Bottom-up forcing and the decline of Steller sea lions (*Eumetopias jubatus*) in Alaska: assessing the ocean climate hypothesis

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ABSTRACT

Declines of Steller sea lion (*Eumetopias jubatus*) populations in the Aleutian Islands and Gulf of Alaska could be a consequence of physical oceanographic changes associated with the 1976–77 climate regime shift. Changes in ocean climate are hypothesized to have affected the quantity, quality, and accessibility of prey, which in turn may have affected the rates of birth and death of sea lions. Recent studies of the spatial and temporal variations in the ocean climate system of the North Pacific support this hypothesis. Ocean climate changes appear to have created adaptive opportunities for various species that are preyed upon by Steller sea lions at mid-trophic levels. The east–west asymmetry of the oceanic response to climate forcing after 1976–77 is consistent with both the temporal aspect (populations decreased after the late 1970s) and the spatial aspect of the decline (western, but not eastern, sea lion populations decreased). These broad-scale climate variations appear to be modulated by regionally sensitive biogeographic structures along the Aleutian Islands and Gulf of Alaska, which include a transition point from coastal to open-ocean conditions at Samalga Pass westward along the Aleutian Islands. These transition points delineate distinct clusterings of different combinations of prey species, which are in turn correlated with differential population sizes and trajectories of Steller sea lions. Archaeological records spanning 4000 yr further indicate that sea lion populations have experienced major shifts in abundance in the past. Shifts in ocean climate are the most parsimonious underlying explanation for the broad suite of ecosystem changes that have been observed in the North Pacific Ocean in recent decades.

Key words: Aleutian Islands, climate regime shift, Gulf of Alaska, Steller sea lion

INTRODUCTION

Steller sea lion populations (*Eumetopias jubatus*) declined by over 80% between the late 1970s and early 1990s in the western Gulf of Alaska and in the

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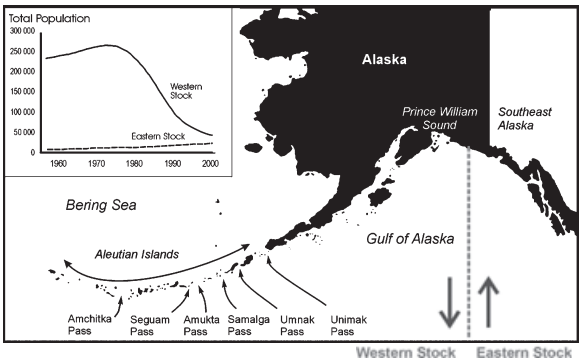
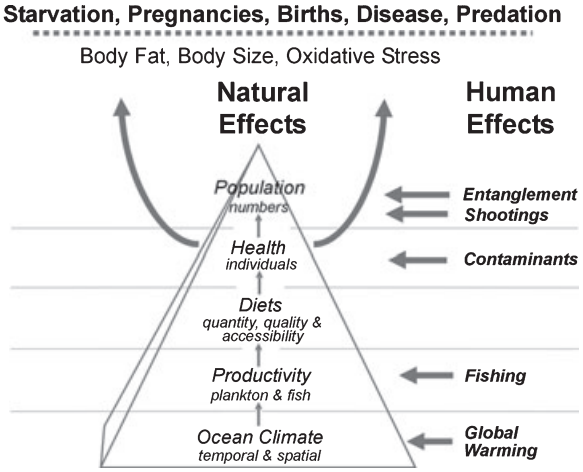
Figure 1. Locations of major geographic features cited in the text. The inserted graph shows estimated numbers of Steller sea lions (all ages) in Alaska from 1956 to 2000 (based on Trites and Larkin, 1996). The dashed line shows the division between the declining (western) and increasing (eastern) populations.



Aleutian Islands (Fig. 1). Concurrent declines also occurred farther west in Russian coastal waters. However, population trends were reversed along the coasts of South-east Alaska, British Columbia, Washington, and Oregon where sea lions increased through the 1980s and 1990s (Trites and Larkin, 1996; Loughlin, 1998). The cause or causes of these population changes have not been resolved and have been the subject of considerable debate and research (DeMaster and Atkinson, 2002; National Research Council, 2003; Trites and Donnelly, 2003).

Much of the search for why Steller sea lions declined in western Alaska has focused on trying to identify a single cause for the changes, rather than recognizing that many of the proposed theories are inter-related. As shown in Fig. 2, the leading hypotheses of epidemic diseases, predation by killer whales, ocean climate change (regime shifts), and nutritional shifts in types of prey available to sea lions (the junk food hypothesis) may all be linked through bottom-up processes. Conceptually, changes in water temperatures, ocean currents and other oceanographic variables can influence the survival and distribution of assemblages of species that are consumed by predators such as sea lions. This in turn will affect the quantity, quality and accessibility of the prey that sea lions consume. Individuals that consume sufficient energy will typically be fat and large, and experience reduced levels of oxidative stress at a cellular level. In contrast, inadequate nutrition can increase oxidative stress (and susceptibility to disease), reduce body fat (and pregnancy rates), and increase rates of predation (as a function of reduced body size or increased vulnerability while spending longer times searching for prey).

Figure 2. Conceptual model showing how sea lion numbers might be affected by ocean climate through bottom-up processes. This hypothesis suggests that water temperatures, ocean currents and other climatic factors determine the relative abundances of fish available to eat, which in turn affects sea lion health (proportion of body fat, rates of growth and at a cellular level – oxidative stress). These three primary measures of individual health ultimately determine pregnancy rates, birth rates, and death rates (through disease and predation). Also shown are the effects of human activities that could have directly or indirectly affected sea lion numbers.



Such changes to the health of individuals ultimately translate into changes in numbers at a population level through decreased birth rates and increased death rates.

A major change in both the physical state and the ecology of the North Pacific Ocean occurred during the mid-1970s, with basin-wide changes noted in temperature, mixed layer depth, primary productivity, fisheries, and other variables (e.g., Beamish, 1993; Miller *et al.*, 1994; Polovina *et al.*, 1995; Mantua *et al.*, 1997; Hare and Mantua, 2000; Benson and Trites, 2002). This linkage between the physical climate and the oceanic ecosystem provided the impetus for the Cooperative Institute for Arctic Research to fund a suite of studies that addressed the hypothesis that large-scale changes in the physical environment of the North Pacific Ocean influenced Steller sea lion populations directly or indirectly. The investigations covered a variety of topics, including physical and biological oceanographic data analysis, ocean modeling experiments, archaeological data, and traditional ecological knowledge.

The following synthesizes a broad range of recently completed research that addressed the climate–ocean regime shift hypothesis of the Steller sea lion decline.

We had two primary goals. The first was to determine whether any spatial and temporal patterns in the physical and biological oceanographic data corresponded with observed differences in the diets and numbers of sea lions since the late 1950s. The second was to put the recent decline in context with similar changes that may have occurred over the past 4000 yr. We begin with a synopsis of the observed features of the Steller sea lion decline along with characteristics of their diets.

STELLER SEA LIONS

Steller sea lions are restricted to the North Pacific Ocean and range along the Pacific Rim from California to northern Japan. Genetically there are two distinct population segments that are split at 144°W near Prince William Sound, AK (Loughlin, 1998; Fig. 1). The sharp decline of the larger western population through the 1980s was mirrored by population growth in the smaller eastern populations in South-east Alaska, British Columbia and Oregon (Calkins *et al.*, 1999; COSEWIC, 2003; Fig. 1).

Counts of Steller sea lions in Alaska began in 1956 and continued sporadically through the 1960s and 1970s. They suggest that sea lion numbers were relatively high and increased slightly through the 1960s and 1970s (Trites and Larkin, 1996). Trouble was not noted until the mid-1970s (Braham *et al.*, 1980), and appeared to spread east and west from the eastern Aleutian Islands in following years (Fig. 3). The frequency and thoroughness of sea lion censuses increased through the 1980s and 1990s and showed an overall rapid decline of sea lions through the 1980s, with an inflection point and slowing of the decline occurring around 1989 (Fig. 1). Recent counts (2002) suggest the possibility that some breeding populations in the eastern Aleutian Islands and Gulf of Alaska may have increased slightly since 1999 (Sease and Gudmundson, 2002).

Analysis of the census data has shown distinct geographic clusterings of rookeries (breeding sites) that shared similarities in their population numbers, trajectories and timings of declines (York *et al.*, 1996; Call and Loughlin, 2006; Winship and Trites, 2006; Fig. 3). Population data from the 1990s (Fig. 3) suggest that in two core regions of sea lion abundance (between Amchitka and Amukta Passes, and around Unimak Pass and the western Alaska Peninsula) numbers have been much higher and population declines slower than in adjoining regions. A few populations in these regions were stable or even increased slightly. In contrast, regions where sea lions have fared much worse are the Aleutian Islands west of Amchitka Pass, the Aleutian Islands between Amukta and Umnak Passes, and the eastern Alaska Peninsula eastward to the central Gulf of Alaska (Fig. 3). Three passes through the Aleutian Islands appear to be the demarcation points for these population segments (Amchitka Pass, Amukta Pass and Umnak Pass; Figs 1 and 3).

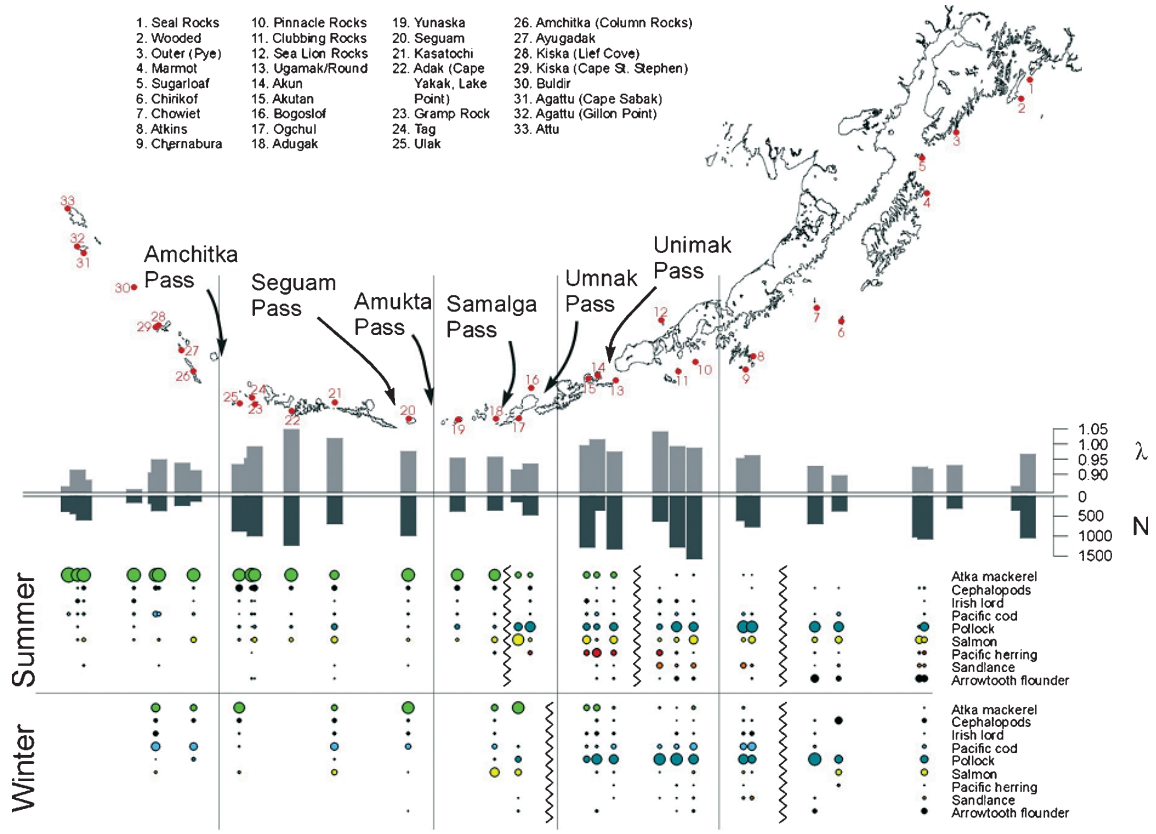
In terms of at-sea distributions, telemetry data indicate that Steller sea lions, particularly females, tend to travel farther from shore in winter than during the summer breeding season (Merrick and Loughlin, 1997), resulting in dramatically different estimates of seasonal distributions (E.J. Gregr and A.W. Trites, unpubl. data; Fig. 4). Steller sea lions regularly haul out on shore at breeding (rookeries) and non-breeding (haulout) sites, and typically spend 1–2 days at sea followed by 1 day resting on shore (Trites and Porter, 2002; Milette and Trites, 2003). Principal prey species include Atka mackerel, walleye pollock, Pacific cod, squid, octopus, salmon, Pacific herring, sand lance and arrowtooth flounder (Sinclair and Zeppelin, 2002).

The most complete set of dietary information for sea lions was collected during the 1990s and also suggests distinct geographic clusterings (Sinclair and Zeppelin, 2002; Fig. 3), with the split points at Samalga Pass and Unimak Pass during summer and Umnak Pass during winter. Demarcation lines for summer diets are roughly in the middle of two population groupings, the one between Amukta and Umnak Passes and the other around Unimak Pass and the western Alaska Peninsula (Fig. 3).

Significant correlations between rates of population decline and the diversity of diets suggest that a possible relationship may exist between what sea lions eat and how their population numbers have fared (Merrick *et al.*, 1997; Winship and Trites, 2003). Sea lions living in regions that incurred the highest rates of declines (e.g., western Aleutian Islands) consumed the least diverse diets with lowest energy prey. In contrast, the increasing populations of sea lions in South-east Alaska had the most energy-rich diet and highest diversity of prey species of all regions studied during summer.

During the 1990s, sea lion diets were dominated by Atka mackerel in the Aleutian Islands, and by walleye pollock in the Gulf of Alaska (Sinclair and Zeppelin, 2002; Fig. 3). Little is known about what sea lions ate prior to their populations declining. Limited insight is only available from two samples from the western Gulf collected in the late 1950s (Mathisen *et al.*, 1962; Thorsteinson and Lensink, 1962) and 1990s (Sinclair and Zeppelin, 2002). Stomachs of animals shot in the

Figure 3. Diets, population trends and sizes for Steller sea lions at 33 rookeries in Alaska during the 1990s. Estimated numbers of sea lions in 2002 (N) and population growth rates (λ) were determined from linear regressions of log-transformed counts of pups and non-pups conducted from 1990 to 2002. Trend and numbers were calculated independently for pups and non-pups, and then averaged. Average population trends ranged between 0.85 and 1.05, with values <1 indicating declines. Bar heights are proportional to the maximum average N and λ, with solid vertical lines denoting distinct geographic shifts in population sizes and trends. Diet data for summer (S) and winter (W) are from Sinclair and Zeppelin (2002), with circles representing the split-sample frequencies of occurrence of prey (proportional to area of circle). The frequencies sum to 100% and were calculated for the nine principal species shown as well as for less important species not shown (grouped into six prey types: flatfish, forage fish, gadids, hexagrammids, other, rockfish). The zig-zag lines indicate seasonal geographic changes in diet (determined through cluster analysis of the summer data by Sinclair and Zeppelin, 2002).

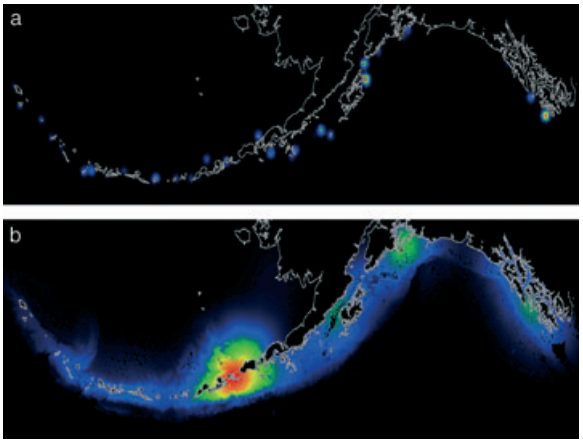


late 1950s at Atkins, Chernabura and Ugamak in the western and central Gulf of Alaska (locations nos. 8, 9 and 13 in Fig. 3) revealed diets dominated by invertebrates and forage fishes, with sand lance occurring in 26% of the sea lions. Flatfish and salmon were rare in the 1950s compared with the 1990s – while pollock were not seen in the 1950s, but were the most frequently occurring prey during the 1990s (at >80% frequency of occurrence at Atkins and Chernabura; Fig. 3). In general, the diet described for the 1950s was strikingly different from that observed for the 1990s.

The National Research Council (2003) review of the causes of the Steller sea lion decline noted that 'levels of groundfish biomass during the 1990s were large relative to the reduced numbers of sea lions, suggesting that there has been no overall decrease in prey available to sea lions'. They also concluded that 'existing data on the more recent period of decline (1990 to present) with regard to the bottom-up and top-down hypotheses indicate that bottom-up hypotheses invoking nutritional stress are unlikely to represent the primary threat to recovery' of sea lions.

The available data support the National Research Council's conclusion that gadid populations were indeed abundant during the population decline, and that Steller sea lions did not starve and incur 'acute' nutritional stress. However, historic data and more recent studies do not support a conclusion that no form of nutritional stress occurred. Instead it appears that sea lions may have experienced 'chronic'

Figure 4. Predicted long-term habitat suitability for female Steller sea lions during summer (a: breeding season) and winter (b: non-breeding season) based on summarized telemetry values, long-term count data, and hypothesized habitat use. Suitability ([0,1]) is shaded from black through blue, green, yellow and red (areas with probabilities $\geqslant 0.75$ are red). Regions with the highest suitability had the highest long-term average census counts from 1956 to 2002.



nutritional stress associated with the high abundances of low-quality species of prey that were present during the 1980s and 1990s (Trites and Donnelly, 2003). This conclusion is based on a growing body of research that includes blood chemistry comparisons, dietary analyses, population modeling, and captive feeding studies (Merrick *et al.*, 1997; Zenteno-Savin *et al.*, 1997; Rosen and Trites, 2000, 2004; Sinclair and Zeppelin, 2002; Holmes and York, 2003; Trites and Donnelly, 2003; Winship and Trites, 2003).

Shifting from a high-energy diet (dominated by fatty fishes) to one dominated by low-energy fish (such as walleye pollock) may have significantly affected young sea lions by increasing the amount of food they would have had to consume to meet their daily energy needs (Alverson, 1992; Rosen and Trites, 2000; Trites, 2003). Bioenergetic models indicate that a yearling sea lion requires about twice the relative energy compared with an adult (i.e., 14% of its body mass versus 7% for an adult on average mixed diets – Winship *et al.*, 2002). Recent feeding experiments with captive sea lions suggest that it may be physically impossible for young sea lions to meet their daily energy requirements if their diet is dominated by low-energy prey (Rosen and Trites, 2004). Adults who have finished growing and have lower metabolic needs than young animals are not similarly constrained and have the stomach capacity to consume sufficient quantities of prey to meet their daily needs. Thus adults could continue to nurse their pups for a second or third year, and forgo giving birth until their pups achieve nutritional independence.

Overall abundance of Steller sea lion prey may have changed in the mid-1970s due to a change in ocean productivity, fisheries removals, and/or other ecosystem interactions. One possible means is schematized in Fig. 2. Decreased prey availability could potentially have increased foraging times and thus the risk of predation. Similarly, abundant prey located farther from shore could also have increased foraging times and exposure to killer whales, which are principal predators of sea lions. Survival and reproduction would have ultimately been compromised if sea lions were unable to efficiently acquire sufficient prey to maintain normal growth and body condition (Fig. 2). A dietary shift to low-energy prey could have further exacerbated any effects of decreased prey availability by increasing food requirements.

Differences in diets and relative prey abundance appear to be associated with pronounced changes in Steller sea lion numbers. Ocean climate could account for these geographic and temporal patterns (Fig. 2). However, the spatial and temporal patterns associated with the available ocean climate data have not been previously explored in the context of Steller sea lion dynamics and their food webs. The following section therefore begins evaluating the ocean climate hypothesis by considering the changes that occurred in the oceanic habitats of sea lions in Alaska.

PHYSICAL OCEANOGRAPHIC DATA

Physical oceanographic data for the North Pacific are generally sparse in time and space – especially in the Gulf of Alaska. Broad-scale changes over recent decades have been identified in sea surface temperatures (SST), which constitute the most complete set of oceanographic data available. The Gulf of Alaska was predominantly cool in the early 1970s and warmed in the late 1970s and throughout the 1980s. There is substantial evidence that this was part of a basin-wide regime shift of the North Pacific that commenced during the winter of 1976–77 (e.g., Ebbesmeyer *et al.*, 1991; Miller *et al.*, 1994; Hare and Mantua, 2000; de Young *et al.*, 2004). These physical changes have been linked to a number of responses within the ecosystem of the Gulf (e.g., Mantua *et al.*, 1997; Benson and Trites, 2002; Mantua, 2004; Miller *et al.*, 2004). For some variables, especially biological ones, the mid-1970s transition was not a sharp change and the duration of the stable time periods before and after the shift may have ranged from 6 yr to more than 20 yr.

The basic issue of identifying regime shifts via statistical techniques is unsettled (Steele, 2004). The method of composite statistical analysis used by Ebbesmeyer *et al.* (1991) and later by Hare and Mantua (2000) to detect regime shifts is questionable based on the findings of Rudnick and Davis (2003) that this composite method will find pseudo regime shifts about 50% of the time when used on short time series arising from Gaussian red noise with stationary statistics. However, identifying whether the shift was driven stochastically or was a consequence of ocean-atmosphere feedbacks is not important here – only the observation that the physical ocean climate and biological populations did change at about the same time.

Besides the issue of detecting significant regime changes from short time series, a greater problem lies in identifying the mechanisms by which the large-scale physical environmental changes drive associated biological regime shifts, which are highly uncertain (Francis and Hare, 1994; Miller and Schneider, 2000; Miller *et al.*, 2004; Wooster and Zhang, 2004). Some detailed mechanisms have been proposed (e.g., Francis and Hare, 1994; Gargett, 1997; Hunt *et al.*, 2002; Wilderbuer *et al.*, 2002), but none have yet been truly tested and validated with field studies. The large-scale surface-derived indices such as the Pacific Decadal Oscillation (PDO – the first principal component of SST north of 20°N in the North Pacific; Mantua *et al.*, 1997) provide little information on how large-scale climate affects local populations. The regional dynamics of climate regimes and the transitions between them need to be understood before ecologically relevant, mechanistic-based indicators of climate state can be developed.

Towards this goal, Bograd *et al.* (2006) uncovered regional and depth-dependent differences in the timing and amplitude of important ocean climate events in the eastern Subarctic Pacific that could have caused local differences in ecosystem response. Their 'common trend' analysis of SST observations, which yields results similar to principal component (PC) analysis, but with the means included, revealed regional differences in the Gulf of Alaska. The structure of their first mode had a pattern that increased from west to east and showed a warming that commenced in the early 1970s and accelerated after the 1976–77 climate shift. The pattern of their second mode accentuated the pattern seen in the first mode, with a strong warming after 1972 – while their third mode had a strong warming in the eastern Gulf of Alaska during the 1957–58 El Niño and after the 1976–77 shift.

Overall, the statistical patterns in SST reflect important large-scale climate impacts in the Gulf of Alaska associated both with El Niño events and the 1976 regime shift. Moreover, the patterns were of sufficient magnitude and duration to potentially foster changes in lower trophic level productivity and structure. But there was also significant spatial heterogeneity in long-term SST patterns across the region. A 'cluster analysis' of SST time series (Bograd *et al.*, 2006) reveals five distinct regions, with common variability within the eastern Gulf of Alaska, the western Gulf of Alaska, as well as the transitional zone to the south. The leading 'common trend' pattern also revealed this robust east–west asymmetry.

The ocean temperature data show temporal and spatial patterns that are visually correlated with some of the observed differences in sea lion numbers and diets shown in Figs 1 and 3. Subsurface observations of temperature, which tend to be in phase with SST in the Gulf of Alaska, can help to describe aspects of the vertical structure of physical oceanographic changes (Bograd *et al.*, 2006). Changes in the seasonality (phase and amplitude of the seasonal cycle) of important environmental processes may have a large ecosystem impact by leading to mismatches in biophysical coupling (Bograd *et al.*, 2002). Unfortunately, the available temperature data are on a much coarser spatial scale than the fine scales over which sea lions forage, making it difficult to draw firmer conclusions in the context of the Steller sea lion decline.

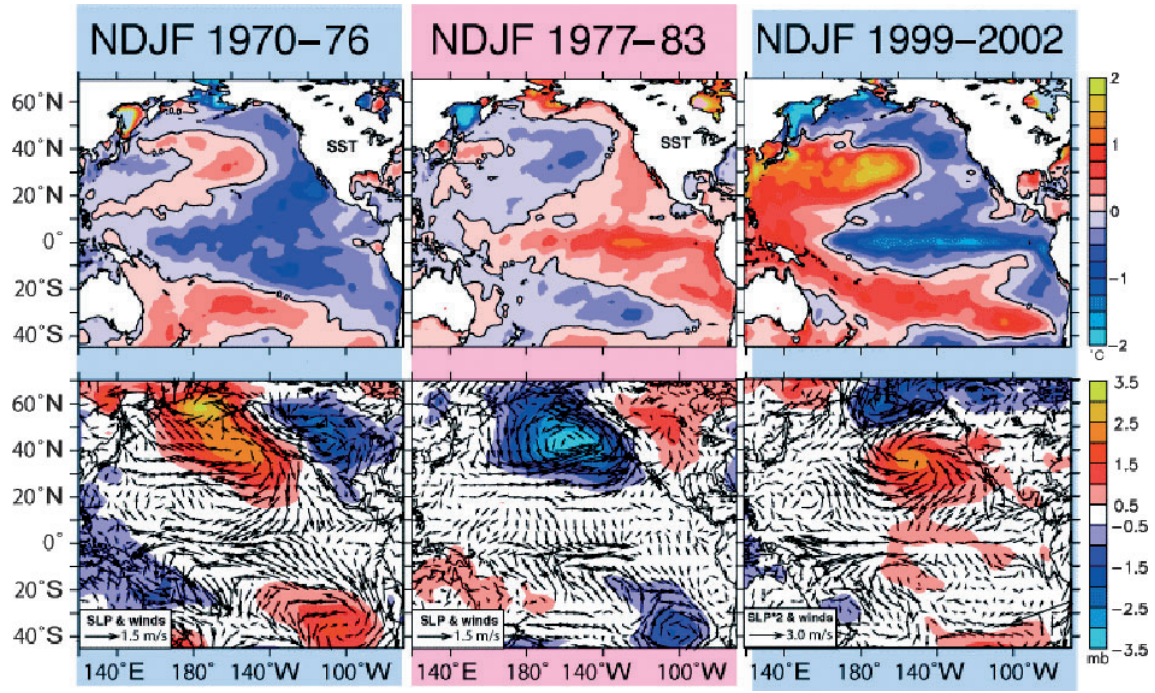
Non-linear statistical analysis provides a complementary view to these linear analyses. A neural-net-based PC analysis was applied to 22 physical indices representing both large-scale and local environmental processes (Marzban *et al.*, 2005). These data contain time series for such large-scale climate processes as the PDO, an Aleutian Low atmospheric pressure index, indices for tropical signatures of ENSO (which can remotely affect the Gulf of Alaska through oceanic and atmospheric teleconnections), and the Arctic Oscillation atmospheric pressure index. They also contain local measures for such things as alongshore (upwelling) winds, coastal SSTs, and Alaska and British Columbia annual river discharge. The results of the non-linear analysis exhibit clear indications of a regime shift around 1976–77, when sea lions began to decline. Sharp changes in the non-linear index in 1989 and 1999 also correspond with inflection points in sea lion numbers in the western population. The time series that most strongly influence the non-linear index include the PDO index, the Aleutian Low index, and coastal SST data. These statistical analyses of the physical indices reiterate the importance of decadal variability in the Gulf of Alaska, especially the importance of the 1976–77 climate shift.

Changes observed across the unique mid-1970s temporal boundary are shown in Fig. 5 for winter SST, sea-level pressure and surface wind anomalies before and after 1976–77 (Peterson and Schwing, 2003). The timing of this major regime shift corresponds to the apparent start of the sea lion decline. Comparing ocean climate conditions across the 1999 temporal boundary also shows similarities between the latest period of sea lion stability (and possibly recovery) and the earlier cool regime (i.e., before 1977). This is noteworthy given some of the early indications that positive changes in sea lion diets and numbers in the Gulf of Alaska may have begun with the start of the 1999 regime shift. However, the 1999 regime shift may not have been a reversal to earlier conditions. Significant differences between regimes (i.e., 1970–76 and 1999–2002 shown in Fig. 5) are evident, such as a strong, displaced Aleutian Low with a strengthened North Pacific High. This suggests that more than two stable climate states may exist, and adds support to the arguments of Bond *et al.* (2003) that a second SST PC has become more important than the PDO in recent years.

The Aleutian Low pressure system affects several oceanic forcing functions, including Ekman pumping, coastal upwelling, surface heat fluxes, turbulent mixing, and surface freshwater fluxes. For example, the mean Ekman pumping in the Gulf weakened appreciably after the climate shift of the mid-1970s in the north-eastern basin, but strengthened in the south-western basin (Capotondi *et al.*, 2006). Anomalous atmospheric forcings may be responsible for driving significant changes in the circulation and density fields of the Alaskan Stream and the Alaska Current.

Streamflow variations along the coastal Gulf of Alaska are linked to density-driven changes in the Alaska Coastal Current (ACC) (Royer, 1981). Coastal discharge into the Gulf of Alaska was calculated based on Royer's (1981) model using National Weather Service temperature and precipitation data since 1980. Royer also estimated discharge using precipitation from the National Centers for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) re-analysis (Kalnay *et al.*, 1996), which in spite of well-known biases in the mean (Roads *et al.*, 2002) substantiates the variability on interannual timescales. These data show that the rate of freshwater discharge with glacial ablation into the ACC increased by about 70% from the early 1970s to

Figure 5. Sea surface temperature anomalies (top panels) and sea level pressure anomalies and surface wind anomalies (bottom panels) for winter periods before and after the 1976–77 regime shift, and for the most recent period. From Peterson and Schwing (2003).



the late 1980s. This suggests that the strength of the coastal current increased significantly through the region designated as critical habitat for Steller sea lions in the North-east Pacific. However, the roles of density stratification and the flow of the ACC in the biological productivity of this coastal system are unclear (Stabeno *et al.*, 2004; S. Strom, pers. comm., Western Washington University, Anacotes, WA, USA).

Royer *et al.* (2001) hypothesized that positive feedback mechanisms could occur in the Gulf of Alaska circulation. Increased fresh water would increase the alongshore transport that brings warmer water northward, which increases cyclogenesis over the Gulf of Alaska and glacial melting. This in turn would further increase freshwater melting. This hypothesis is consistent with the observation that increases in freshwater and coastal stratification have been occurring concurrently with increases in water temperatures since 1970 (Royer *et al.*, 2003).

East–west patterns of sea lion population dynamics may be associated with the east–west asymmetries in key physical oceanographic observations, such as SST and thermocline depth. Atmospherically controlled oceanic forcing functions, such as Ekman pumping patterns and streamflow discharge into the Alaska Current, also indicate that basin-scale ocean changes may have occurred after the 1976–77 climate shift when sea lion populations decreased significantly in the western Gulf of Alaska. These results imply a linkage between the distinct observed climate changes and sea lion populations, but the specific physical forcing mechanisms affecting the animals are unclear. Limited observations in space and time prevent a more detailed historical assessment of the small-scale regional effects of climate as well as of the broad-scale influences of unobserved oceanographic variables such as velocity, lateral mixing and vertical mixing. However, numerical simulations of oceanic processes can be used to gain further insight into how these physical changes may have influenced sea lions and other species.

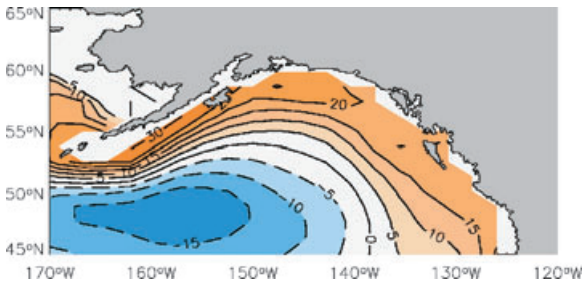
OCEAN MODELING

Due to the sparseness of oceanographic observations in space and time (especially before the 1976–77 climate shift), a number of modeling studies were designed to elucidate the physical processes that may have led to changes in the sea lions' food web. These studies included hindcasts forced by observed atmospheric variations to determine the magnitude of phasing of oceanic events in the water column. They also involved process studies in which the effects of eddies, such as eddy interactions with topography and mean conditions, were explored. Coarse resolution models allow a broad-scale perspective of the physical oceanographic changes induced by climate forcing, while eddy-permitting models can suggest roles for eddies in altering the mean background states of the ocean and driving fluxes of nutrients across the shelf-slope system (Hermann *et al.*, 2002).

A coarse-resolution hindcast of the Gulf of Alaska was analyzed by Capotondi *et al.* (2006) to determine how pycnocline depth may have changed after 1976–77. The changes in pycnocline depth were diagnosed from the output of an NCAR ocean model driven by NCEP/NCAR re-analysis winds over the period 1958–97. The analysis showed a shoaling of the pycnocline in the central part of the Gulf of Alaska after the mid-1970s, consistent with the findings of Freeland *et al.* (1997), and a deepening in a broad band that follows the coast (Fig. 6). The deepening was particularly pronounced in the northern and western part of the Gulf of Alaska, to the south-west of Kodiak Island, where the pycnocline deepened by 25–30 m after 1976. The surface forcing responsible for these changes was the local Ekman pumping, which can account for a large fraction of the pycnocline depth changes as a local response (Cummins and Lagerloef, 2002; Capotondi *et al.*, 2006).

Pycnocline depth changes are relevant for biological productivity in the North-east Pacific. First, changes in pycnocline depth can indicate changes in upwelling, a process responsible for transport of nutrients from the deep ocean to the upper ocean. Secondly, the North-east Pacific is characterized by a well-mixed fresh surface layer bounded at the bottom by a halocline. The halocline tends to coincide with the pycnocline because water density is mainly controlled by salinity in the Gulf of Alaska. Thus, the depth of the top of the maximum seasonal pycnocline

Figure 6. Modeled pycnocline depth changes (CI = 5 m) for the period 1977–97 relative to the period 1964–75, based on the depth of the sigma = 26.4 isopycnal of the model hindcast. Blue indicates shoaling. From Capotondi *et al.* (2006).



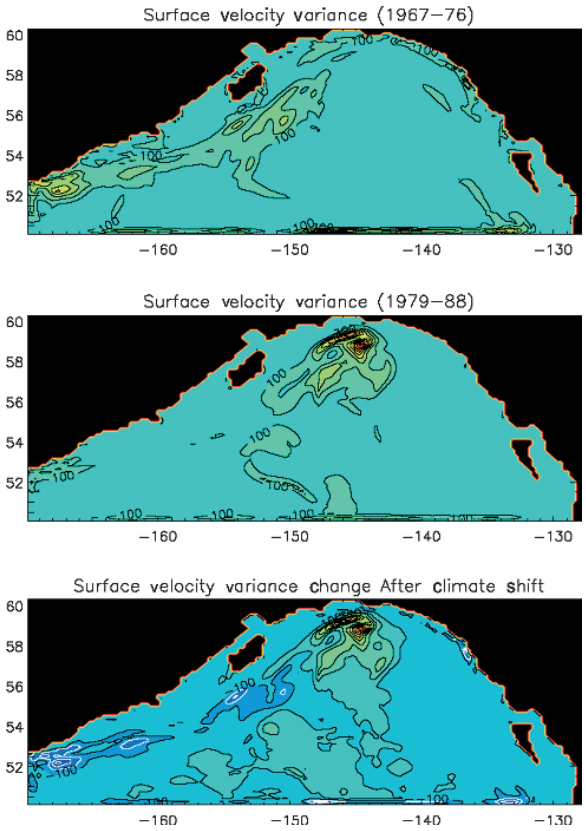
is a good approximation for winter mixed layer depth in this area.

The changes noted in pycnocline depth between 1964–75 and 1976–97 (Fig. 6) were associated with a strengthening of the Alaskan Stream in the western Gulf of Alaska. Such a result is intuitively expected following an intensification of the Aleutian Low, which is the main driver of the mean Gulf of Alaska ocean circulation. However, Lagerloef's (1995) observational analysis of dynamic height suggests that the Alaskan Stream weakened rather than strengthened after the 1976–77 regime shift. Such a conclusion might reflect the sparseness of data used in the objective analysis over these time intervals and motivates further analysis of observations and model results.

Changes in the distribution of mesoscale eddies in the Gulf of Alaska after the 1976–77 regime shift were studied using monthly mean wind stresses (taken from the NCEP/NCAR re-analysis) to force a regional eddy-permitting ocean model, with a 16-km grid and 20 layers, over the 1950–99 time period (Miller *et al.*, 2006). The model suggests that the Alaskan Stream was strengthened considerably after the shift in the north-west part of the Gulf of Alaska, and weakened in the south-western domain. The increase in the strength of the Alaskan Stream is consistent with coarse resolution model results of Capotondi *et al.* (2006). Such changes in the mean strength of the Alaskan Stream over decadal timescales would have altered the stability properties of the flow field, which consequently changed the mesoscale eddy variance distribution.

Figure 7 shows the modeled surface current velocity variance for two 10-yr epochs, along with the difference in variance, before and after the 1976–77 climate shift. Before the shift, mesoscale eddy variance was highest south-east of Kodiak Island and along the Alaskan Stream to the south-west of Kodiak. After the shift, model mesoscale eddy variance increased dramatically in the north-western Gulf of Alaska, and decreased to the south and west of Kodiak Island. The consequences of this modeled change included altered cross-shelf/slope mixing of water masses of the open-ocean and shelf regions. As mesoscale eddies provide a mechanism for transporting nutrient-rich open-ocean waters to the productive near-shore shelf region (Okkonen *et al.*, 2003; S. Strom, pers. comm.), the fundamental flow of energy through the food web may have been altered due to this physical oceanographic change. This mechanism may have altered the relative abundances of key prey species available to Steller sea lions prior to and following the 1977 regime shift.

Figure 7. Modeled variance (CI = 100 cm^2 s^{-2}) of the anomalous monthly mean surface currents for the 10-yr epochs 1967–76 (top) and 1979–88 (middle), and the difference between the two epochs (bottom). Anomalies are defined with respect to the monthly mean seasonal cycle of the respective 10-yr epoch. From Miller *et al.* (2006).



In contrast to the western Gulf of Alaska, the model mean flows of the Alaska Current in the eastern Gulf were nearly unchanged after the shift (Miller *et al.*, 2006). Likewise, the model surface velocity variance was only weakly altered, being reduced slightly compared with pre-shift conditions. Hence, an east–west asymmetry occurred in the Gulf of Alaska circulation response to the strengthened Aleutian Low. This is consistent with eastern populations of Steller sea lions in south-east Alaska continuing their steady increase across the temporal boundary of the 1976–77 climate shift.

While the physical ocean models provide a sense of how the basic ocean environment might have changed after the shift, an ecosystem model is useful to attempt to understand how the physical changes could have altered the food web. Towards this end, M.A. Alexander, A. Capotondi, A.J. Miller and F. Chai (unpubl. data) analyzed the results of the coarse-resolution

physical-ecosystem ocean model hindcast of Chai *et al.* (2003) to examine whether changes in the physical environment associated with the 1976–77 transition could have influenced the lower trophic levels of the food web in the North-east Pacific. The physical component of the analysis simulated ocean temperatures, salinity, horizontal currents and upwelling, while the biological component consisted of 10 compartments with small and large classes of phytoplankton and zooplankton, two forms of dissolved inorganic nitrogen, detrital nitrogen, silicate, detrital silicate, and CO_2. Processes simulated by the model included: primary productivity through new and regenerated production, grazing, predation, excretion, and sinking of organic matter (Chai *et al.*, 2002, 2003). The model extended over most of the Pacific and was forced with observed atmospheric fields over the period 1960–1999.

The model simulation indicated that the biomass of large zooplankton would have been substantially reduced during May in the Gulf of Alaska and eastern Bering Sea in 1977–98 relative to 1960–76. A similar decrease was projected in April for the large phytoplankton and small zooplankton classes, representing about a 20% decrease in plankton during the spring bloom. As production during the spring bloom may establish the availability levels of prey year-round, this predicted decrease in plankton biomass (1977–98) could have reduced the food available to higher trophic levels and ultimately negatively affected Steller sea lions. The difference in the plankton concentration between the two epochs, however, is relatively unchanged in seasons other than spring, and is negligible for the small phytoplankton class throughout the year.

This coarse resolution model, with its limited number of biological variables, may be incapable of indicating a change in the flow of energy up the food web, such as alterations in small pelagic fish populations, which may be more important than a change in total productivity. These model findings of decreased phytoplankton counter those of Brodeur and Ware (1992) who concluded that zooplankton increased in the Gulf of Alaska after the 1976 transition. But the observations they used were only collected during summer and were widely spaced in time and location. Likewise, salmon stocks increased in the Gulf after the climate shift (Mantua *et al.*, 1997). While no direct link was found between any single modeled physical process (e.g., upwelling) and the modeled biological changes, the increased model mixed layer depth in April along the southern coast of Alaska could have reduced the light available for photosynthesis in that region during later winter seasons of 1976–98 relative to 1960–76.

Basin-scale models designed to study oceanic processes are not of sufficient resolution to investigate coastal ecosystem dynamics. Instead, limited domain models of ocean circulation with higher resolution allow focused, regional studies of critical processes and circulation. Such an approach allows for proper representation of the complex flow-topography interactions and their influence on exchanges between adjacent water masses and through the Aleutian Island passes.

A pan-Arctic coupled sea ice–ocean model provides insight into the circulation and exchanges between the sub-arctic and arctic basins (Maslowski and Walczowski, 2002; Maslowski and Lipscomb, 2003; Maslowski *et al.*, 2004), particularly on the exchange between the North Pacific Ocean and the Bering Sea through the passes of the Aleutians, which can influence biological productivity along the Aleutian Island chain. This eddy-permitting model extended over much of the Northern Hemisphere and was integrated with realistic daily-averaged 1979–93 re-analyzed data and 1994–2001 operational products from the European Centre of Medium-range Weather Forecasts to investigate interannual-to-interdecadal variations in transport through these straits.

One of the important features of ocean circulation in the Gulf is the Alaskan Stream, and its interannual variability and effects on the mass and property transport through the Aleutian Island passes. A comparison of transport estimates of the Alaskan Stream (Thompson, 1972; Favorite, 1974; Reed, 1984; Warren and Owens, 1988; Roden, 1995; Reed and Stabeno, 1999; Onishi, 2001) with those through the eastern and central passes (Schumacher *et al.*, 1982; Reed, 1990; Reed and Stabeno, 1997; Stabeno *et al.*, 1999, 2006) suggests that even small variations in the magnitude and position of the Alaskan Stream could have significant consequences on the dynamics and hydrographic conditions within and to the north of the passes. Analyses of model output suggest that the dominant mechanism of interannual variability in volume transport is related to anticyclonic mesoscale eddies (100–250 km diameter) propagating westward along the Alaskan Stream with mean speed of a few kilometers per day. Similar eddies have been observed from satellites (Okkonen, 1992, 1996; Crawford *et al.*, 2000) and in field observations (Reed *et al.*, 1980; Musgrave *et al.*, 1992; Ladd *et al.*, 2005).

Model-simulated eddies along the Alaskan Stream have significant influence on both the circulation and water mass properties across the eastern and central

Aleutian Island passes. S.R. Okkonen and W. Maslowski (unpubl. data) examined depth-averaged (0–100 m) velocity snapshots and salinity differences across Amukta Pass for eddy and no-eddy conditions in 1984. Amukta Pass is the major pass that delineates the eastern and central Aleutian Island clusters of sea lion rookeries (Fig. 3). In March, no eddy is present in the Alaskan Stream, and the dominant flow in the region to the south of Amukta Pass is westward and parallel to the pass. Two months later - when a mesoscale eddy enters the region – the flow of the Alaskan Stream is significantly modified down to over 1000 m, with a strong northward velocity component into Amukta Pass and a strong southward component some 200 km to the east. This pattern has implications both on the transport of Alaskan Stream and on the flow through, and conditions in, Amukta Pass (Maslowski *et al.*, 2004).

Eddy-related upwelling of salty water along the southern slope affects the water column down to about 1000 m. A salinity increase of 0.1 psu extends all the way to the surface within the Amukta Pass region when the eddy is present in the Okkonen and Maslowski simulation. Given the high correlation between salinity and nutrient content at depths, the increased salinity in the upper ocean over the pass can represent nutrient input for enhanced and/or prolonged primary productivity (Mordy *et al.*, 2006). As modeled eddies along the Alaskan Stream occur throughout a year, their contribution to high surface nutrient concentrations within the Aleutian Island passes could be especially significant during otherwise low primary productivity seasons. This effect would be most important during years with mesoscale eddies frequently propagating along the Alaskan Stream. An overall net increase of salinity in the upper water column is experienced within the region adjacent to Amukta Pass after the eddy moves farther to the west.

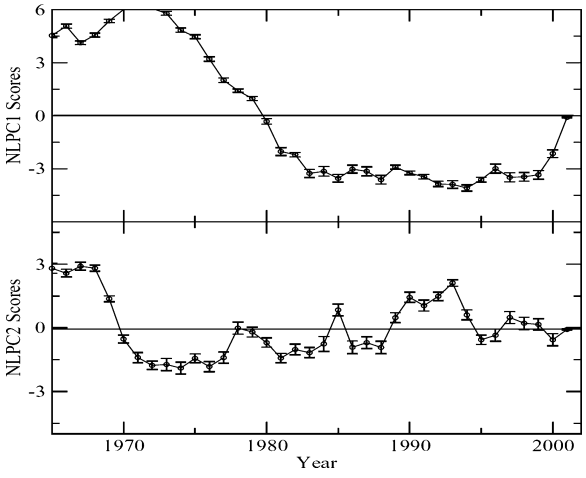
In summary, there is strong evidence that climate-forced changes occurred in both the strength of the mean currents of the Alaskan Stream and the spatial distribution of the mesoscale eddy field of the Alaskan Stream after the mid-1970s climate regime shift. These changes were strongest in the western Gulf of Alaska, where sea lion populations contemporaneously experienced precipitous declines. Ocean models also demonstrate that mesoscale eddies provide an important mechanism for mixing nutrient-rich waters with nutrient-depleted waters along the Alaskan Stream and across the Aleutian Island passes. Hence, the flow of energy through the ecosystem in the Gulf of Alaska may have been fundamentally altered by changes in these basic physical oceanographic processes. However, the specific mechanisms that link eddies, mixing, advection and wind forcing to the basin-scale and regional structures of the biological environment – not only related to primary productivity but also to higher trophic levels including Steller sea lions – are still unclear. Yet, as described in the following section, there are indications that the broad suite of concurrent food web changes that occurred at basin and regional scales were influenced by the effects of physical oceanography.

ECOSYSTEM AND BIOGEOGRAPHIC LINKS

The oceanographic studies described thus far provide evidence of medium and long-term changes in the physical dynamics in the northern Gulf of Alaska and Aleutian Islands. It is therefore reasonable to expect these changes to be reflected in observations of the broad-scale ecosystem and the biogeography of the regional fauna. Several studies have addressed these issues.

Following the earlier work of Hare and Mantua (2000), Marzban *et al.* (2005) applied a non-linear PC analysis to a multivariate data set they created with 45 fishery and survey records from the Bering Sea and Gulf of Alaska for the period 1965–2001. These data contained time series for such variables as annual salmon landings for five species and three regions in Alaska, rockfish and herring recruitment indices, herring biomass, and zooplankton biomass estimates for subregions of the Gulf of Alaska and Bering Sea. The results (Fig. 8) were similar to those found by

Figure 8. Non-linear principal component analysis results from a multivariate data set of 45 biotic indices (fishery and survey records) from the Bering Sea and Gulf of Alaska from 1965 to 2001.



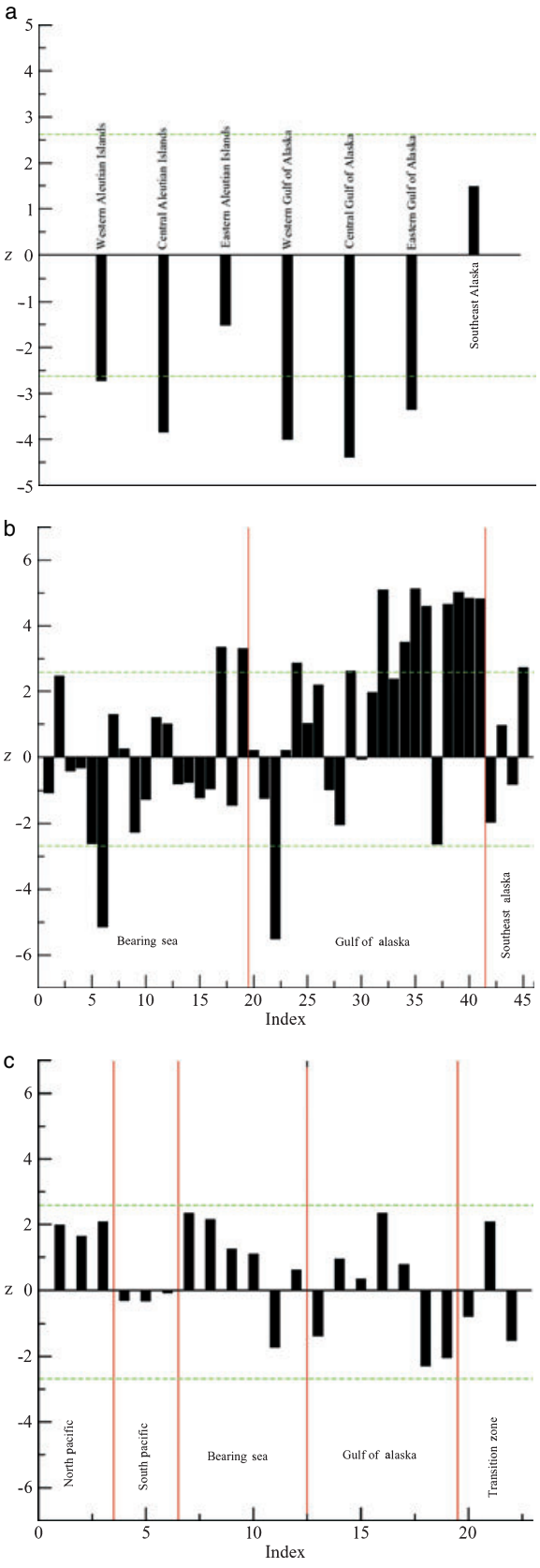


Figure 9. Non-parametric Kendall's tau statistic to assess the statistical significance of trends in (a) Steller sea lion data, (b) Pacific fishery data and (c) Pacific climate data. While a 'trend' often means a linear trend, Kendall's tau assesses the trend non-linearly (though monotonically). The Z-statistic assesses the statistical significance of that trend such that if $Z \geqslant 2.575$ then the hypothesis that the true tau is zero can be rejected with 99% confidence.

Hare and Mantua (2000), whereby the leading PC indicated a pattern with all positive scores from 1965 to 1979, and all negative scores from 1980 to 2000. However, the index of the abiotic series had stronger interannual variations than the PC of the fishery/survey (biotic) data, which highlights decadal-scale changes. The time series that most strongly influenced the first non-linear principal component (NLPC1) included Alaska salmon landings and many rockfish recruitment records, while records for shrimp catches in the Gulf of Alaska acted negatively on NLPC1. The explained variance in NLPC1 from this analysis was 39%, while PC1 from a linear analysis accounted for only 27% of the variance in these data.

An intriguing aspect of the NLPC1 is how it appears to emulate the pattern of decline of Steller sea lions (compare Figs 1 and 8). A closer inspection of the PC suggest that the NLPC1 preceded the overall decline of the western stock of sea lions by about 4 yr, which is roughly the age of sexual maturity of sea lions and may correspond with the start of the decline in the eastern Aleutians.

Marzban *et al.* (2005) also computed the non-parametric Kendall's tau statistic to assess the statistical significance of trends in the climate, fishery, and sea lion data used in their analysis. While a 'trend' often means a linear trend, Kendall's tau assesses trend non-linearly (though monotonically). The adult sea lion count data showed statistically significant negative trends in five of the seven regions (Fig. 9a). In contrast, there were many positive trends in the Alaska fishery and survey data for the period 1965–2001, with a few negative trends (Fig. 9b). Most of the very strong trends were in the Gulf of Alaska records, including many of the salmon catch records. The two series with large negative trends were for the indices that tracked eastern Bering Sea turbot recruitment and Gulf of Alaska shrimp catch per unit effort. Kendall's tau was also computed for climate/environmental data, but did not reveal any statistically significant trends for 1965–2001 period (Fig. 9c).

Research cruises to the passes of the eastern and central Aleutian Islands during May/June of 2001 and

2002 revealed a number of intriguing biogeographic features of the region that correspond to the population and dietary divisions of sea lions shown in Fig. 3. Sharp fronts in surface salinity were found at Unimak and Samalga Passes (Fig. 10) that coincided with demarcation points for sea lion diets and population dynamics (Fig. 4). Samalga Pass appears to be a boundary between shelf-derived waters to the east and open-ocean-derived waters to the west, with the ACC influencing the waters east of the pass, and the Alaskan Stream influencing the waters farther west (Ladd *et al.*, 2006). The difference in source waters in the two regions influences the distributions of nutrients (Mordy *et al.*, 2006) and biota (Coyle, 2006; Jahncke *et al.*, 2006) around the different passes. In addition, the different sources may imply that climate variability influences the eastern and the central passes in different ways. For example, increasing freshwater discharge into the ACC (Royer *et al.*, 2001) would influence the eastern passes while changes in eddy variability would influence the central passes.

Changes in the abundance and composition of zooplankton species are associated with seasonal changes in water mass and other physical properties along the Aleutian Island chain (Coyle, 2006). Declines noted in the abundance of *Neocalanus plumchrus* and *N. flemingeri* at Akutan and Unimak in June reflected them leaving the surface waters and migrating down to depths over 300 m – while elevated abundances of *Calanus marshallae* and *Acartia* spp. at Umnak, Akutan, and Unimak Passes were due to their preference for warmer neretic conditions. Abundance of two species of euphausiid along the islands showed a preference by *Thysanoessa inermis* for neretic water of Akutan, Unimak, and Samalga Passes, and a preference by *Euphausia pacifica* for the open ocean conditions of the passes west of Samalga Pass.

In addition to zooplankton and fish, the western extent of the ACC at Samalga Pass also operates as a biogeographical 'boundary' for seabirds (Jahncke *et al.*, 2006). At-sea surveys of seabirds during the cruises in May/June 2001 and 2002 showed that the avifauna east of Samalga Pass was dominated by migrant short-tailed shearwaters (*Puffinus tenuirostris*), which were foraging on neritic species of euphausiids, and piscivorous tufted puffins (Jahncke *et al.*, 2006). West of Samalga Pass, the marine avifauna was dominated by small auklets (*Aethia spp.*) and northern fulmars (*Fulmarus glacialis*), species that were foraging mostly on large species of oceanic copepods (Fig. 11). Although there is no break point in the distribution of breeding seabirds at Samalga Pass (Byrd *et al.*, 2006), there are large-scale patterns that suggest that the central and western Aleutian Islands support the vast majority of breeding seabirds dependent upon oceanic zooplankton, whereas the eastern Aleutian Islands support the majority of piscivorous seabirds. For example, about 68% of the 1.6 million piscivorous seabirds nesting in the Aleutian Islands occur to the east of Samalga Pass, whereas only 7.5% of the 7.9 million planktivorous seabirds nesting in the Aleutians are found to the east of Samalga Pass (US Fish and Wildlife Service, 2000). These data support the premise that the eastern Aleutians provide a very different habitat than regions of the archipelago west of Samalga Pass. At smaller spatial scales, the passes of the Aleutian Islands are the focal point of much seabird foraging activity.

For breeding seabirds, Byrd *et al.* (2006) found no evidence 'that average reproductive rates for any species groups were consistently different among island groups within the Aleutians.' The only 'species showing widespread declines across the Aleutians were three nearshore-feeding piscivores.' In contrast, murres, tufted puffins, and kittiwakes increased at Buldir Island, far west of the region investigated by Jahncke *et al.* (2006). In some other areas, they declined.

Figure 10. Underway sea surface salinity (psu) during May/June 2001 cruise. (a) Salinity plotted against latitude. (b) Salinity represented by colored line on map. Average salinity in the regions east of Unimak Pass, between Unimak and Samalga Passes, and between Samalga Pass and Amukta Pass are noted. From Ladd *et al.* (2006).

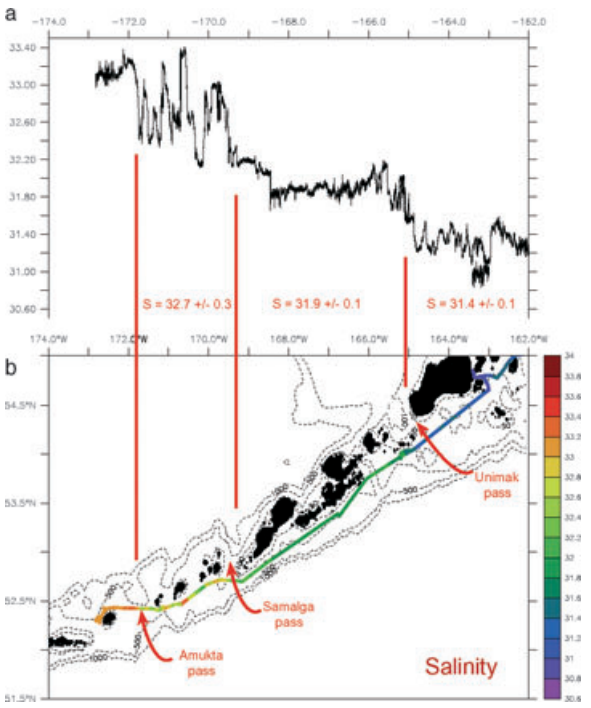
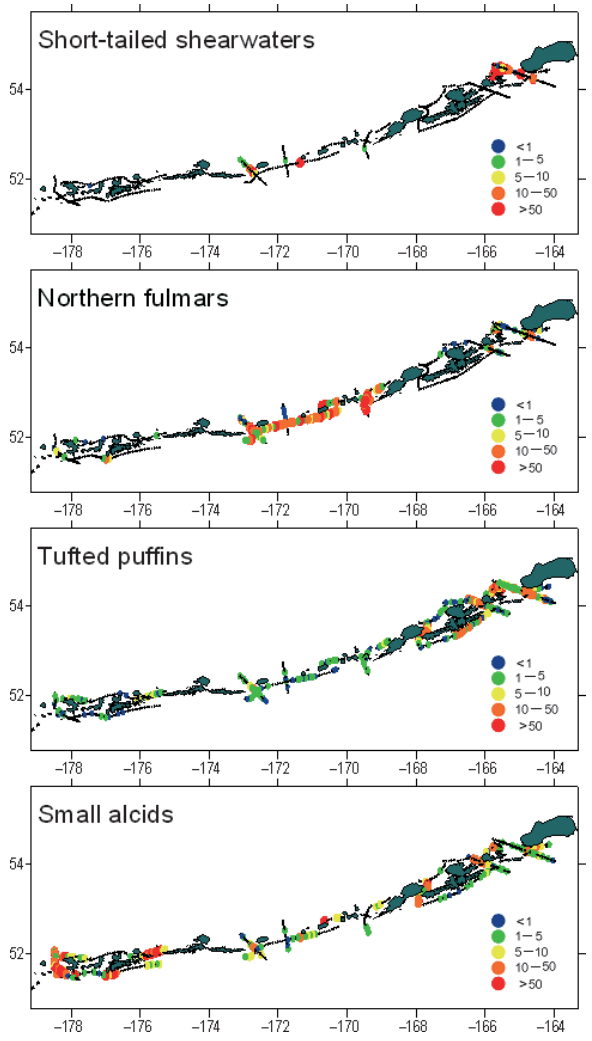


Figure 11. Seabird abundances along the Aleutian Islands from data collected in 2001 and 2002. From Jahncke *et al.* (2006).



According to Springer *et al.* (1996), birds nesting at Buldir have a greater dependence on the oceanic environment than at other islands, and it may be that the inshore environments of the Aleutians are suffering while the offshore communities remain relatively healthy. But no information exists to test this hypothesis.

Changes in the benthic and pelagic fish communities within the Gulf of Alaska and Aleutian Islands in response to the regime shift of 1976 were dramatic. Population increases occurred in flatfish (Wilderbuer *et al.*, 2002), gadids (Hollowed *et al.*, 2001) and salmonids (Hare and Francis, 1995) resulting from an increase in the frequency of strong year classes after 1976. At around the same time, decreases occurred in shrimp and crab stocks (Orensanz *et al.*, 1998). A small mesh trawl survey conducted near Kodiak Island between 1953 and 1997 provided a documentation of the 'community reorganization' in the Gulf of Alaska (Anderson and Piatt, 1999). The catch composition of the trawl catches in this survey prior to 1977 was dominated by forage species such as capelin and shrimp. Following the regime shift, the catches were primarily high-trophic-level groundfish.

Further up the food chain, concurrent changes were also noted in the few populations of marine mammals that have been counted since the 1960s and 1970s. At Tugidak Island, for example, the largest population of harbor seals in Alaska began an unexplained decline in the mid-1970s, falling to <20% of its peak abundance by the mid-1980s (Pitcher, 1990). Steller sea lions at the nearby rookery on Chowiet Island also fell rapidly through the 1980s (Trites and Larkin, 1996). Similarly the Pribilof Islands' population of northern fur seals that accounts for about 80% of the world population also declined unexpectedly from the late 1970s to mid-1980s (Trites and Larkin, 1989; Trites, 1992). All three populations of pinniped species appear to have declined at about the same time (DeMaster *et al.*, 2006), coincidental with the 1976–77 regime shift.

These broad-scale ecological changes across all trophic levels are generally coincident in time, and are widely believed to be driven by differences and changes in the oceanic environment. This is not to say that the other primary force affecting fish populations (i.e., fishing) is without impact. Fishing can, and does, affect community dynamics. The effect of fishing is added to natural sources of variability. Paleoecological studies have repeatedly demonstrated wide swings in abundance of fish species long before the development of large-scale fisheries (Soutar and Isaacs, 1969; Finney *et al.*, 2002). Generally, fishing impacts the adult portion of fish populations. An important link between climate and population size occurs at the larval and juvenile stages for many marine animals. Making the transition from egg (marine fishes) or smolt (salmon) to successful recruit requires oceanic and ecological conditions conducive to survival. Under the regime shift hypothesis, certain species are favored under one set of ocean conditions while other species flourish when conditions change.

Though the precise mechanisms regulating recruitment of species under different climate regimes are not known with certainty, it is likely that both zooplankton and water temperature play key roles. The Alaska-wide increase in salmon production coincides with the observed increase in summer zooplankton production and distribution around the northern

periphery of the Alaska Gyre (Brodeur and Ware, 1992; Francis and Hare, 1994). Hare *et al.* (1999) hypothesized that this resulted from increased advection of zooplankton-rich subarctic water into the coastal regions of the Alaska Gyre, which is favorable to young migrating salmon. At the same time that Alaska salmon populations flourished, those off of Washington and Oregon declined. Hare *et al.* (1999) hypothesized that this resulted from decreased zooplankton production because of increased stratification in the California Current, which is unfavorable to young migrating salmon. Gargett (1997) suggested that coastal water column stability changes, driven by climate forcing, could explain these inverse production regimes along the North American West Coast.

Another significant change that occurred following the regime shift was a change in the developmental timing of *N. plumchrus*, the dominant copepod in the Gulf of Alaska. Between the early 1970s and 1990s the spring bloom moved as much as 1 month earlier in the year (Mackas *et al.*, 1998). Such a change will impact marine fish populations by favoring those species with earlier hatch dates. The decline of crabs and shrimps appears to have been the result of both fishing and recruitment failure (Orensanz *et al.*, 1998). Mueter and Norcross (2000) examined the precise timing of the decline in crabs and shrimps and found that it followed, rather than preceded, the increase in groundfish. This result suggests that predation by groundfish, possibly on recruiting juveniles, could have been the mechanism behind the crab/shrimp decline.

The effects of broad-scale changes in ocean climate on Steller sea lion habitat appear to be moderated through a number of indirect mechanisms. For example, increased storm activity may have reduced the suitability of certain haulouts and rookeries, while bottom-up effects mediated through at least three trophic levels (i.e., phytoplankton, zooplankton, forage fish) have the potential to affect the distribution of Steller sea lion prey species. In light of the spatial distributions of different species in the food web, and the potential foraging distances of individual sea lions (Fig. 4), further range-wide studies encompassing areas of both decreased and increased habitat suitability will be required to fully elucidate the effects that changing climate can have on apex predators.

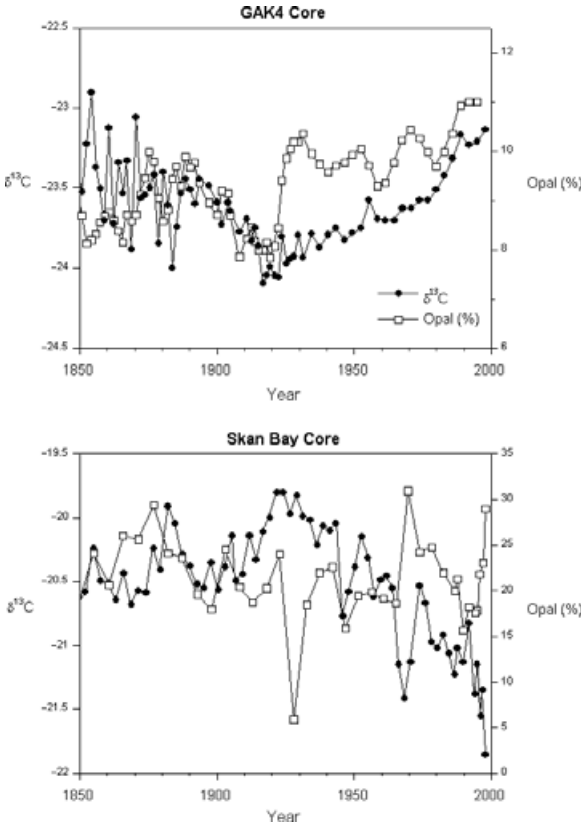
In summary, a suite of changes occurred across all trophic levels of the Gulf of Alaska and Aleutian Islands ecosystems that corresponded to the timing of the 1976–77 regime shift and the decline of Steller sea lions in the western Gulf of Alaska and Aleutian Islands. The detailed regional influences of these climate changes are difficult to pinpoint among the sparsely observed populations, but they appear to be modulated by the effects of biogeographic features such as the Samalga Pass transition from coastal influence to open-ocean conditions and the fine structure of island distributions. These transition points delineate distinct clusterings of prey species, which are in turn correlated with differential population sizes and trajectories of Steller sea lions. The results support the idea that a fundamental change in the ecosystem occurred after the mid-1970s, which may have cascaded up through the food web to influence the regional diets and health of sea lions. Other studies suggest that such changes were not unique to the 20th century.

PALEOECOLOGICAL PERSPECTIVE

Paleoecological studies provide a long-term perspective to changes seen in recent decades. Finney studied indicators of oceanic productivity in two sediment cores – one from the GAK-4 site in the central Gulf of Alaska shelf and one from the Bering Sea (Skan Bay). Increases in productivity are inferred from two proxies whereby an increase in opal content may represent diatom productivity, while an increase in the $\delta^{13}C$ of organic matter may imply increases in overall organic productivity. Results showed that considerable variability occurred in ocean productivity over the last 150 yr for each region (Fig. 12). In the Gulf of Alaska, both productivity proxies increased since the 1976–77 regime shift, while the signals were mixed in the Bering Sea, with a decrease in organic matter $\delta^{13}C$ and highly variable but no overall change in opal. The Bering Sea data imply significant changes in the phytoplankton community. Such changes in productivity could have affected the flow of energy up the food web and altered the relative abundances of favored species upon which Steller sea lions feed. This paleoecological record averages out seasonal changes, which may be an important effect in addition to total productivity. The regional differences in the paleoecological records may be important in explaining regional differences in numbers and diets of Steller sea lions.

Long-term changes in the North Pacific and southern Bering Sea ecosystems have also been the subject of intensive investigations using archaeological and anthropological data (Maschner, 2000; Savinetsky *et al.*, 2004). The archaeological data indicate that significant variations occurred in the distributions of key species over the last 5000 yr (Yesner, 1988). Correlations between changes in relative abundances of species such as Steller sea lions and regional

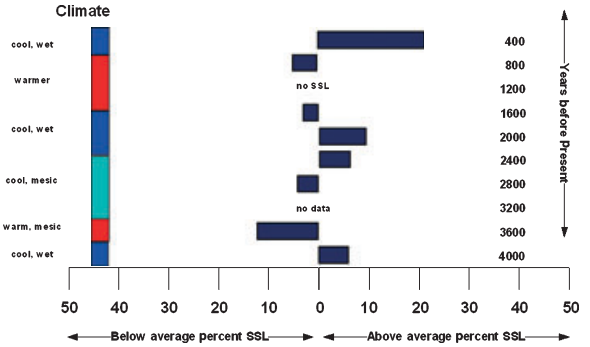
Figure 12. Paleoproductivity indicators over the last 150 yr derived from two cores in the Gulf of Alaska (GAK 4 site central gulf shelf) and Bering Sea (Skan Bay). Two productivity indicators are plotted for each core: opal, which represents diatom productivity (open squares) and the $\delta^{13}C$ of organic matter (closed circles), which represents all organic productivity. Increases in productivity would be indicated by an increase in either indicator. The dating of the cores is based on ^{137}Cs and ^{210}Pb.



climatic regimes are only suggestive at this time, with cooler periods having near average harvests of sea lions by Aleuts, and warmer periods having below average harvests (Fig. 13). Notably, the greatest abundance of Steller sea lion occurred during the Little Ice Age, which may be significant. The end of the Little Ice Age appears to have had an impact on Steller sea lion populations, as Collins *et al.* (1945) noted, 'Once abundant, this animal is now greatly reduced in numbers, and it has disappeared from many of its former haunts.'

While it is impossible to use archaeological data to determine absolute abundances of individual species, the thousands of bones from archaeological sites allow the reconstruction of relative abundances if the ancient Aleut harvested species in numbers relative to their actual abundance on the landscape. If true,

Figure 13. Long-term trends in the percentage of Steller sea lions harvested by Alaska Peninsula Aleut in relation to their total sea mammal harvest. This chart shows the percentage difference from the mean harvest over the last 4000 yr. Climate data-based pollen cores and other data of the Alaska Peninsula Project (Jordan and Maschner, 2000; Jordan and Krumhardt, 2003) and data provided by Finney.



changes in the proportions of phocid (true seals) and otariid (sea lion) bones, for example, can be used as indicators of changes in the proportions of these animals on the natural landscape. Centennial-scale changes in species abundance can thereby measure long-term and region-wide fluctuations in the marine environment.

Decadal-scale changes in the marine ecosystem spanning nearly 150 yr are identifiable using both ethnohistoric data and traditional ecological knowledge of local Aleut fishermen (e.g., Veniaminov, 1840; Black, 1981). Based on Russian and early American accounts of the region, there has been at least one period in the last few centuries with a collapse in the Steller sea lion population (Collins *et al.*, 1945). This occurred in the 1870s, coinciding with a warming period observed in the Sitka air temperatures, and lasted until at least 1910. By the late 1870s, sea lions were rare in many areas of the Bering Sea and North Pacific (Nelson, 1887). While in 1800, several hundred thousand sea lions inhabited St George Island (Elliot, 1881) and may have dominated the landscape at the expense of the fur seal (Choris, 1822), by 1880 so few were found that the total Aleut harvest did not meet basic needs in the Pribilof Islands (Nelson, 1887). This was also a problem in the western Aleutians where, at Attu, the local Aleut could not find any sea lions, which caused them to stop making kayaks altogether sometime before 1909. The lack of sea lion skins further caused all the Aleut to stop making their large, ocean-going transport boats (Jochelson, 1933). This limited their ability to move between islands and adapt to changing conditions, and curtailed their hunting and

fishing, which would have caused widespread subsistence problems (H. Maschner and K. Reedy-Maschner, unpubl. data). US Census officials remarked that the failure of the Steller sea lion throughout the region was so acute at this time that sea lion skins were being imported from southern California so that the Aleut hunters would be able to construct their kayaks (US Census, 1890). While some early references imply that this crash was caused by over hunting, those same sources report that the only people killing sea lions were Aleut trying to meet basic needs (Elliot, 1881). Aleut populations were so low at this time that this depression in the Steller sea lion population levels cannot, therefore, be correlated with any human-based harvesting of either the sea lions or their food sources.

Savinetsky *et al.* (2004) also examined bones recovered from archeological sites throughout the Bering Sea. They concluded that most species of marine mammals had maintained their geographic distributions during the past 2000 to 3000 yr, but that the abundance patterns had changed. In particular they noted that sea lions were once numerous on Nunivak Island (along south-western Alaska in the Bering Sea), but are now rare. They further concluded that the changes they noted in population sizes of marine mammals over the past thousands of years were primarily due to exogenous factors, i.e., temperature, precipitation, summer ice cover and changes in sea level (Savinetsky *et al.*, 2004). Some breeding areas have been lost in the past because of catastrophic environmental events such as earthquakes, volcanic eruptions, and tsunami (Black, 1981), which have been documented for Unalaska, the Sanak Islands, the Shumagin Islands, and the Attu area over the last 200 yr. However, changes in environmental conditions appear to be the primary explanation for the changes noted in the relative abundances of Steller sea lions and other species of marine mammals over the past thousands of years. Hunting was not a significant factor (Savinetsky *et al.*, 2004).

Traditional knowledge of local fishermen indicates that the North Pacific ecosystem underwent a series of disruptions over the last 100 yr that may or may not have been due to commercial fishing. For example, the North Pacific was heavily fished for cod between the 1880s and the mid-1930s, when the fishery collapsed. Cod appear to have been completely absent in many areas south of the Alaska Peninsula between 1945 and 1970 (Reedy-Maschner and Maschner, field notes, 2003), during which time shrimp and crab were dominant components of the ecosystem (Anderson and Piatt, 1999; Anderson, 2000). The extent to which these changes were mitigated by predator–prey interactions, fishing, or changes in ocean climate is not known. However, it is interesting to note that the Aleut term for codfish can be rendered into English as 'the fish that stops,' meaning it disappears periodically (Black, 1981). It is also noteworthy that the major shifts in species abundances line up reasonably well with the major documented regime shifts recorded over the past century.

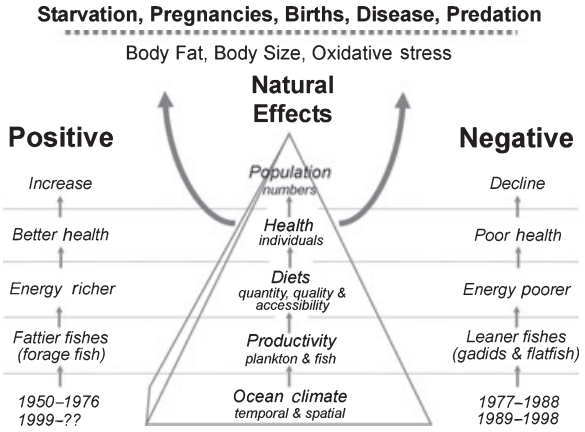
In summary the archaeological and anthropological analyses provide data on time scales that are currently not available in any other form of analysis. They demonstrate that the North Pacific and southern Bering Sea have been dynamic and volatile, and subject to great fluctuations over the last hundreds to thousands of years. This requires careful evaluation of current models to determine where sea lion populations are currently positioned within the large amplitude swings in population sizes that are evident from the past. The results also provide additional evidence that climate may very well underpin ecosystem restructurings that can be manifested as large, regional changes in Steller sea lion abundance.

SUMMARY

We examined the hypothesis that the decline of the Steller sea lion populations in the Aleutian Islands and Gulf of Alaska was a consequence of physical oceanographic changes due to the 1976–77 climate shift. The available data suggest that ocean climate can affect the survivorship of key species of prey consumed by Steller sea lions. The change in climatic conditions following the 1976–77 regime shift enhanced the survivorship and distribution of leaner species of prey (such as pollock and flatfish) that in turn negatively affected the survival of young sea lions from 1977 to 1998 and reduced the birth rates of their mothers (Fig. 14). Thus, physical environmental changes could have had consequential effects on the health and fecundity of Steller sea lions. Higher temperatures appear to be associated with an increased abundance of cod and pollock, while a return to cooler temperatures would favor Steller sea lions.

In broad terms, the suite of studies that have been undertaken to investigate the temporal and spatial differences in ocean climate in the North Pacific have identified ocean climate patterns that are consistent with the patterns of sea lion distributions, population trends, numbers, and diets. The oceanic response to climate forcing after 1976–77 has an east–west asymmetry, with stronger changes occurring in the western Gulf of Alaska. The geographic clustering of sea lion

Figure 14. Conceptual model showing how regime shifts might have positively or negatively affected sea lion numbers through bottom-up processes that influenced suites of species.



diets and population trajectories, and their correspondence with key biogeographic and oceanographic features of the Gulf of Alaska and Aleutian Islands add credence to the view that there is a linkage between Steller sea lions and the physical environment. However, additional studies will be required on finer spatial scales to draw firmer conclusions, particularly in regions closer to shore where sea lions spend more time foraging.

Our assessment of the ocean climate hypothesis does not discount the other leading hypotheses that have been proposed to explain the decline of Steller sea lions, such as the nutritional stress hypothesis, fishing hypothesis, disease hypothesis and killer whale predation hypothesis (see DeMaster and Atkinson, 2002; Burek *et al.*, 2003; National Research Council, 2003; Trites and Donnelly, 2003). Instead, the ocean climate hypothesis provides a holistic framework within which each of the alternative hypotheses can be aligned (Fig. 14).

The available data suggest that ocean climate is the most likely underlying mechanism that drove the decline of the Steller sea lion populations in the Aleutians and western Gulf of Alaska. The major shift in oceanic conditions that began in the mid-1970s is a parsimonious explanation to account for the suite of changes that were unleashed throughout the North Pacific ecosystem. Spatial and temporal variations in the ocean climate system can create adaptive opportunities for high trophic-level species. The east–west asymmetry of the oceanic response to climate forcing after 1976–77 is consistent with both the temporal changes (sea lion populations decreased after the late 1970s) and the spatial issue of the decline (western, but not eastern, populations decreased). The regional impacts of these broad-scale changes appear to have been modulated by biogeographic structures in the Gulf, which include a transition point from coastal to open-ocean conditions at Samalga Pass westward along the Aleutian Islands. Making such links between local complexities and broad-scale regularities is an important and necessary step in assessing the impact of climate on ecosystems.

The ethnohistoric and archaeological records indicate that the decline of Steller sea lions observed through the 1980s and 1990s was not the first time such an event has occurred. Sea lions appear to have experienced major shifts in numbers long before the advent of commercial fisheries. While fisheries could be a confounding factor in the current decline (Fig. 2), ocean climate appears to be the only major driving force that can link changes over so many eras and across so many trophic levels.

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