km of shoreline at 26 islands/locations, for an average track length of 214 km per island/location. Track lengths ranged from a minimum of 21 km at Little Kiska Island to 1,792 km in Prince William

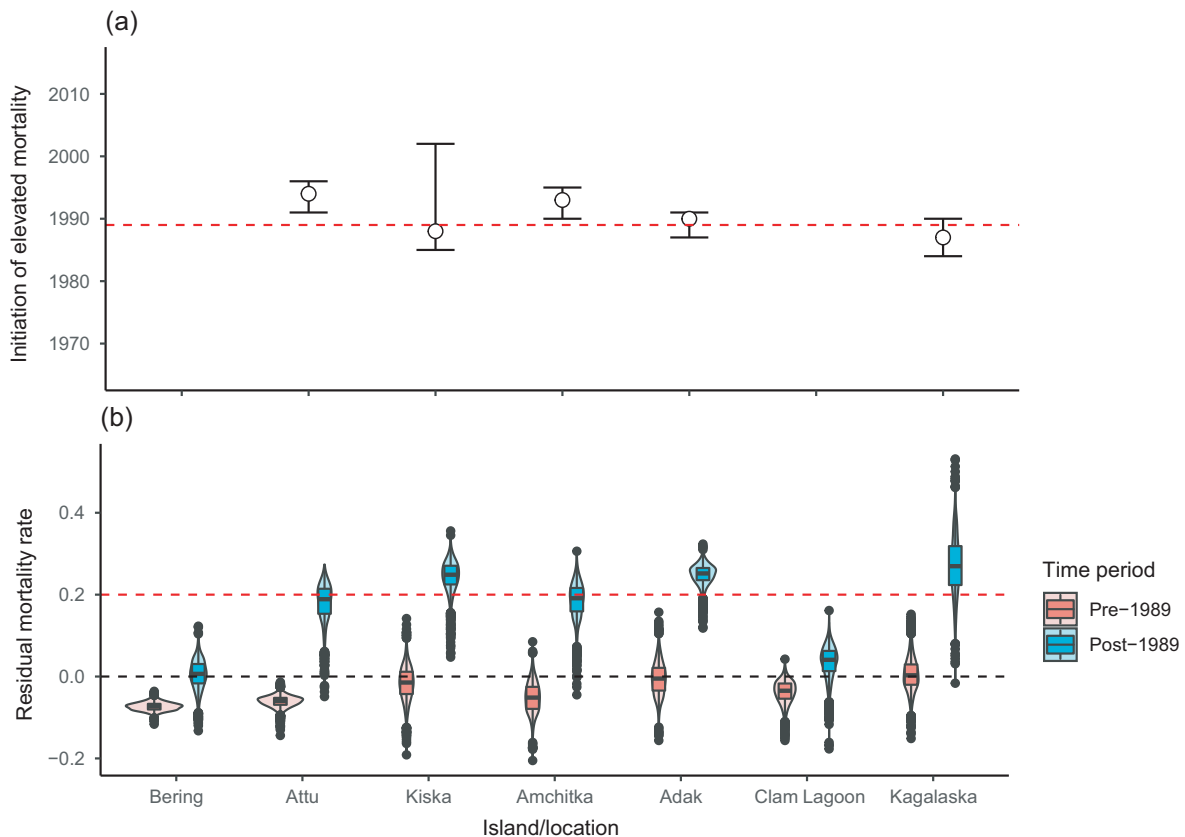


FIG. 3. Comparison across index islands (plotted from west to east) of (a) the year at which estimated residual mortality rates ($\delta_{i,t}$) first exceeded the threshold value of 0.2 (a value sufficient to cause a sustained decline); and (b) the mean estimated residual mortality rates for years prior to 1989 and years after 1989. In plot (a), estimates are not plotted for Bering Island and Clam Lagoon (as these locations did not experience a sustained decline) and the dashed line indicates the best-supported timing of a shift to greater variation in residual mortality. In plot (b), the black dashed line indicates 0 (the expected mean value of residual mortality for a stable population) and the red dashed line indicates the threshold value of 0.2.

Sound. Measured linear densities of sea otters ranged from a high of 16.06 otters/km at Bering Island to a low of 0.02/km on the Kupreanof Peninsula (Table 4). Mean distance to shore of observed sea otters also varied considerably, from 740 m at Bering Island to <50 m at many of the islands in the central and western Aleutians. A k-means cluster analysis showed support for two distinct groupings of the survey data (Appendix S1: Fig. S2): cluster 1 was defined by a high proportion of otters <20 m from shore and low population densities, and cluster 2 was defined by a low proportion of otters <20 m from shore and high population densities (Fig. 4a). Cluster 1 corresponded to islands/locations that had experienced a decline, and cluster 2 corresponded to those that had not declined. Results of a MANOVA indicated that islands/sites within the two clusters differed significantly with respect to density ($F = 18.4$, $P = 0.0002$) and distance to shore ($F = 79.5$, $P < 0.0001$) but not average pup ratios ($F = 1.28$, $P = 0.268$), which tended to be slightly higher in cluster 1 (Fig. 4b). Cluster membership of islands/

locations, when arranged on an east–west longitudinal axis, indicated clear boundaries of the area of decline (Fig. 4c): the western boundary occurred between Attu and Bering Island, while the eastern boundary occurred near Castle Cape, on the south Alaska Peninsula (Fig. 1). Pup: independent ratios ranged from 0.10 to 0.50 with a mean of 0.29.

Stranded carcass recoveries

In 2008–2009 we surveyed the beaches for carcasses and remains of sea otters at 10 locations ranging from Bering Island in the west to Prince William Sound in the east (Table 5). We combined data from contemporary carcass surveys with the results of six earlier surveys (see below) to provide historical context for current patterns. The combined data set represented 1,924 km of shoreline and resulted in recovery of 1,258 sea otter skulls. In stable/growing populations we surveyed 1,308 km and recovered 1,059 skulls, in declining populations we surveyed 514 km

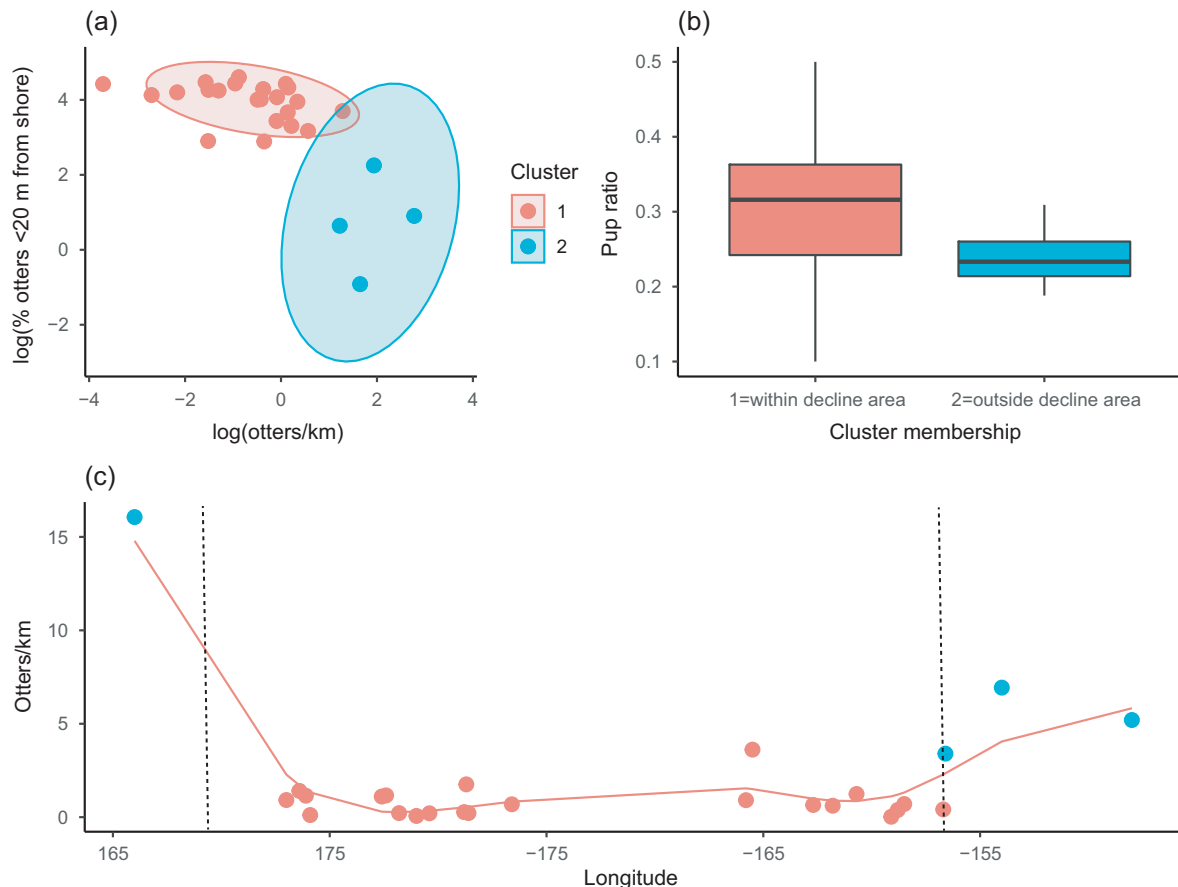


FIG. 4. Results of analyses of spatial variation in sea otter density, habitat selection (distance from shore) and reproductive output (pup:adult ratio) at locations sampled between 2005 and 2010. The results of a cluster analysis (a) indicate that sampling locations group into two clusters based on density and the proportion of otters <20 m from shore. Average pup ratios were slightly (though not significantly) higher at locations in cluster 1 (low density, more otters close to shore) vs. cluster 2 (higher density, fewer otters close to shore). The two clusters were clearly partitioned on a longitudinal axis (c), indicating the east and west boundaries of the area of decline (black dashed lines).

and recovered 195 skulls, and in postdecline populations we surveyed 102 km and recovered four skulls.

Prior to the onset of the decline of sea otters in southwest Alaska, large numbers of stranded carcasses were routinely recovered from selected beaches at Amchitka, in the central Aleutian archipelago, and estimated annual mortality (200/yr) was about 10% of the population (Kenyon 1969). Most of these animals died in late winter/early spring, apparent casualties of limiting food resources and disease following the challenges of a long, harsh winter. However, by the early 1990s, during the initial phases of the decline and when otters were still relatively common, there appeared to be a reduction in the numbers of beach-cast carcasses. For example, 50 km of Amchitka Island's coastline (roughly 25% of the island's perimeter) was surveyed monthly for carcasses from summer of 1992 through late winter of 1994 with more extensive surveys (>70% of the Island's perimeter) conducted in spring of 1992 and late winter of 1994. A total of 174 otter remains were collected over this 3-yr period, averaging about 60/yr. Of these, most (85%) were weathered skeletons or detached skulls, likely representing mortality from previous years (Monson et al. 2000b). Some fraction of these remains therefore likely came from animals that died prior to the onset of the decline. At Adak Island, three beach sections of approximately 10 km each were surveyed monthly in 1995–1996, one in Clam Lagoon (where the population remained near equilibrium density) and two along the outer coast (where the population declined). Over the 13-month study at Adak between 1995 and 1996, during the peak period of decline (Doroff et al. 2003), only a single

carcass (an adult female) was recovered from the outer coast sections, while 26 were recovered from Clam Lagoon (the only area on Adak that did not decline; Fig. 2), including seven bleached skulls and 19 within-the-year mortalities. The low carcass recovery rates at Adak (outer coast) and Amchitka during the decline contrasted with much higher rates of carcass recoveries during beach surveys in the 1960s (Kenyon 1969) and early 1970s (Estes 1977) when the population was stable. These findings suggested that the causal factor of the rapid decline at Adak and Amchitka islands (Fig. 2) involved the disappearance of a large number of animals but produced relatively few beach-cast carcasses (Estes et al. 1998). Further, the age structure of the dying population represented by carcass collections would not necessarily reflect the mortality factor driving the decline.

The per capita rate of recovery of skulls varied among regions ($SD = 0.751$) and as a function of population status (Appendix S1: Table S3). In stable or growing populations the annual rate of recovery was approximately 10% of the estimated population size, but this rate dropped to approximately 3% in declining populations ($Z = -3.773$, $P = 0.0002$) and 2% in postdecline populations ($Z = -2.960$, $P = 0.0031$; Fig. 5). After accounting for the effect of population status, there was no significant effect of population density on carcass recovery rates ($Z = 0.030$, $P = 0.976$).

Morphometrics

Removing individuals with missing age, length, or mass data resulted in a total sample size of 724 sea otters

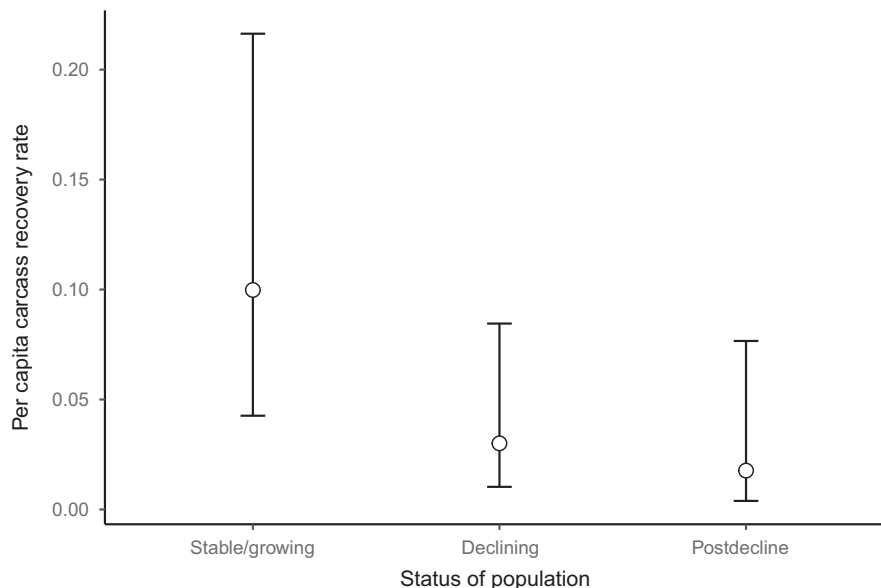


FIG. 5. Comparison of mean per capita carcass recovery rates for sea otter populations at locations/time periods that were classified a priori into one of three categories: (1) stable or growing populations, (2) declining populations, and (3) postdecline populations. Points show the marginal mean values for each category (after removing random effects of region), and error bars show 95% credible intervals around each estimate, based on a generalized linear mixed model fit to the data.

among 13 study groups (each group represented one island/location by time combination, although in some cases adjacent islands/locations and time periods were combined due to sample size limitations). We augmented this data set with historical data on sea otter body size based on samples obtained from Kodiak Island in the late 1980s (Monson & Degange 1995) and the Aleutian Islands in the 1960s (Laidre et al. 2006), for an additional 1,467 records (Table 6).

There was considerable variation among study groups in all three indices of body size and condition (Table 6). The general pattern of differences was similar across all three indices and for both sexes: stable populations had the lowest values while growing and postdecline populations had the highest values, with declining populations tending to be similar or slightly higher than stable populations (Fig. 6). For both males and females, the BMI showed the clearest differences (Fig. 6a, d; also see Appendix S1: Table S4): females had a significantly higher BMI in growing ($t = 2.633$, $P = 0.0424$) and postdecline populations ($t = 3.697$, $P = 0.0026$) relative to stable populations, and declining populations were not significantly different from stable populations ($t = 0.032$, $P = 0.8211$). Males showed a similar pattern with a significantly higher BMI in growing populations relative to stable populations ($t = 3.295$, $P = 0.0073$), and a marginally significant ($t = 1.812$, $P = 0.0911$) and nonsignificant ($t = 0.618$, $P = 0.5494$) increase in postdecline and declining populations, respectively. The overall pattern of relative index values was similar for SSI and DCI indices, though with fewer significant differences (Appendix S1: Table S4), so we focused our spatial and temporal contrasts on the BMI.

Based on samples collected in the postdecline period (i.e., after 2004), the spatial patterns in BMI showed a consistent pattern of variation on a west-to-east longitudinal axis (Fig. 7a). Low values of BMI were found at Bering Island (to the west of the area of decline) and at Clam Lagoon, while the highest recorded values were found at postdecline populations in the western Aleutians and the western end of the south Alaska Peninsula. Moving east of the decline area, we found high values of the BMI in growing populations at Katmai and Kodiak Island and Kachemak Bay, and lower values (comparable to Bering Island and Clam Lagoon) within longer-established, stable populations at NE Kodiak archipelago and Prince William Sound (PWS). Temporal trends in BMI in the western Aleutians showed a clear and significant pattern of increase ($t = 4.012$, $P = 0.0278$) both during and after the period of decline (Fig. 7b).

Diet and energy intake rate (EIR)

Between 2004 and 2013, we collected data on sea otter foraging behavior at 18 islands/locations (Table 2), ranging from Bering Island (to the west of the decline), through the Aleutian archipelago and western Alaskan

Peninsula (the area of the decline), to Katmai, Kodiak, Kenai Peninsula, and Prince William Sound (all east of the decline). We partitioned the resulting data set into 11 study groups (Table 8), each representing an island/location by time combination. We recorded a total of 367 h of feeding observations, recording information on 2,117 feeding bouts comprising 12,754 dives and 66,437 prey captures. We added these data to previously collected foraging data from the late 1980s at Kodiak (Doroff & Degange 1994, Monson 1995) and the early-mid 1990s at Adak and Amchitka islands (Estes et al. 1998, Watt et al. 2000), which consisted of 332 h of observations, recording information on 944 feeding bouts comprising 10,516 dives and 34,847 prey captures (Table 8).

The relative abundance of 16 prey categories (Table 9) in the otter's diets varied among islands/locations, and these differences for the most part corresponded to known habitat differences among regions: sea urchins (*Strongylocentrotus* spp.) were the most common prey type in rocky-substrate-dominated regions (Bering Island, Aleutian Islands, and western Alaska Peninsula), whereas clams and crabs were the most common prey types in the soft-sediment-dominated regions to the east of Castle Cape, and also in the mud-bottomed Clam Lagoon on Adak Island (Table 8). Other regional differences included a near absence of fish in otter diets in all eastern regions, and the relative importance of octopus in otter diets along the Alaska Peninsula. Despite these differences in diet composition, there were no obvious patterns of diet diversity related to region (Table 8) and no significant variation among populations of different status (Appendix S1: Table S5).

Foraging success, as measured by the rate of energy intake while feeding (EIR), differed considerably among the various study populations. Much of this variation in EIR was explained by differences in population status, with higher EIR values in growing ($t = 5.541$, $P = 0.0002$) and postdecline populations ($t = 12.311$, $P < 0.0001$) relative to stable populations, but no significant difference between stable and declining populations (Fig. 8, Appendix S1: Table S5). Based on samples collected in the postdecline period (i.e., after 2004), the spatial patterns in EIR showed a clear pattern of high values (>15 kcal/min) at islands within the area of decline, lower values (<10 kcal/min) in the stable populations to the east and west of the decline area, and intermediate values in the growing populations east of the decline (Fig. 9a). Temporal trends evaluated for the western Aleutians, where a long time series was available, revealed a significant increase in EIR ($t = 16.610$, $P = 0.0036$) both during and after the period of decline (Fig. 9b).

Variation in the rate of energy gain was a significant predictor of sea otter morphometric indices: there was a positive relationship between EIR and SSI ($t = 2.762$, $P = 0.0246$), BMI ($t = 5.200$, $P = 0.0008$) and DCI, though the latter was only marginally significant ($t = 2.052$, $P = 0.0743$). The relationship between EIR

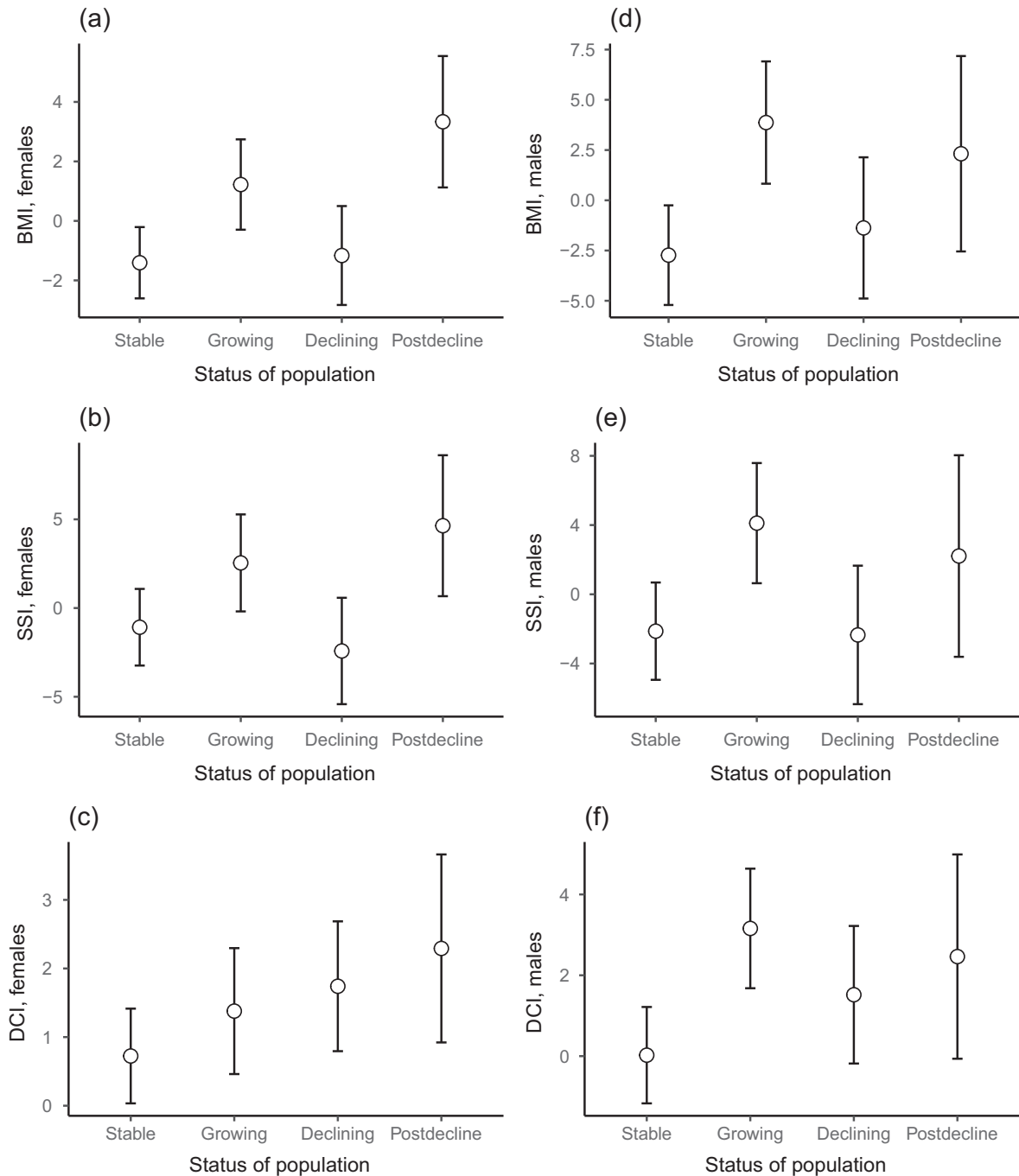


FIG. 6. Comparison of three morphometric indices for sea urchin populations that have been classified into one of four categories based on their demographic trends. Plots are shown for females (a)–(c) and males (d)–(f) and for three different indices: body mass index [BMI: plots (a) and (d)], structural size index [SSI: plots (b) and (e)], and dynamic condition index [DCI: plots (c) and (f)]. Points show the marginal mean values for each category (after removing random effects of region) whereas error bars show 95% credible intervals around each estimate, based on a generalized linear mixed model fit to the data.

and BMI explained the greatest amount of variation in EIR among populations ($R^2 = 0.772$; Appendix S1: Table S5), and populations of different status were well differentiated along the trendline predicted by this relationship (Fig. 10).

Food availability

The average biomass density of sea urchins varied among the various sample locations and time periods by almost four orders of magnitude, from 0.1 g 0.25 m⁻² to

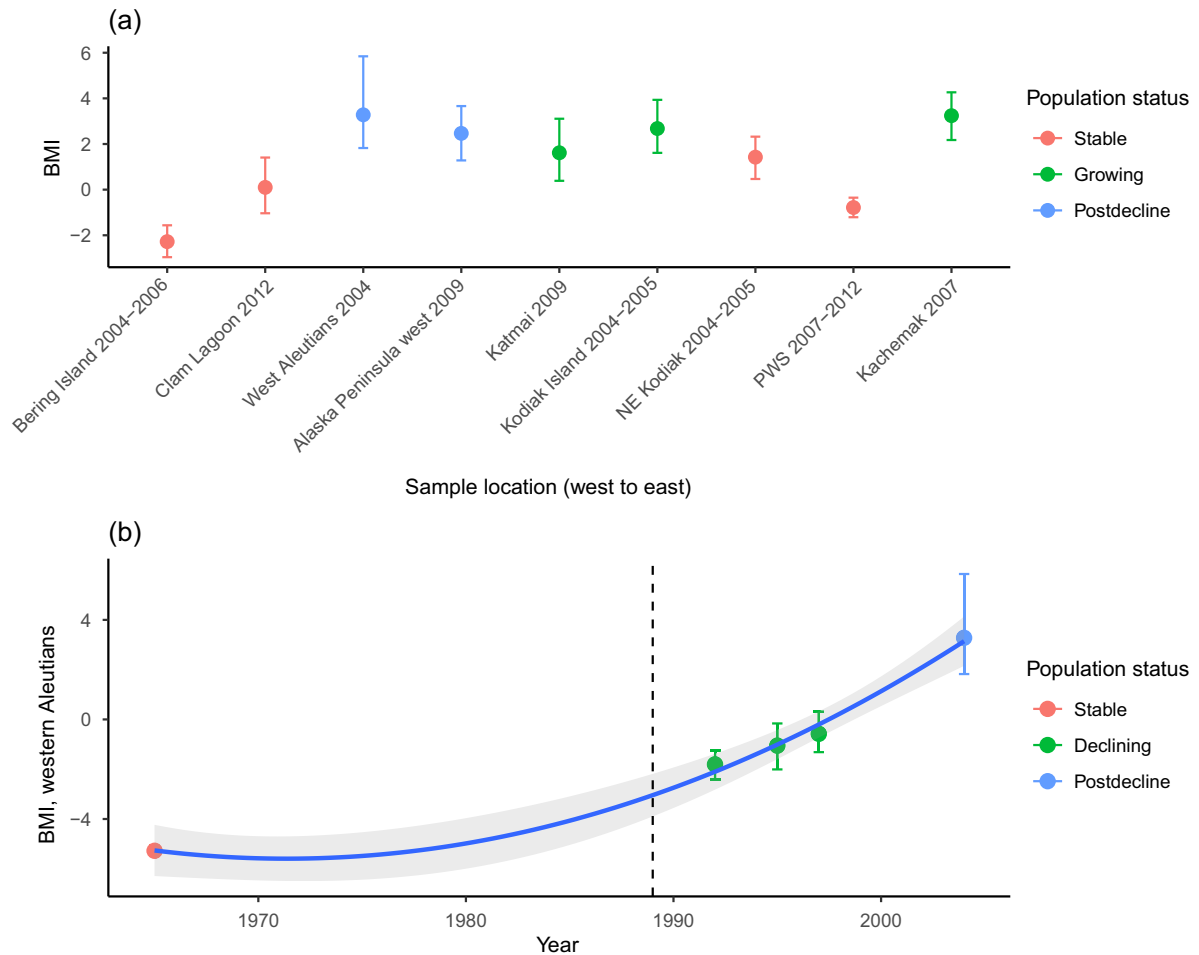


FIG. 7. Spatial variation and temporal trends in the body mass index (BMI) for females and males combined. Top panel (a) shows comparison of BMI for populations across a longitudinal gradient (west–east) sampled after 2004: points are color coded by status with respect to the decline, and error bars indicate 95% credible interval. Lower panel (b) shows temporal trends in BMI for the western Aleutian Islands based on samples collected before, during, and after the period of decline.

984.9 g per 0.25 m^{-2} (Table 9). Some of this variation was explained by differences among regions and islands within regions, but there was also a strong effect of sea otter population status. After controlling for random effects of location, urchin biomass density was 7–10 $\times$ higher in growing ($t = 9.796$, $P < 0.0001$), declining ($t = 9.884$, $P < 0.0001$) and postdecline populations ($t = 11.306$, $P < 0.0001$) as compared to stable populations (Fig. 11a, Appendix S1: Table S6). The effect of population status on urchin recruitment was less clear: growing populations exhibited 2.7 $\times$ higher recruitment than stable populations ($t = 3.537$, $P = 0.0004$), although postdecline populations exhibited approximately 50% lower recruitment ($t = 4.208$, $P < 0.0001$), and there were no significant differences in recruitment index between stable and declining populations (Appendix S1: Table S6).

Limiting consideration to data collected during the 2005–2009 sampling period, and more closely examining

spatial patterns, provided a clearer picture of variation in sea urchin recruitment. A spatial break in recruitment values was evident between the western and eastern Aleutians, with high levels of recruitment to the west of Samalga Pass (Fig. 1) and much lower recruitment to the east (Fig. 12b). After accounting for this approximately ninefold regional difference ($t = 3.597$, $P = 0.0003$), there were no significant differences in recruitment index between stable, growing, and postdecline populations (Appendix S1: Table S6). However, there were significant differences in urchin biomass explained by population status after accounting for regional differences: higher biomass densities occurred in postdecline ($t = 1.983$, $P = 0.0473$) and growing populations (marginally significant difference, $t = 1.750$, $P = 0.0801$) relative to stable populations (Fig. 12a).

Focusing on three islands in the western Aleutians, for which the best time series of data were available, revealed temporal trends in urchin biomass and recruitment. On

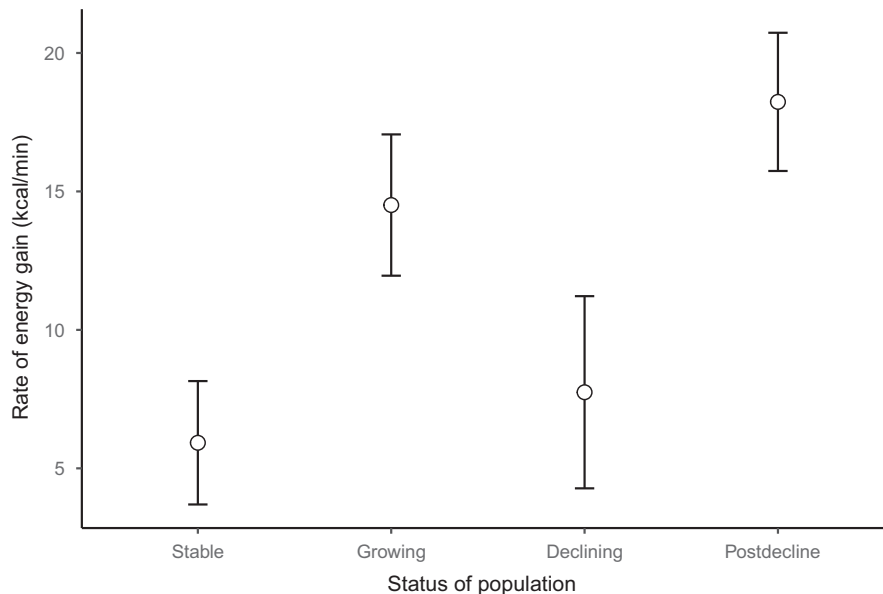


FIG. 8. Comparison of estimated energy intake rate (EIR) of foraging sea otter populations that have been classified into one of four categories based on their demographic trends at the time of data collection: stable (no significant trend, assumed to be at or near K), growing (significant positive trend in abundance), declining (islands within area of decline between 1989 and 2001), and postdecline (islands within area of decline after 2001). Points show the marginal mean values for each category (after removing random effects of region) and error bars show 95% credible interval around each estimate, based on a linear mixed model fit to the data.

average there was an increasing trend in urchin biomass (Fig. 13), with higher biomass density during the decline ($t = 9.003$, $P < 0.0001$) and in the postdecline period ($t = 8.188$, $P < 0.0001$) relative to the predecline period (Fig. 13). However, there were significant interactions between Island and population status (Appendix S1: Table S6), with Attu Island showing a somewhat different trajectory than Adak and Amchitka islands. Specifically, at Attu Island there was slightly lower urchin biomass density during the decline relative to the predecline period, although by the postdecline period the urchin biomass density at Attu had increased to one of the highest recorded values (Fig. 13). The urchin recruitment index also varied over time, though the trends were less consistent. Overall, there was a lower recruitment index during the decline relative to the predecline period ($t = 3.288$, $P = 0.0015$), but no significant difference in recruitment between the postdecline and predecline periods ($t = 1.262$, $P = 0.2078$). Attu Island had a significantly lower recruitment index than Adak and Amchitka islands ($t = 2.575$, $P = 0.0104$), and Amchitka Island had a significantly higher recruitment index than the other islands during the period of decline ($t = 3.491$, $P = 0.0005$).

Health and disease assessment

Between 2004 and 2010, a total of 301 sea otters were captured for health sampling at locations within and outside (east and west of) the area of decline. Comprehensive physical exams were conducted for 181 of these animals, including 42 animals from two locations within the area

of decline, and 139 animals from four locations outside of the area of decline (Table 11). The incidence of observable disease symptoms was generally similar for postdecline and nondeclined populations: there were no differences in the frequency of dental disease (Barnard score = -1.33 , $P = 0.1932$), papilloma (Barnard score = 0.419 , $P = 0.8203$), neoplasia (Barnard score = -0.551 , $P = 0.7345$), cardiac disease (Barnard score = -0.782 , $P = 0.5781$), abscesses (Barnard score = 0.903 , $P = 0.4338$), or lymphadenopathy (Barnard score = -0.551 , $P = 0.7346$). There was a slightly higher frequency of intraspecific wounds in the postdecline populations (19% as compared to 7% in nondecline populations; Barnard score = 2.25 , $P = 0.0253$); however, this likely reflected to some degree the higher ratio of males to females sampled in postdecline populations (M/F ratio = 0.68) vs. nondecline populations (M/F ratio = 0.39), as intraspecific wounds were twice as prevalent overall in males (16% incidence) as compared to females (8% incidence).

Blood samples were collected from all 301 animals for serological analysis (Table 13), and hematological analyses were conducted for 115 of these animals (Table 14). Serum parameters showed a great deal of variation among locations, although there were no obvious and consistent patterns of variation (Fig. 14). For example, GLU levels were higher in PWS and the western Aleutians than at other locations, BUN was highest at Bering Island, and sodium and albumin were particularly high at Katmai and Alaska Peninsula West (Fig. 14). However, although there were some statistically significant differences in specific parameters between populations,

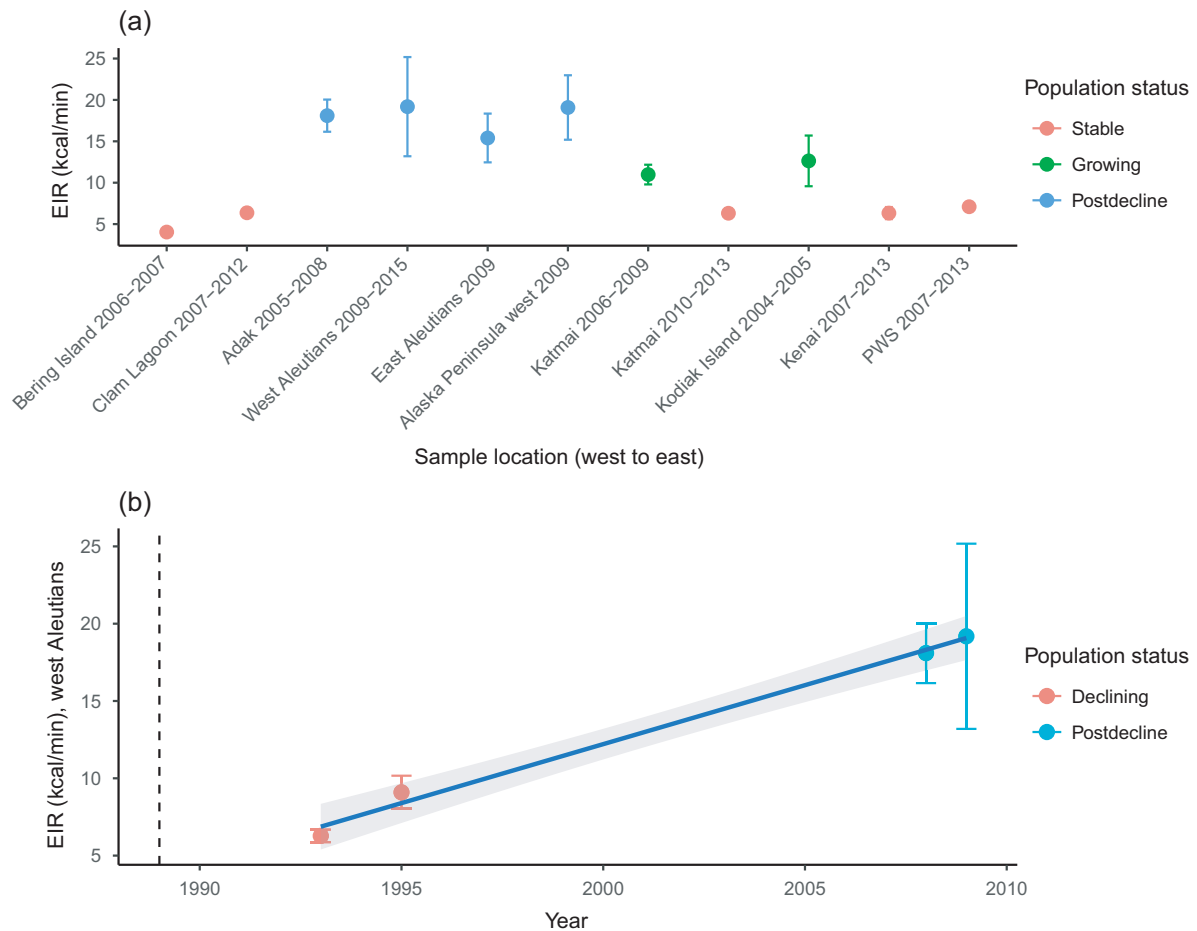


Fig. 9. Spatial variation and temporal trends in the estimated energy intake rate (EIR) of foraging sea otters. Top panel (a) shows comparison of populations across a longitudinal gradient (west–east) sampled after 2004: points are color coded by status with respect to the decline, and error bars indicate 95% credible interval. Lower panel (b) shows temporal trends in EIR for the western Aleutian Islands based on observations conducted during and after the period of decline.

the mean values for all parameters at all locations fell within published reference ranges (Rebar et al. 1995). Similarly, there was some predictable variation in hematology parameters among populations (Fig. 15) that could reflect either artifacts of sample handling or actual differences in animal status, but here again, mean values for all parameters fell within reference ranges. Despite some degree of variation in parameters between populations, the mean values were within the upper and lower limits observed if the tests were performed on otherwise healthy sea otters.

The NMDS model fit to serum parameters converged successfully, with Stress value of 0.149 (Appendix S1: Table S7). A k-means cluster analysis of the NMDS scores showed weak support for two clusters based on silhouette scores and no obvious clusters based on an elbow plot (Appendix S1: Fig. S3). An ordination of NMDS scores indicated a high degree of overlap between populations within and outside the area of decline (Fig. 16a). Only one location—Bering Island—

showed a different distribution from other locations in NMDS space, and this was mostly driven by differences in the second NMDS axis (Fig. 16c). Based on combined NMDS scores, Bering Island was statistically distinguishable from western Aleutians ($t = 3.199$, $P = 0.0326$), Clam Lagoon ($t = 3.977$, $P = 0.0022$), Alaska Peninsula West ($t = 4.434$, $P = 0.0003$), and Katmai ($t = 3.980$, $P = 0.0022$). However, except for Bering Island (Appendix S1: Table S7), populations within the area of decline did not differ from populations outside the decline area.

The NMDS model fit to hematology parameters also converged successfully, with stress value of 0.089 (Appendix S1: Table S8). A k-means cluster analysis of the NMDS scores showed consistent support for three clusters based on evaluation of silhouette scores and an elbow plot (Appendix S1: Fig. S4). An ordination of NMDS scores showed clear separation of the three clusters. Most samples from Alaska Peninsula West (within the decline area) fell within cluster 2, along with samples

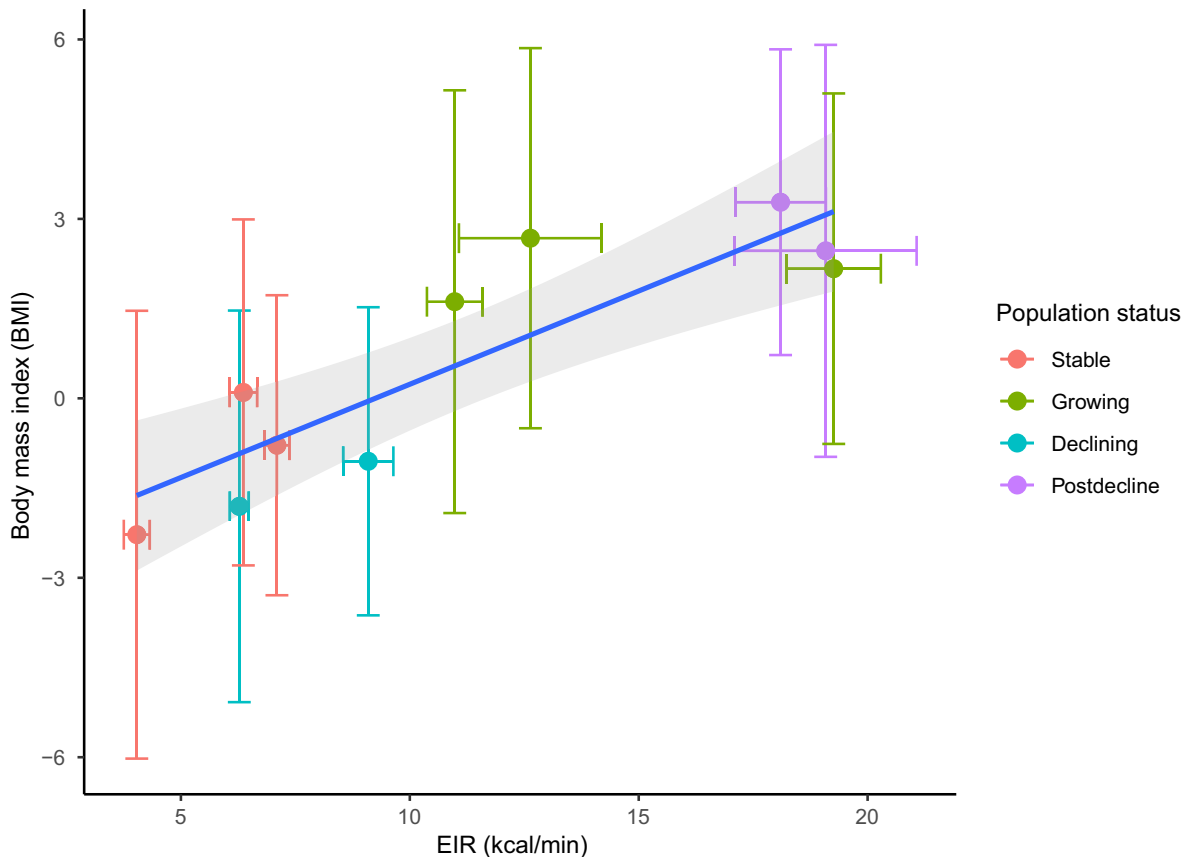


FIG. 10. Relationship between body mass index (BMI) and estimated energy intake rate (EIR) while feeding, for nine sea otter populations, where both metrics were measured at approximately the same time. Points are color coded according to the status of each population (at time of data collection) with respect to the Aleutian sea otter decline. Vertical and horizontal error bars indicate 95% credible interval associated with the estimate of each index. The solid line and gray shaded band indicate (respectively) a linear regression model fit to the data and the associated 95% prediction interval.

from Katmai and PWS (populations outside the decline area; Fig. 17). Bering Island samples were distinct from other populations in NMDS space, falling almost entirely within cluster 1, and cluster 3 included a small proportion of samples from PWS, Katmai, and Alaska Peninsula West (Fig. 17a). Bering Island was statistically distinguishable from Alaska Peninsula West ($t = -6.858$, $P < 0.0001$), Katmai ($t = -6.456$, $P < 0.0001$), and PWS ($t = -6.950$, $P < 0.0001$), but there were no significant differences between the other three populations (Appendix S1: Table S8).

Gene transcription

The geometric mean values for 10 genes of interest, for each sampled sea otter population, are provided in Table 15. Geometric mean transcript values were highest (i.e., lowest cycle threshold or C_T values) at Kodiak for 8 of the 10 genes (AHR, COX2, CYT, HDC, HSP70, IL10, Mx1, THR β ; Fig. 18). Geometric mean transcript values were lowest (i.e., highest C_T values) at Clam Lagoon for 8 of the 10 genes (AHR, COX2, DBR,

HDC, HSP70, IL10, Mx1, THR β ; Fig. 18). The largest ranges of geometric means among groups (most variable transcription) were identified for HDC and IL10, whereas the smallest ranges occurred for DRB, IL18, and CYT (with CYT showing no significant variation among any groups). Genes with larger ranges may be subject to greater environmental variation in a given system than genes with smaller ranges.

Univariate, linear models fit to each gene, with location and sex as predictive variables (Appendix S1: Table S9) revealed two general patterns: (1) sex was not a significant predictor of gene transcription levels for any of the genes of interest; and (2) most genes showed significant differences between the reference group (captive animals) and three locations: Kodiak, PWS, and Clam Lagoon. Katmai samples differed from captive animals in the case of four genes, COX2, HDC, IL18, and Mx1, whereas the samples from Alaska Peninsula West (the only population within the decline area for which gene transcription data were available) did not differ significantly from captive animals for any of the genes of interest (Appendix S1: Table S9).

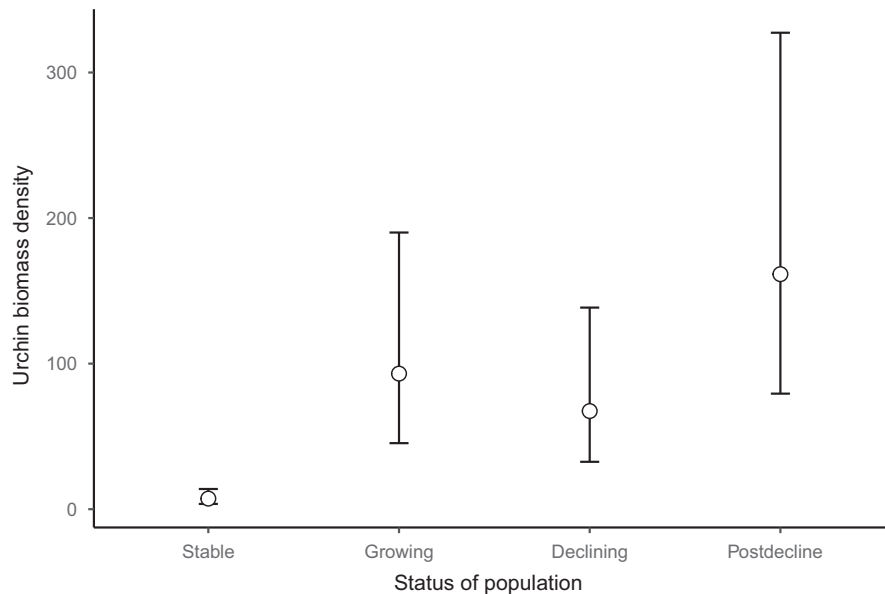


FIG. 11. Comparison of estimated urchin biomass density at locations having sea otter populations of differing status, including: stable (no significant trend, assumed to be at or near K), growing (significant positive trend in abundance), declining (islands within area of decline between 1989 and 2001), and postdecline (islands within area of decline after 2001). Points show the estimated mean value of each index at locations assigned to each category (after removing random effects of region), and error bars show a 95% credible interval around each estimate, based on a generalized linear mixed model fit to the data.

The NMDS model fit to gene transcription data converged successfully, with Stress value of 0.091 (Appendix S1: Table S9). A k-means cluster analysis of the NMDS scores showed consistent support for three clusters (Appendix S1: Fig. S5), and an ordination of NMDS scores showed clear separation of the three clusters. The first cluster included most samples from PWS and Clam Lagoon, the second cluster included most samples from captive animals, Katmai, and Alaska Peninsula West (the latter population was inside the decline area), whereas the third cluster consisted exclusively of samples from Kodiak (Fig. 19a). Kodiak was statistically distinguishable from all other locations in NMDS space ($P < 0.0001$), whereas PWS and Clam Lagoon did not differ from each other but did differ from all other populations (except Alaska Peninsula West). Captive animals and Katmai and Alaska Peninsula West sea otters were not statistically different (Appendix S1: Table S9).

Contaminants

Concentrations of persistent organic compounds (POC) in blue mussels from 39 islands across the Aleutian archipelago and five locations in southeast Alaska (Table 16) show several interesting patterns of variation along an east–west axis (Fig. 20). For Σ PCB concentrations, there were three clear peaks within the Aleutian archipelago (corresponding to 6 of the 39 sites), where values were greatly elevated above the range of values observed at islands/locations throughout the rest of the Aleutians and in SE Alaska (Fig. 20a). All three peaks—

one near Sweeper Cove on Adak Island, a second at Constanine Harbor on Amchitka Island, and a third at Dutch Harbor at Unalaska Island—corresponded to the location of current or recently decommissioned military bases. When these military sites were excluded, Σ PCB concentrations in Aleutian mussels were actually 50% lower (on average) than in southeast Alaska, where no outliers were identified. For all remaining POC groups analyzed, overall concentrations, while generally low by U.S. and international mussel watch standards (Farrington & Tripp 1993, Lauenstein 1995), were on average about 2 $\times$ greater in the Aleutians than they were in southeast Alaska. However, the sites with the highest levels tended to occur on islands with military bases and/or islands with large breeding colonies of seabirds (e.g., Buldir and Yunaska islands), which can serve as vectors through foraging activity (Ricca et al. 2008, Reese et al. 2012). At remaining sites, levels were comparable to southeast Alaska.

The spatial patterns of POC concentrations in sea otter blood samples (Table 17) were consistent with the patterns evident from mussels. In particular, median values of Σ PCB, Beta-HCH, and Σ chlordan concentrations measured from otters at sites near military bases (Adak Island in Kuluk Bay and Amchitka Island at Kiriloff Point) were substantially higher than similar measures from animals in southeast Alaska (Fig. 21). However, median blood concentrations of these same contaminants at other locations in the Aleutian Islands (Bay of Islands on the west side of Adak Island, and Kanaga and Kiska islands) were similar or slightly lower

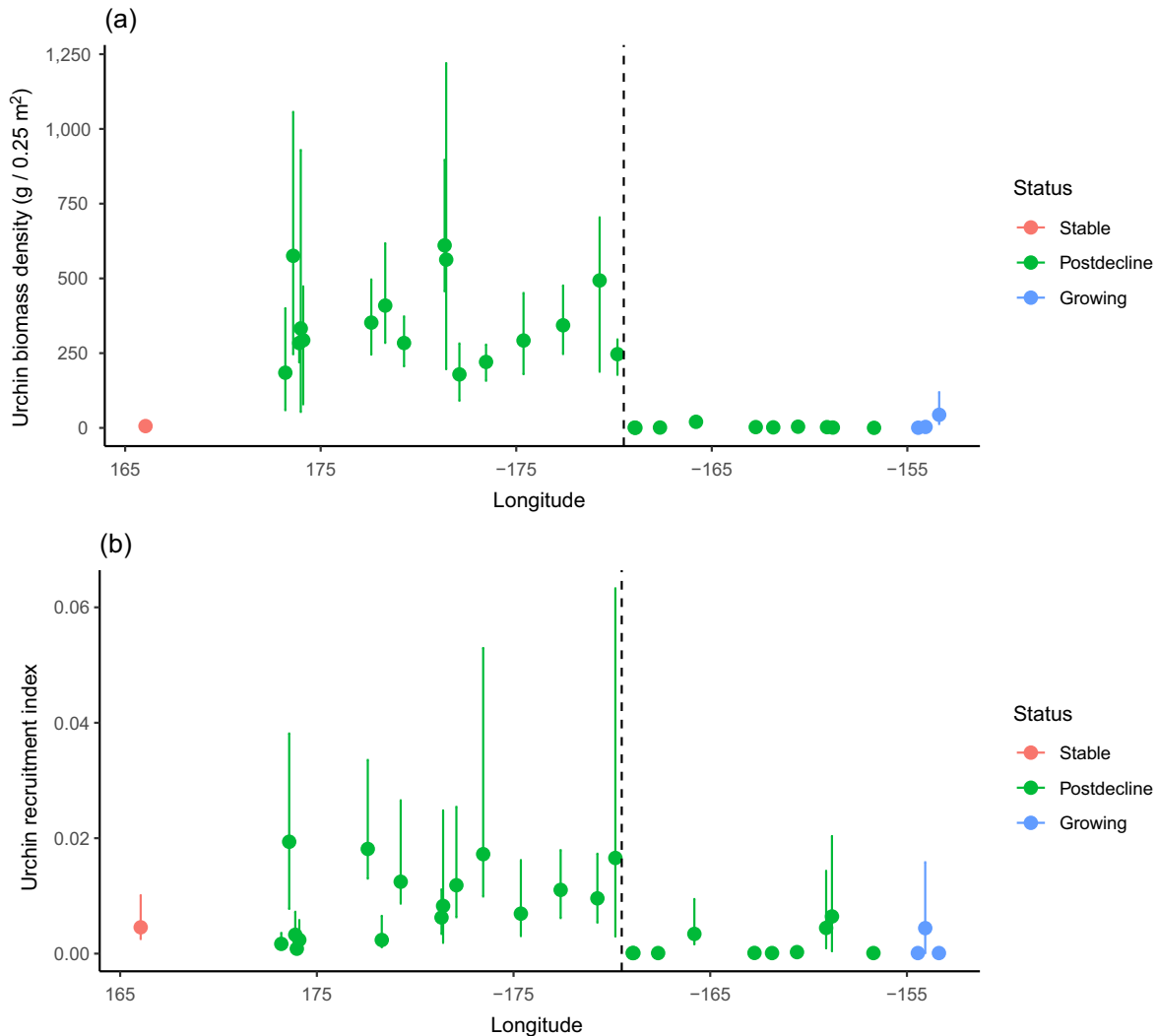


FIG. 12. Spatial variation in estimated urchin biomass density (a) and urchin recruitment index (b) at locations sampled after 2005 and arranged across a longitudinal gradient (west to east). Mean values for each index and location are plotted as points (color coded by status with respect to the decline) and error bars indicate 95% credible interval. The vertical dashed line indicates the position of Samalga Pass along the longitudinal axis.

than in southeast Alaska (Fig. 21). Blood POC concentrations of other contaminants at islands throughout the Aleutians were also similar or lower than at locations in southeast Alaska (Table 17).

Comparing support for alternative hypotheses

The results of analyses of multiple data sets, as presented above, provided varying degrees of support or lack of support for the predictions associated with alternative hypotheses for the cause of the sea otter decline in southwest Alaska (Table 1). In many cases it was possible to score combinations of hypotheses and data types as either a “1” (the analysis results were consistent with hypothesized predictions) or “0” (the analysis results were inconsistent with the hypothesized predictions),

while in other cases a score of NA indicated either no relevancy or no conclusive inferences about degree of support (Table 18). For example, data on foraging success and urchin abundance both suggest that there was an increase in the availability of food for sea otters during the decline: these data sets are thus inconsistent with the nutritional limitation hypothesis, but consistent with both the fisheries/harvest and predation hypotheses (both of which imply top-down control of sea otters and thus increases in prey in response to reduced sea otter predation); alternatively, no conclusive inferences could be made about hypotheses of reproductive failure, disease, contaminants, or large-scale redistribution. A tabulation of all consistencies and inconsistencies can be used to gauge the overall weight of evidence for or against each hypothesized causal factor.

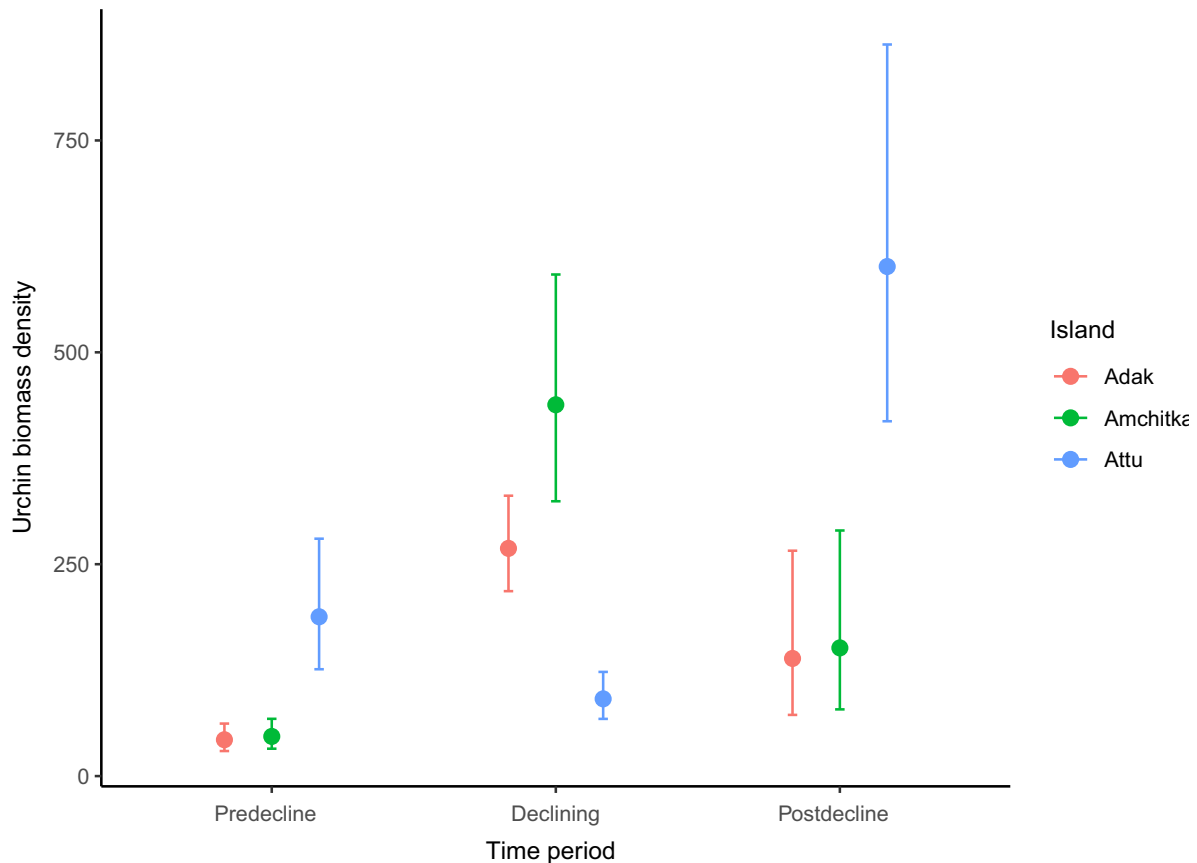


FIG. 13. Temporal trends in estimated urchin biomass density at three islands in the western Aleutian archipelago. Estimates are based on sampling conducted at each island during three time periods: prior to the start of the decline (before 1989), during the period of decline (1989–2001), and postdecline (after 2001). Mean values for each island and time period are plotted as points, and error bars indicate 95% credible interval.

A review of the completed consistency matrix (Table 18) shows that the available data sets did not allow for an equal degree of assessment for all hypotheses. For example, the nutritional limitation hypothesis was addressed in various ways by eight of the available data sets (all of which were inconsistent with this hypothesized cause), whereas reproductive failure was addressed by four data sets and large-scale redistribution was addressed by just two data sets. This means that our level of certainty about the degree of support for different hypotheses will not be equivalent for all causes. Similarly, some data sets (such as abundance trends or carcass production) provided insights into the degree of consistency of most alternative hypotheses, whereas other data types (e.g., contaminant exposure) were more specific to one or a few alternative hypotheses.

In the case of the final data type, “documented observations of deaths,” we rely on previously published accounts of sea otter mortality that directly pertain to one or more hypothesized causal agents, and their distribution in time and space. Published reports on the spatiotemporal distribution (in Alaska) of exposure to and/or mortality from disease (Goldstein et al. 2009,

Goldstein et al. 2011, Carrasco et al. 2014, Lefebvre et al. 2016), fisheries interactions and human harvest (DeGange & Vacca 1989, Raymond et al. 2019) and predation (Estes et al. 1998, Hatfield et al. 1998) were inconsistent with disease or fisheries/harvest mortality as a primary cause of decline but were consistent with predation as a primary cause of decline assuming the predator left no remains to be found.

A qualitative evaluation of the degree of consistency between multiple data sets and the alternative hypotheses suggests a high degree of consistency with the predation hypothesis (zero inconsistencies out of seven relevant data sets) and a low degree of consistency with all other hypotheses (50–100% of available data sets showing inconsistency). A Bayesian-based information theoretic approach provided a more quantitative assessment of the relative weight of evidence, subject to the assumption that each data set represented an independent experimental test of support for each hypothesis. Based on data and analysis of results presented here, we found that the relative degree of support for the predation hypothesis (0.8) was 3–4 times higher than the relative degree of support for all other hypotheses (Fig. 22).

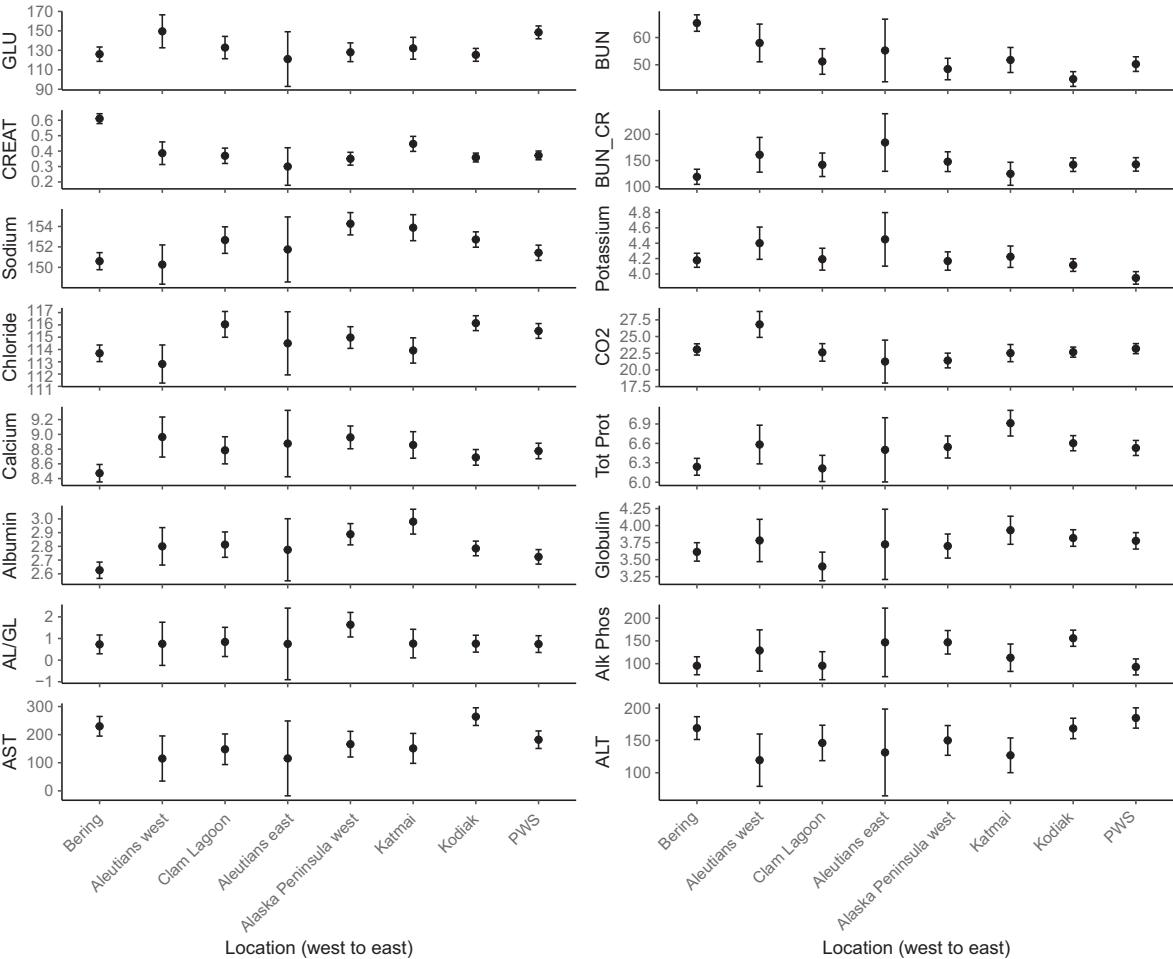


FIG. 14. Univariate comparisons of 16 serum chemistry parameters measured from sea otters captured and sampled at eight locations across Alaska between 2004 and 2012, arranged west to east.

There was considerable uncertainty around point estimates for degree of hypothesis support, although the upper bounds of the 95% CI for hypotheses 1–7 were all <0.6, and there was no overlap in 95% CI between the predation hypothesis and any other hypotheses (Fig. 22).

DISCUSSION

Understanding the distribution and abundance of organisms is a central goal of ecology (Scheiner & Willig 2008). This endeavor is commonly pursued through an initial description of pattern and the subsequent quest to comprehend causal process. A variety of approaches have been used in an effort to understand ecological process, which range from almost purely observational to rigorously experimental. Observational approaches are applicable to almost any pattern but seldom lead to a strong causal inference because such inferences always rest on unconfirmed assumptions. Properly done

experiments exclude the potentially confounding influences of unconfirmed assumptions, thereby leading to stronger inference (Platt 1964). Many modern ecologists thus embrace the experimental method as superior (Underwood 1990). However, relevant experiments are not always feasible, usually for logistical, legal, and ethical reasons (Quinn & Dunham 1983).

Logistical constraints, which often arise from temporal and spatial scales of pattern and process that are unmanageably large (Levin 1992), are the most fundamental obstacle to understanding ecological process by way of experimentation. For example, generation times vary among species by nearly five orders of magnitude (from hours to millennia) and the longer of these are simply too great for an experimental approach to provide useful results in a timely manner (Fukami & Wardle 2005). Similarly, many potential causal processes are difficult or impossible to manipulate (i.e., vary by adding them to or removing them from an experimental unit) at manageable spatial scales (Carpenter 1990). Although

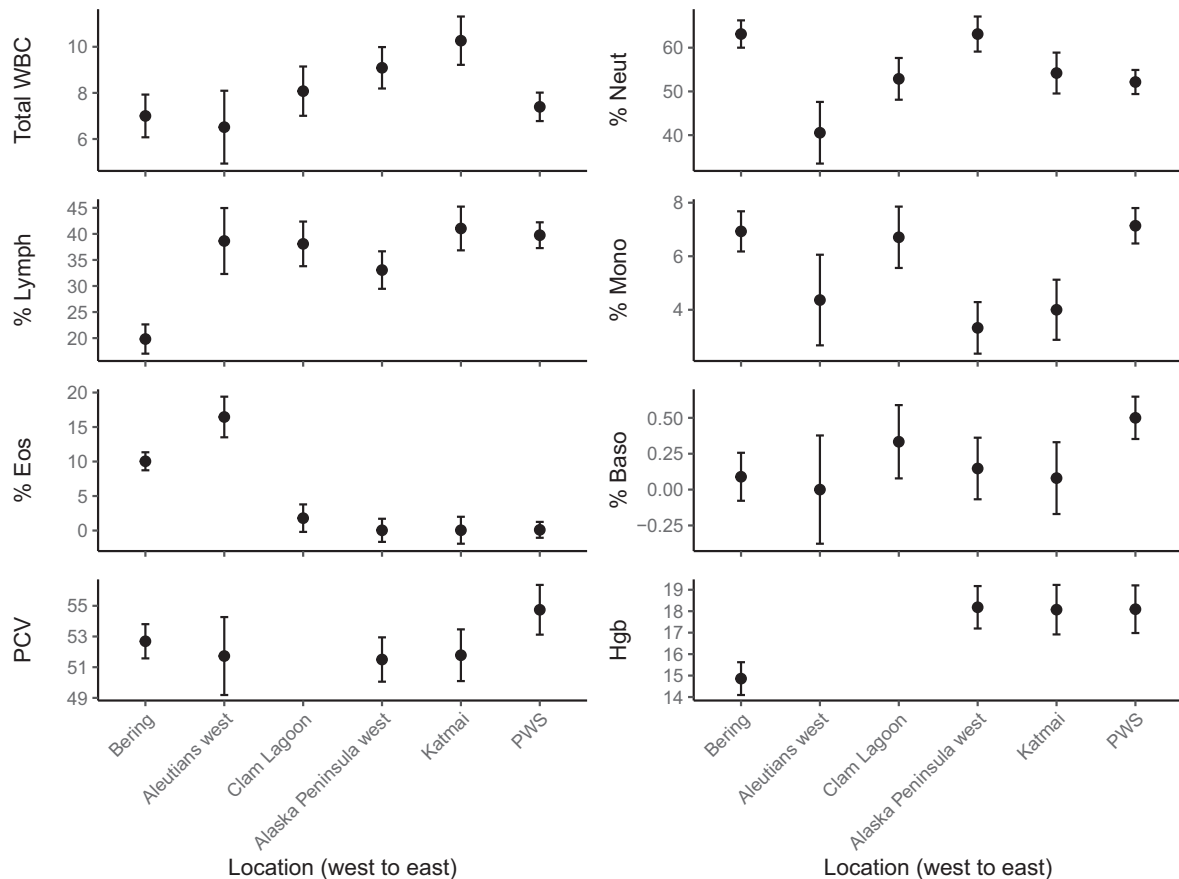


FIG. 15. Univariate comparisons of eight hematology parameters measured from sea otters captured and sampled at various locations across Alaska between 2004 and 2012, arranged from west to east.

the experimental method has been a boon to ecology, virtually all of the many thousands of published studies that are rigorously experimental involve processes that can be manipulated on sufficiently small and brief scales of space and time. This fact leads to a philosophical conundrum—should the many questions about nature that are not experimentally addressable be dismissed as rigorously unanswerable, or should ecologists attempt to answer these questions, but with appropriate caveats of uncertainty? Many modern ecologists opt for the latter, if not by preference then out of necessity.

Although efforts to understand questions that are not experimentally addressable will always be plagued by uncertainty, it is often possible to reduce the level of uncertainty through the use of natural experiments and the comparative method. Natural experiments, though usually unreplicated and never well controlled, nonetheless can be illuminating because, as with any purposeful experiment, they provide the opportunity to observe the system's response to a perturbation (Carpenter 1990, Butsic et al. 2017). The challenge to all who use natural experiments and the comparative method is to make the resulting inferences as objective and compelling as

possible. This can be accomplished by adhering to two principles. The first principle is to consider competing alternative hypotheses broadly. In contrast with purposeful experiments, which are nearly always done to test specific hypotheses, natural experiments are never purposefully designed and their results therefore must be interpreted from the weight of evidence for and against all possible (or at least all reasonably imaginable) hypotheses. The second principle is to consider multiple data types. Even though there may be uncertainty in the interpretation of any particular kind of information, a consistency of pattern across multiple data sets, in the context of expectations under the multiple alternative hypotheses, can reduce the level of overall uncertainty.

The aforementioned discussion provides a conceptual backdrop for this monograph. After almost 50 yr of recovery from near extinction from the maritime fur trade (Kenyon 1969, Estes 1990a), sea otter populations abruptly and unexpectedly collapsed in the central and western Aleutian archipelago (Doroff et al. 2003). Scientists, managers, and the public at large wish to know why. Although predation by killer whales has been identified as the most likely cause of the sea otter collapse

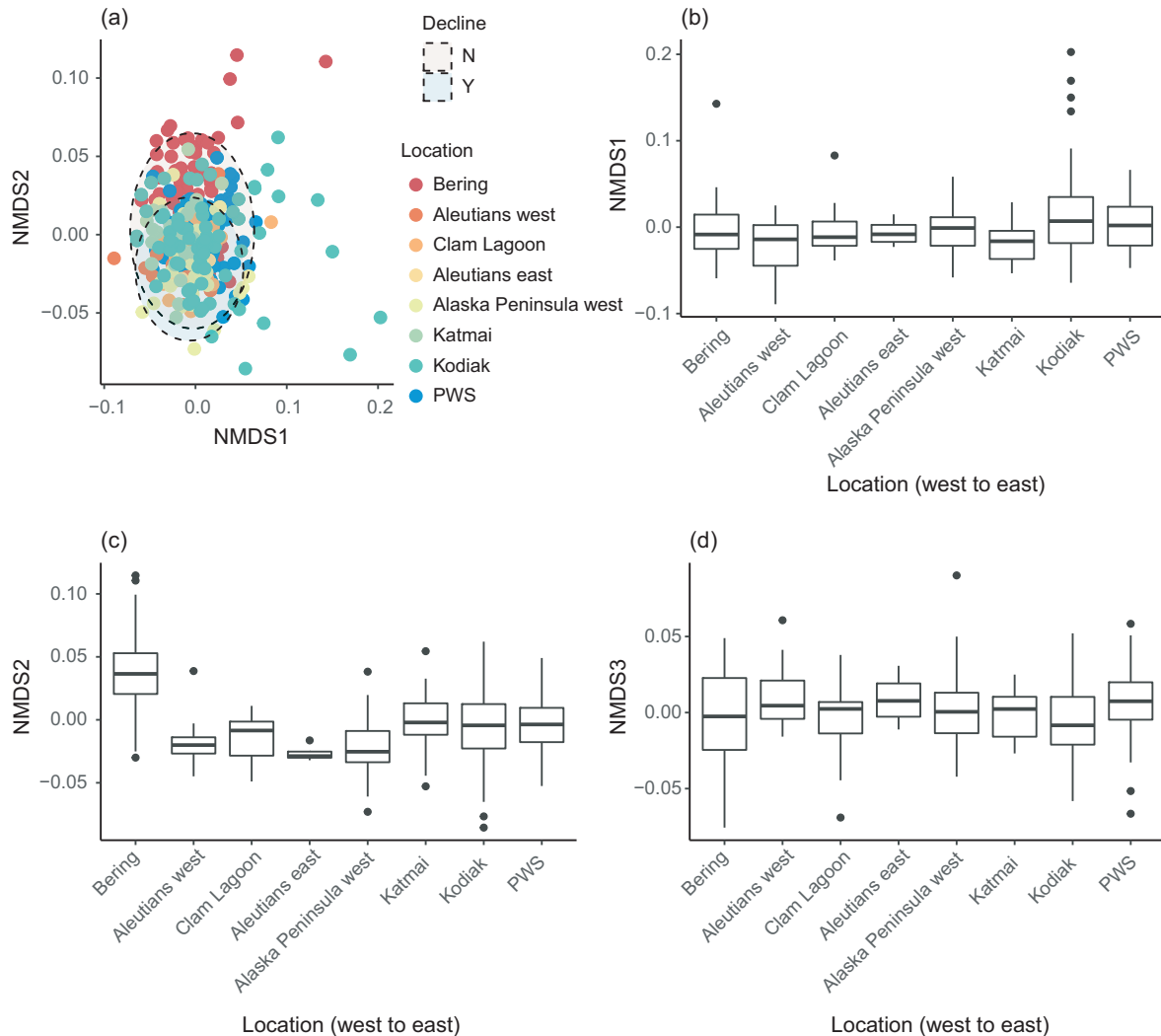


FIG. 16. Results of multivariate analysis of serum chemistry parameters measured from sea otters captured and sampled at eight locations across Alaska between 2004 and 2012. A nonparametric multidimensional scaling analysis (NMDS) ordination of all data (a) showed a high degree of overlap between individuals from all populations, with no clear differentiation between otters sampled within the area of decline (blue-filled 95% confidence ellipse) and outside the area of decline (red-filled 95% confidence ellipse). Comparisons of values for each of three NMDS axes (b), (c) show high overlap across populations, with some outliers on NMDS1 for Kodiak and elevated values of NMDS2 for Bering Island, both of which are locations outside the area of decline.

(Estes et al. 1998, Williams et al. 2004, USFWS 2013), there is at least one dissenting view (Kuker & Barrett-Lennard 2010) and the direct evidence for killer whale predation is indeed limited. Fortunately, we have been studying sea otters and coastal ecosystems in this region for decades and have amassed a great deal of information on basic natural history, demography, and ecological interactions. We have used various information from those studies (1) to describe the spatiotemporal pattern of decline more rigorously, and (2) to understand the underlying responsible process better.

The spatiotemporal pattern of decline was determined from two kinds of data—(1) time series of counts from seven islands or coastal locations over the course of the

decline, and (2) a large-scale resurvey of otter populations across larger regions at or near the end of the period of decline. We used population densities at the ends of the time-series measurements for islands that had declined and our knowledge of where and to what degree sea otters had recovered after the maritime fur trade—beginning with Kenyon (1969) and including subsequent published and unpublished survey results obtained through the 1970s and 1980s from Prince William Sound to the Commander Islands—as guidelines for a regional-scale geographic assessment. With this historical information, we could determine with confidence whether a low sea otter population density at any given island/location within the overall area of interest was the result of a

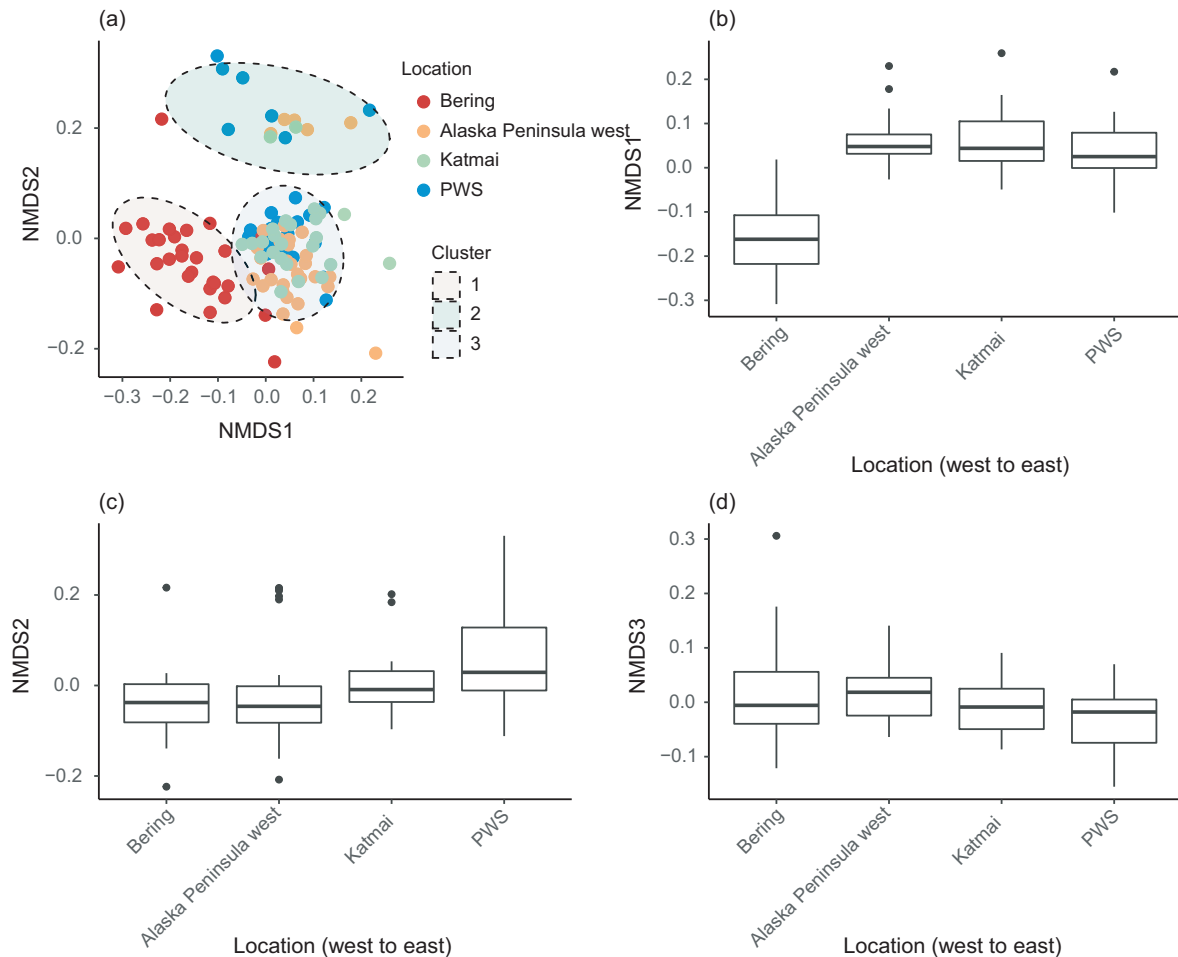


FIG. 17. Results of multivariate analysis of hematology parameters measured from sea otters captured and sampled at four locations across Alaska between 2004 and 2012. A nonparametric multidimensional scaling analysis (NMDS) ordination of all data (a) showed support for three distinct clusters (defined by color-coded 95% confidence ellipses), and samples from Alaska Peninsula west (within the decline area) clustered together with samples from Katmai (outside the decline area). Comparisons of values for each of three NMDS axes (b), (c) showed high overlap across populations, although Bering Island had lower than average values of NMDS1 and PWS had higher than average values on NMDS2.

decline or the failure to recover from the fur trade. This geographical assessment generated several notable patterns. One of these is a clear delineation of the range of the decline, which extends from Attu Island (westernmost of the Aleutian archipelago) in the west to Castle Cape (on the south coast of the Alaska Peninsula) in the east (Fig. 1). Sea otter populations in the Commander Islands (the next point of land to the west of Attu) had recovered from the fur trade by the late 1980s (Fig. 2) and remained stable there through 2007 (the year of the most recent available survey). The change in population density between Attu and Bering islands is sharply truncated (i.e., there is no indication from the pattern of population densities across the western Aleutians through the Commander Islands and Kamchatka Peninsula of a spatially graded decline). The history of post-fur-trade sea otter recovery along the Alaska Peninsula is less clear, owing largely to a general lack of surveys in this

region through the 1970s and 1980s. However, remnant colonies are known to have survived at Kodiak, and somewhere around the eastern Aleutians or western Alaska Peninsula (Kenyon 1969). These remnant colonies seeded populations that spread and increased across this area through the 1970s and 1980s (Schneider 1981, Brueggeman et al. 1988, USFWS 2013, Bodkin 2015, Coletti et al. 2016). Thus, at the time of the decline's onset in the central and western Aleutians in the late 1980s or early 1990s, sea otter populations had recovered to a large degree across all or much of the area to the east. The low sea otter population densities west of Castle Cape are therefore almost certainly a result of the decline, not an intrinsically low carrying capacity of that environment. The transition to a high sea otter density to the east of Castle Cape, while not as dramatic as that between Attu and the Commander islands in the west, is similarly sharply truncated. Thus, regional differences

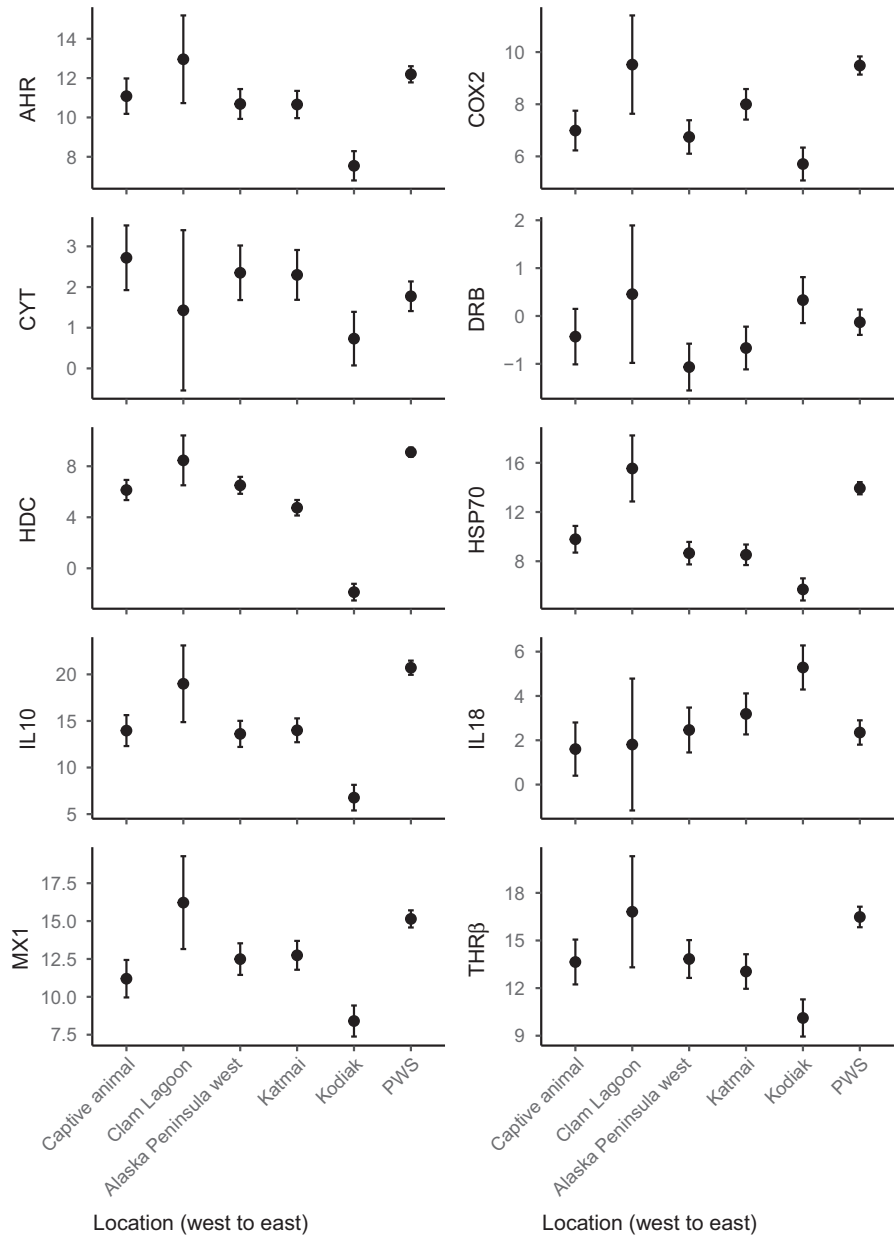


FIG. 18. Univariate comparisons of gene transcription results for 10 index genes sampled from captive sea otters as well as wild sea otters captured and sampled at five locations across Alaska between 2004 and 2012, arranged from west to east.

and uncertainties notwithstanding, our data indicate that (1) sea otter populations have declined across the entire area from Attu Island to Castle Cape (Fig. 2); (2) the resulting low population densities are broadly similar throughout this area (Fig. 4c); (3) the behavioral tendency of otters to remain very close to shore, a phenomenon first observed in SW Alaska after the 1990s, was witnessed consistently within the area between Attu Island to Castle Cape, but not at islands/locations outside this area (Fig. 4a); and thus (4) the reason or reasons for the decline are probably not geographically

graded but instead begin and end abruptly at the decline's range limits. The data further indicate that the decline began and progressed to a low, steady-state density in a nearly synchronous manner throughout this area (Fig. 2).

Given the enormous spatial scale of the decline, the logistical inaccessibility of most of this region and thus the near impossibility of directly observing sea otter mortality, there is little opportunity for experimentally testing hypotheses about the cause of the decline. What then can be reasonably inferred from the

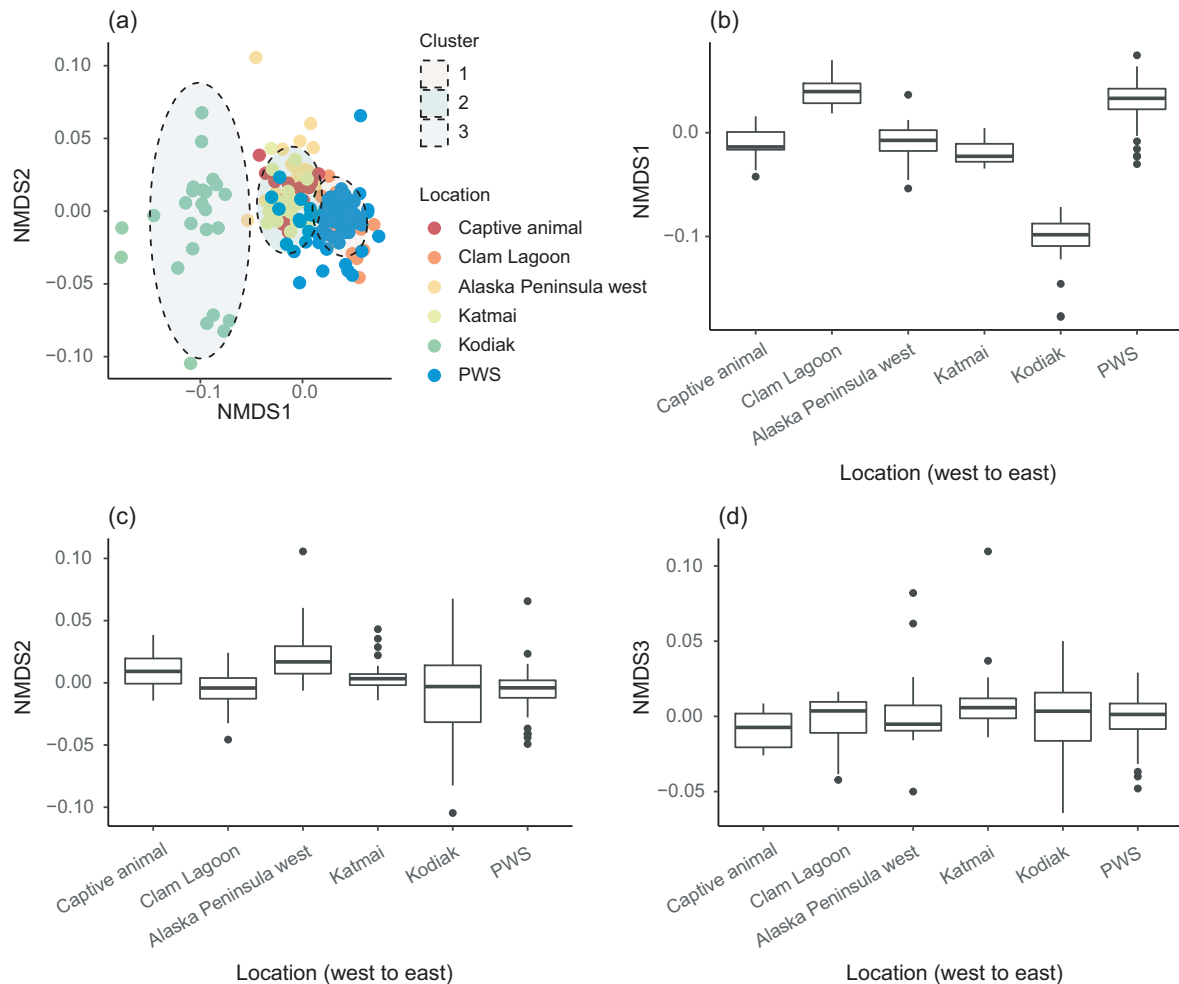


FIG. 19. Results of multivariate analysis of gene transcription biomarkers measured from captive sea otters as well as wild sea otters captured and sampled at five locations across Alaska between 2004 and 2012. A nonparametric multidimensional scaling analysis (NMDS) ordination of the data followed by k-means cluster analysis (a) shows that animals tend to group into three clusters (illustrated by the three 95% confidence ellipses): the first cluster consists of animals from Prince William Sound and Clam Lagoon (on Adak Island); the second cluster includes animals from Katmai, western Alaska Peninsula (within the area of decline) and captive animals; and the third cluster consists of animals from Kodiak. Comparisons of values for each of three NMDS axes (b) and (c) show significant differences between populations on NMDS1 and NMDS2, consistent with the three clusters.

available indirect evidence? Only three general demographic processes—births, large-scale movements (immigration and emigration), and deaths—must be responsible for any and all changes in population size (Gotelli 2001). We can exclude reduced or failed reproduction as an explanation for the sea otter population decline because the data unequivocally show that reproductive rates were similar across the various populations we studied and did not decrease (and may even have increased) through the period of decline (Table 4, Fig. 4). Moreover, even a complete failure of reproduction could not explain the rapid rate of population decline in the 1990s (25% per year), as typical mortality rates of nonpup otters (Gerber et al. 2004) combined with zero recruitment can only account for a rate of decline of 10–15% per year. Large-scale

redistribution can also be excluded because sea otters rarely move over large (>1,000 km) distances (Garsheles and Garsheles 1984, Ralls et al. 1996, Bodkin et al. 2000, Tinker et al. 2008b, Laidre et al. 2009), and even if they did, the corresponding increases in abundance at islands/locations beyond the range of the decline have not been seen. This is clearly true in the west, where otter numbers in the Commander Islands and along the adjacent coast of Russia remained more or less constant over the period of the decline (Fig. 2f, l). Otter populations along the Katmai coast and in lower Cook Inlet (to the east) (Fig. 1) have increased markedly in recent decades, but these increases are thought to be the result of intrinsic growth processes in an area that is still recovering from the fur trade (Monson & Degange 1995, Bodkin 2015, Coletti et al. 2016).

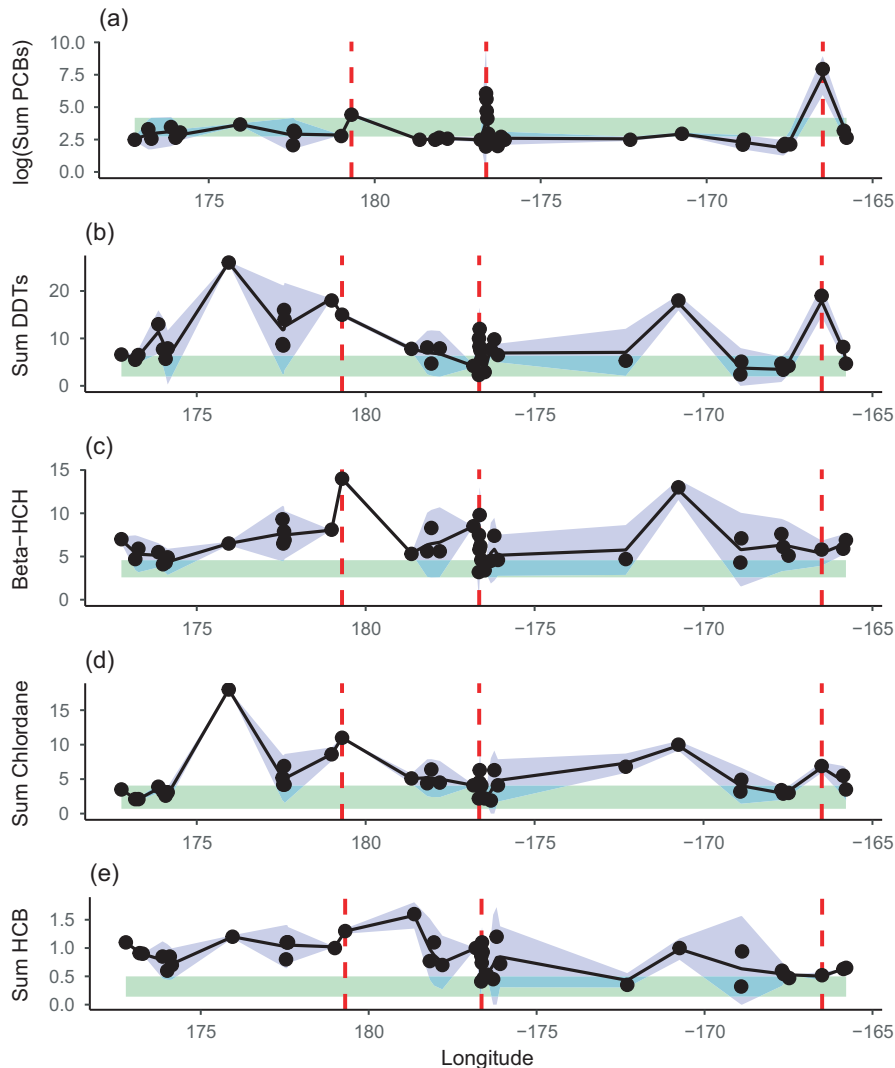


FIG. 20. Spatial variation in the concentration of five organic contaminants sampled from mussels in the Aleutian archipelago. Data from 39 sites are plotted along a longitudinal axis (increasing from west to east). A LOESS curve fit to the data is plotted as a black line, with blue shaded band indicating the 95% prediction interval. The green shaded band shows the 95% credible interval for concentrations measured from samples collected at five sites in southeast Alaska. The vertical red dashed lines indicate the sites of military bases.

This leaves elevated mortality as the only possible explanation for the sea otter decline in southwest Alaska. The state-space demographic model fit to the survey data at seven index islands/locations supports this inference, indicating that residual variation in vital rates (i.e., variation not explained by typical density-dependent processes) increased dramatically around 1989 at the five outer coast islands within the area of decline, but did not increase in Clam Lagoon on Adak, or at Bering Island, outside the decline area (Fig. 2). This demographic volatility was associated with multi-year increases in mortality rates (above 0.2, the intrinsic rate of population increase for sea otters) at the outer coast islands within the decline area, sufficient to drive a steep decline through the mid-1990s and to constrain

recovery of the remaining low-density populations through the subsequent 20 yr. Similar increases in residual mortality were not seen in the Bering Island population, whose dynamics between 1970 and 2015 were well explained by typical density-dependent processes (Bodkin et al. 2000). For Clam Lagoon, the model results indicate a brief spike in residual mortality in the early 2000s, sufficient to cause a short-lived dip in numbers (Fig. 2a, g); however, anecdotal reports by USFWS maritime refuge staff stationed at Adak during that time suggest that this pattern may instead have been caused by an episodic emigration event, as a group of some 30–40 otters appeared in Kuluk Bay (the outer coast immediately adjacent to Clam Lagoon) in late winter/spring of 2000 (J. Williams, *personal communication*), which

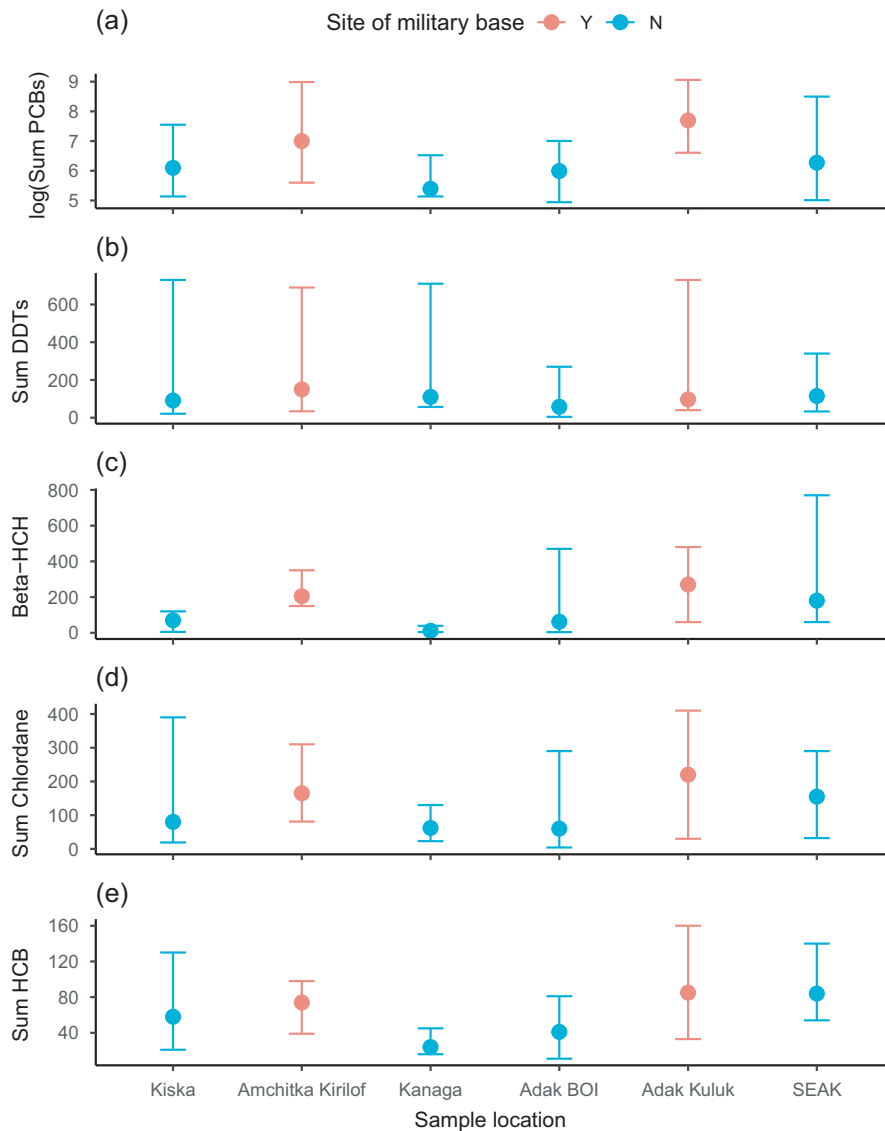


FIG. 21. Spatial variation in the concentration of five organic contaminants in sea otter blood. Samples from five sites in the Aleutian archipelago (plotted along a longitudinal axis increasing from west to east) are compared to samples from southeast Alaska (rightmost points), with error bars indicating the range of values from each sample. Data are color coded based on proximity to past or present military bases.

had disappeared by the following summer. The number of animals in Clam Lagoon subsequently recovered, reaching 90% of estimated local carrying capacity by 2015, while population density on the outer coast of Adak remained low.

An unexpected result of the state-space model analysis was the evidence for cyclicity in the magnitude of residual mortality at those islands where otter numbers declined (Fig. 2). Each of these islands appears to have experienced 2–3 peaks in unexplained mortality since 1990, with negligible levels of residual mortality between those peaks. The islands with the most complete time series of survey data (Attu, Amchitka, and Adak, each in different

island groups) most clearly illustrate this “peak and valley” pattern of mortality (Fig. 2g–i). The “valleys” are evident in the survey time series as short-lived periods of population growth (Fig. 2a–c), followed by renewed declines after the next “peak.” The reasons for this cyclicity are presently unknown: one possible explanation is that they are related to movements of predators across the area of decline, but additional information about predator behavior would be required to evaluate this hypothesis properly. Clam Lagoon and Bering Island, while exhibiting minor variation in residual mortality (and one large spike for Clam Lagoon, discussed above), did not exhibit large cyclical peaks in mortality.

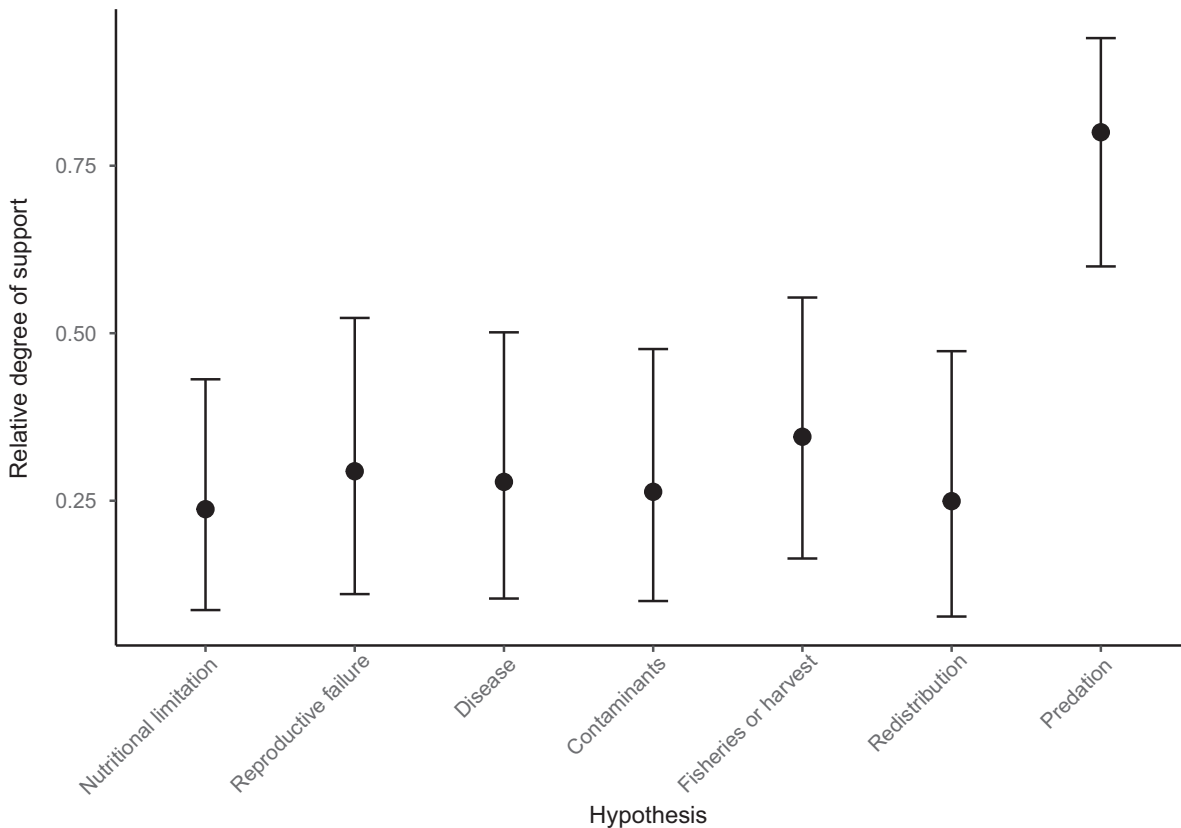


FIG. 22. Results of a quantitative analysis of consistency between multiple data types and the predictions of seven alternative hypotheses about the cause of the southwest Alaska sea otter decline. Points and error bars indicate the posterior mean and 95% credible interval for the inferred degree of support for each hypothesis, based on overall consistency with all available data.

Although the available survey data strongly imply increased mortality (rather than reduced reproduction or dispersal) as the demographic driver of decline, the source of this elevated mortality is less clear. Potential causes of increased mortality that we could envision included nutritional limitation (food resources that are insufficient in abundance or quality to maintain high numbers of sea otters), disease (parasites and pathogens), toxins (anthropogenic contaminants or biotoxins), predation, and direct or indirect anthropogenic killing (e.g., illegal harvest, incidental losses in fishing gear). It is also possible that two or more of these factors acted in concert. For example, nutritional limitation might have led to an increased susceptibility to toxins, parasites, pathogens, or even predators. However, we can envision no other obvious causes of the decline, and no others have been suggested in the literature. Using a weight-of-evidence approach, we can evaluate the degree of consistency between the predictions associated with each hypothesized cause of mortality (Table 1) and the available data sets.

The data are strongly inconsistent with nutritional limitation as a cause of or contributing factor to the sea otter decline. Elevated prey abundance and biomass (Fig. 10a), large structural body size and good condition of sea otters (Fig. 6), and high rates of energy gain by

foraging otters (Figs. 8, 9) within vs. outside the area of decline all run counter to the expected effects of nutritional limitation. The nutritional limitation hypothesis can thus be dismissed with high confidence.

The data also are inconsistent with disease or toxicity as causes of the decline. Either of these factors should have produced substantial numbers of stranded carcasses or their remains during the height of the decline, but few of either were found; in fact, the per capita carcass recovery rate decreased during the decline (Fig. 5). Nor did we find any direct evidence for toxicity or disease in sampled animals (Tables 11, 15, 17) or their coastal environments (Table 16). Broad-spectrum assays for persistent organic compounds (POCs) in both intertidal mussels and in tissue samples from the remaining living sea otters revealed generally low concentrations of these compounds within the range of the decline, except for localized spikes in certain organic compounds (e.g., PCBs) at three sites of current or previous military activity, and localized increases of other persistent organic compounds (e.g., DDTs, chloro-danes) near breeding seabird colonies (Ricca et al. 2008, Reese et al. 2012). Gene transcription analysis also showed no evidence of increased exposure to disease or toxins within the area of decline: to the contrary, gene transcription patterns for animals within the decline area

were most similar to those observed in healthy captive otters and otters from a growing population in a pristine area (Figs. 18, 19). We also found no consistent differences in hematologic/blood serum assays between populations that had declined and populations adjacent to the decline area that were stable or growing. These results are consistent with a previous analysis (Hanni et al. 2003) contrasting pathogen exposure rates and hematologic/blood serum assays between the declining sea otter populations in the west-central Aleutian Islands and the stable population in central California, which demonstrated higher disease exposure levels and stronger indications of pathology in central California.

Conceivably, the decline was caused by an unknown toxin or pathogen, or an epidemic that swept through the population, leaving the survivors with bountiful resources. However, efforts to chronicle disease and toxicity during and after the decline (data presented here and by Jessup et al. 2010, Goldstein et al. 2011, Reese et al. 2012) provided no indication of unusual levels of either factor within the area of decline. Moreover, the failure of the small sea otter population in Clam Lagoon on Adak Island to decline while widespread declines occurred elsewhere (Figs. 1, 2) is difficult to reconcile with toxicity or disease. The results of demographic modeling presented here indicate that elevated levels of mortality within the area of decline have continued through 2015, thereby explaining the continued lack of recovery (Fig. 2). If disease or toxicity were responsible for the decline we would expect to see continued evidence of these processes during our more recent sampling events (e.g., abundant beach-cast emaciated carcasses, irregularities in body condition, health metrics, gene transcription indices and hematologic/blood serum assays of captured animals), which we did not. Finally, the magnitude and duration of the decline is inconsistent with how episodic diseases normally affect populations (Härkönen et al. 2006, Krog et al. 2015) and the spatial extent of the decline is inconsistent with toxins that generally affect more localized populations exposed to an identifiable source (de Marche et al. 1998, Miles et al. 2007, Ricca et al. 2008, Miles et al. 2009). Even a large-scale contamination event such as the 1989 *Exxon Valdez* Oil spill only affected a subset of the Prince William Sound sea otter population (Monson et al. 2011) and had no discernable population effects outside of Prince William Sound.

Purposeful or inadvertent human take might have been responsible for or contributed substantially to the decline. Food resources would expectedly increase in response to a reduction in sea otter population density and the resulting release from density-dependent population limitation, as would foraging efficiency, body condition, and general health profiles. The absence of stranded carcasses could also be consistent with human take if the carcasses sank (as might be expected after drowning in fishing gear) or were otherwise disposed of (as might be expected with illegal take). However, the

observed behavioral shift in habitat selection by sea otters after the decline is not consistent with a predicted response to human take. Specifically, at islands that experienced population declines, the remaining sea otters are now found almost exclusively in areas very close to shore (Fig. 4), having more complex underwater bathymetry (Stewart et al. 2015) or else within shallow estuaries (e.g. Clam Lagoon), a distributional pattern which would not discourage lethal take by humans (but would limit access for large marine predators). In fact, the observed shift in habitat use would likely facilitate hunting from shore or from small boats. For this reason, and because there are no known coastal human activities in this remote region that could have removed so many animals so quickly (and any such events should have been observed and reported at one point or another), we view the human take hypotheses as unlikely.

Predation is therefore the only remaining explanation for the decline. This conclusion is supported by our Bayesian analysis of the weight of evidence, reflecting the combined degree of consistency between each hypothesis and the available data sets. In light of available data, the relative degree of support for predation as a cause of the decline was more than 2× higher than the relative support for any of the other hypotheses (Fig. 22). Although any number of species are capable of killing adult sea otters, two groups of predators—killer whales and sharks—stand out as being most likely, based on behavior and their existing distributions. The evidence is consistent with either of these predators. Killer whales have been observed on several occasions to attack and consume sea otters (Hatfield et al. 1998); of these observations in southwest Alaska, all occurred since the onset of the decline; and several prior analyses (Estes et al. 1998, Williams et al. 2004) demonstrate both the feasibility of killer whale predation and a consistency between the observed rate of predation on sea otters and the rate and magnitude of sea otter population decline. There is no direct evidence of shark predation on sea otters in southwest Alaska, despite studies of hundreds of predatory shark stomachs from the area of sea otter decline (Yang & Page 1999, Hulbert & Rice 2002, Sigler et al. 2006, Kubodera et al. 2007). White sharks have had significant impacts on sea otter populations in California; however, in that region sea otters appear to be the victims of investigative bites rather than targets for consumption, resulting in many identifiably shark-bite carcasses washing up on beaches (Ames & Morejohn 1980, Tinker et al. 2016, Moxley et al. 2019). Although this does not exclude sharks, we consider sharks less likely than killer whales because of the lack of any direct evidence or observations of consumption. Further, the spatial extent of the decline and the irregular pulses in excess mortality suggest the decline could be the result of one or several groups of killer whales moving extensively throughout the region (or only occurring within the region part time), making periodic visits to individual islands (Durban et al. 2010).

CONCLUSIONS

The disappearance of large predators is a defining feature of the Anthropocene (Estes et al. 2011, Ripple et al. 2014). The reasons for these disappearances are fairly obvious in some cases, but they are less certain or entirely unknown in many others. This is especially so in remote ocean ecosystems, where observation is difficult and, except for fisheries (Myers & Worm 2003), the culture of ecology has largely embraced physical forcing and bottom-up control as a default explanation for population change (Ocean Studies Board 2017). These uncertainties and predilections in the process of population regulation are not matters of concern for increasing populations, as limiting process under this circumstance is not an issue to be reckoned with. They are matters of substantial concern for the many populations that are in decline or are failing to recover, especially for those cases in which the goals of management and conservation are to arrest a declining trend or recover a depleted species. Mitigation in these cases requires a proper understanding of limiting process.

The approach we have taken in an effort to identify causal process in the decline of sea otters in southwest Alaska and their ongoing failure to recover should be applicable to other species and ecosystems, especially where comparisons can be made between areas/times of population recovery or stability and areas/times of population decline or recovery failure. Rather than seeking support for favored explanations (or simply giving up in the face of uncertainty, which unfortunately occurs), a weight-of-evidence analysis, such as we have used here to understand the sea otter decline in southwest Alaska better, can be informative and even helpful for the advance of management and policy. The approach requires four basic steps. Step 1 is to assemble an exhaustive list of causal hypotheses. Although these hypotheses may vary in detail from system to system, those we have developed for the sea otter decline, with minor modifications, ought to be generally applicable to other cases. Step 2 is to make a series of testable predictions for each hypothesis, that is, predictions about the patterns that would be expected in data sets that are available (or could be obtained) if each hypothesis were true. Step 3 is to assemble the available evidence (and conduct field studies to collect additional data if necessary and feasible). The only instances in which there is no evidence are cases for which nothing is known at all. This is rarely the situation because if there is enough information to identify a problem and the problem is of sufficient interest or importance to society, at least some additional work usually will have been done. The evidence is simply a compilation of that information. In many cases this exercise will lead to a clearer vision of additional obtainable data that bears on the issue, an approach providing the added benefit of avoiding the costs of gathering superfluous or largely irrelevant information. The fourth and final step is to line up the

evidence with the hypotheses and determine which hypothesis is best supported by the available evidence. The Bayesian approach we used for our sea otter example provides one possible quantitative, probabilistic way of comparing the weight of evidence across hypotheses, though there are others. A key requirement of this final step is that the underlying logic for consistency/inconsistency between each element of evidence and each specific hypothesis be reasonably clear and unequivocal. In some cases that may not be possible, but in most cases it should be. Seldom will this approach lead to a definitive explanation for a population decline. However, it will nearly always identify inconsistencies that can be used to exclude particular hypotheses—an undertaking that always will bring one closer to the truth.

ACKNOWLEDGMENTS

Support for this work was provided by the U.S. Geological Survey, the U.S. Fish and Wildlife Service (Office of Marine Mammals Management), the Monterey Bay Aquarium, the Alaska SeaLife Center, the *Exxon Valdez* Oil Spill Trustee Council, the National Science Foundation (grant numbers DPP-8421362, DPP-9101134, 0647635, and PLR-1316141) and the North Pacific Research Board (NPRB Project 717). We thank the crews of the *M/V Tiglax*, *R/V Alpha Helix*, *R/V Norseman*, *R/V Alaskan Gyre*, *M/V Alexandra*, and the *M/V Typhoon* for vessel support, the Alaska Maritime National Wildlife Refuge for logistic support, and the National Park Service for supporting capture work along the Katmai coast (permit number KATM-2009-SCI-0009). We are grateful to Marissa Young (RVT) for invaluable assistance with health assessments and diagnostics, C. McCormick, P. Snyder, P. Tuomi, and V. Vanick for assistance with veterinary services, S. Reese and J. Chapman for administrative support, and H. McCormick and M. Novak for help with data management and analysis. We thank the many people who assisted with fieldwork including C. Alfano, J. Ames, R. Anthony, B. Baker, D. Bruden, D. Burn, L. Carswell, E. Danner, J. DeGroot, M. Deiman, J. deLaBruere, A. Doroff, D. Duggins, M. Edwards, R. Estes, M. Fedorko, J. Figurski, E. Forsman, V. Gill, D. Irons, R. Jameson, W. Jarman, D. Jenski, A. Kage, B. Krause, P. Lane, D. Lindberg, M. Lindeberg, S. McCloskey, A. McKay, J. Meehan, M. Murphy, K. Nolan, J. Pierce, J. Reed, S. Reese, M. Ricca, G. Saunders, C. Simenstad, G. Snedgen, M. Staedler, J. Stewart, K. Vicknair, J. Watson, J. Watt, J. Williams, and L. Yeates. We are grateful to T. Gelatt and 2 anonymous reviewers for helpful comments and suggestions on an earlier draft. Capture and handling of sea otters was authorized under a permit from the U.S. Fish and Wildlife Service (DMA PRT MA067925-1 and MA067095-1) and conducted in accordance with U.S. Geological Survey Alaska Science Center Institutional Animal Care and Use Committee (IACUC) guidelines. This manuscript has been approved for publication consistent with USGS Fundamental Science Practices (<http://pubs.usgs.gov/circ/1367/>). Any use of trade, firm or product is for descriptive purposes only and does not imply endorsement by the U.S. government.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1472/full>

OPEN RESEARCH

All data used for analyses presented here are available for download at publicly available data repositories, including survey data on population trends, distribution, and reproductive rates (Kenner et al. 2021); carcass recovery rates (Kloecker & Monson 2020, Kenner et al. 2021); body size and condition (Monson et al. 2021); diet and energy recovery rates (Kloecker & Monson 2017); urchin abundance (Ebert et al. 2018); health metrics and blood chemistry (Kenner et al. 2021); and gene transcription data (Bowen et al. 2017). Contaminant data from mussels and urchins are available in Jessup et al. (2010, 2021).