Ocean Climate Changes and the Steller Sea Lion Decline

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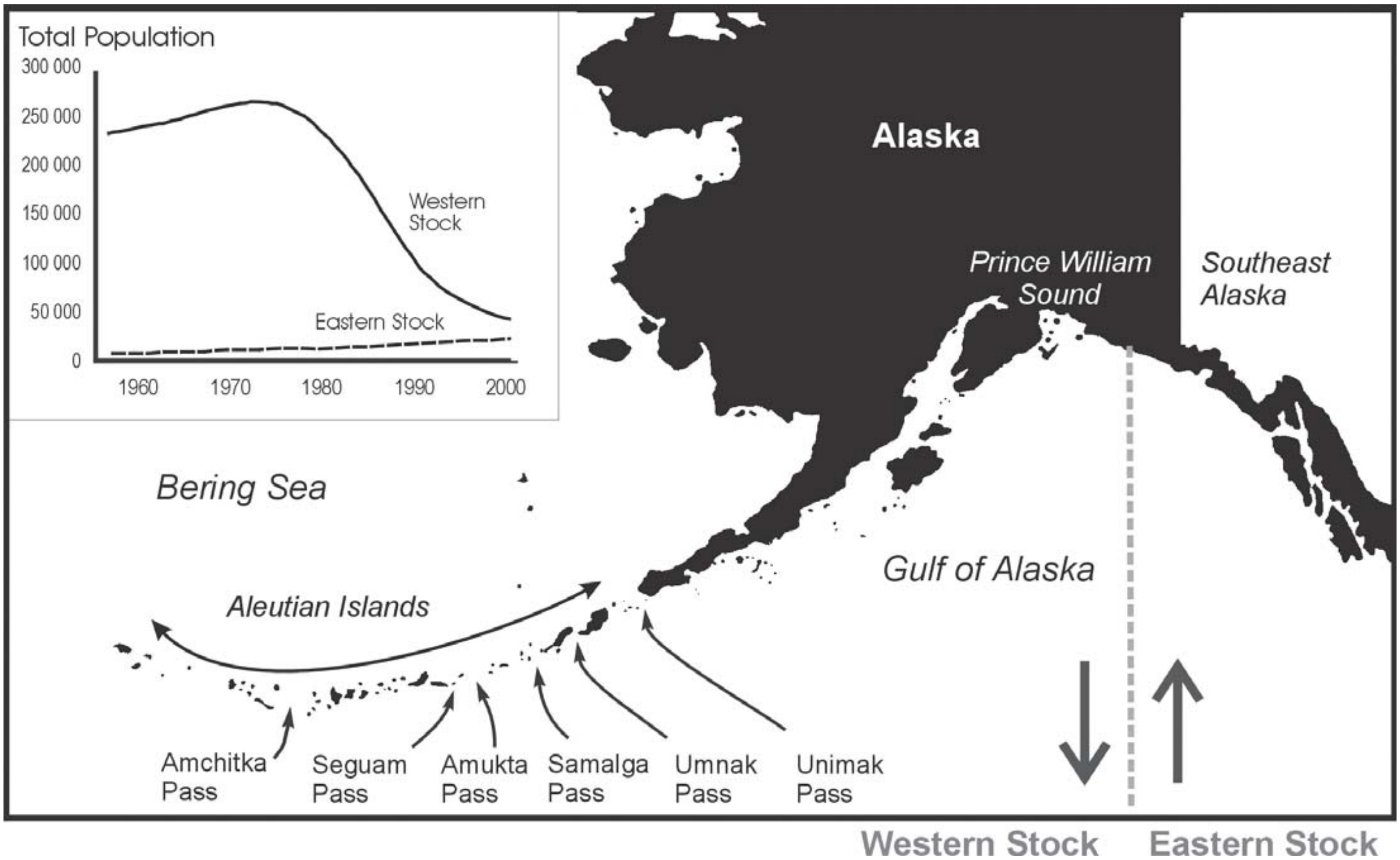
Steller sea lion populations declined by over 80% between the late 1970s and early 1990s in the western Gulf of Alaska and the Aleutian Islands. Concurrent declines also occurred farther west in the Russian coastal waters. Yet population trends were reversed along the coasts of southeast Alaska, British Columbia, Washington, and Oregon, where sea lions increased through the 1980s and 1990s. The cause or causes of these population changes have not been resolved and have been the subject of considerable debate and research because their preferred prey often coincides with economically important fisheries.

Much of the search for an explanation of the Steller sea lion decline in western Alaska has focused on trying to identify a single cause, rather than recognizing that many of the proposed theories are interrelated. 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 are typically 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). 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

Steller sea lions.



Habitats of the western and eastern stocks of the Steller sea lion. The graph shows the estimated numbers of Steller sea lions (all ages) in Alaska from 1956 to 2000. The dashed line shows the division between the declining (western) and increasing (eastern) populations.

during the mid-1970s, with basin-wide changes in temperature, mixed layer depth, primary productivity, fisheries, and other variables. This linkage between the physical climate and the oceanic ecosystem provided the impetus for the Cooperative Institute for Arctic Research (CIFAR) 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, and archaeological evidence.

CIFAR also sponsored a synthesis workshop in December 2004 that resulted in a detailed publication in *Fisheries Oceanography*, which is briefly summarized here. It 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 years.

Characteristics of 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, Alaska. The sharp decline of the larger western population through the 1980s was mirrored by population growth in the smaller eastern populations in southeast Alaska, British Columbia, and Oregon.

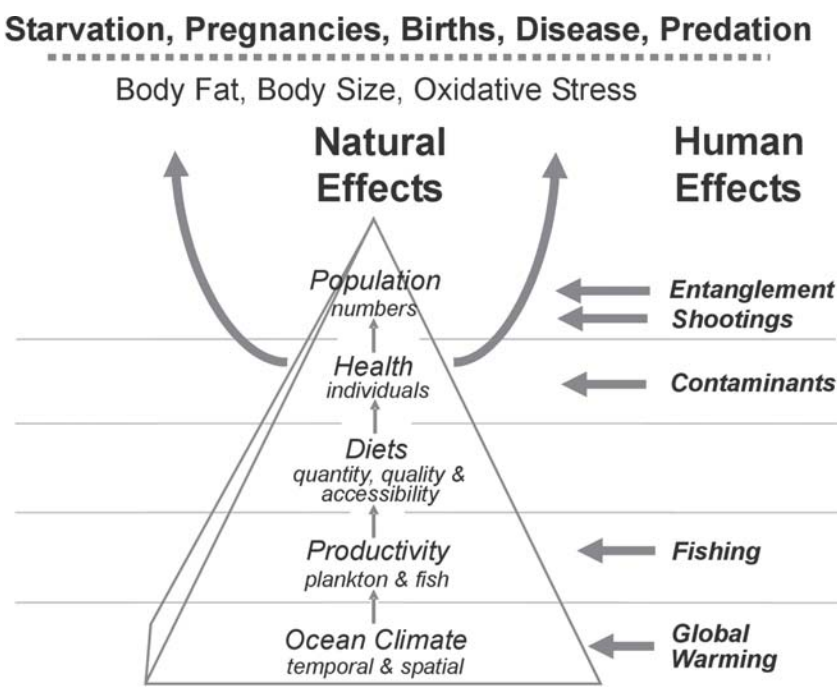
Counts of Steller sea lions in Alaska began in 1956 and continued sporadically through the 1960s and 1970s. They suggest that sea lion numbers were relatively high and increased slightly through the 1960s and 1970s. Trouble was not noted until the mid-1970s, and it appeared to spread east and west from the eastern Aleutian Islands in following years. 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 around 1989. 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.

Steller sea lions regularly haul out on shore at breeding (rookeries) and nonbreeding (haulout) sites. They typically spend one to two days at sea followed by one day resting on shore. Principal prey species include Atka mackerel, walleye pollock, Pacific cod, squid, octopus, salmon, Pacific herring, sand lance, and arrowtooth flounder. The most complete set of dietary information for sea lions was collected during the 1990s. It also suggests distinct geographic clusterings, with the split points centered on major Aleutian passes (Samalga Pass and Unimak Pass during summer and Umnak Pass during winter).

Significant correlations between rates of population decline and the diversity of diets suggest that a relationship may exist between what sea lions eat and how their populations have fared. Sea lions living in regions with the highest rates of declines, such as the western Aleutian Islands, consumed the least diverse diets with the lowest energy prey. In contrast, the increasing populations of sea lions in southeast Alaska had the most energy-rich diet and the 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. Little is known about what sea lions ate prior to their population decline.

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, as measured by the 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.



The National Research Council 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–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" nutritional stress associated with the high abundances of low-quality species of prey that were present during the 1980s and 1990s. This conclusion is based on a growing body of research that includes blood chemistry comparisons, dietary analyses, population modeling, and captive feeding studies.

Shifting from a high-energy diet (dominated by fatty fishes) to one dominated by lower-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. Bioenergetic models indicate that a yearling sea lion requires about twice the relative energy compared to an adult. 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 low-energy prey species dominate their diet. 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.

The overall abundance of Steller sea lion prey may have changed in the mid-1970s because of changes in ocean productivity, fishery removals, and/or other ecosystem interactions. Decreased prey availability could potentially have increased foraging times and thus the risk of predation. Similarly, abundant prey located farther from shore could also increase foraging times and exposure to killer whales, which are the 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. A dietary shift to low-energy prey could have further exacerbated any effects of decreased prey availability by increasing food requirements.

Differences in diet and relative prey abundance appear to be associated with pronounced changes in Steller sea lion numbers. The ocean climate could account for these geographic and temporal patterns. 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 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

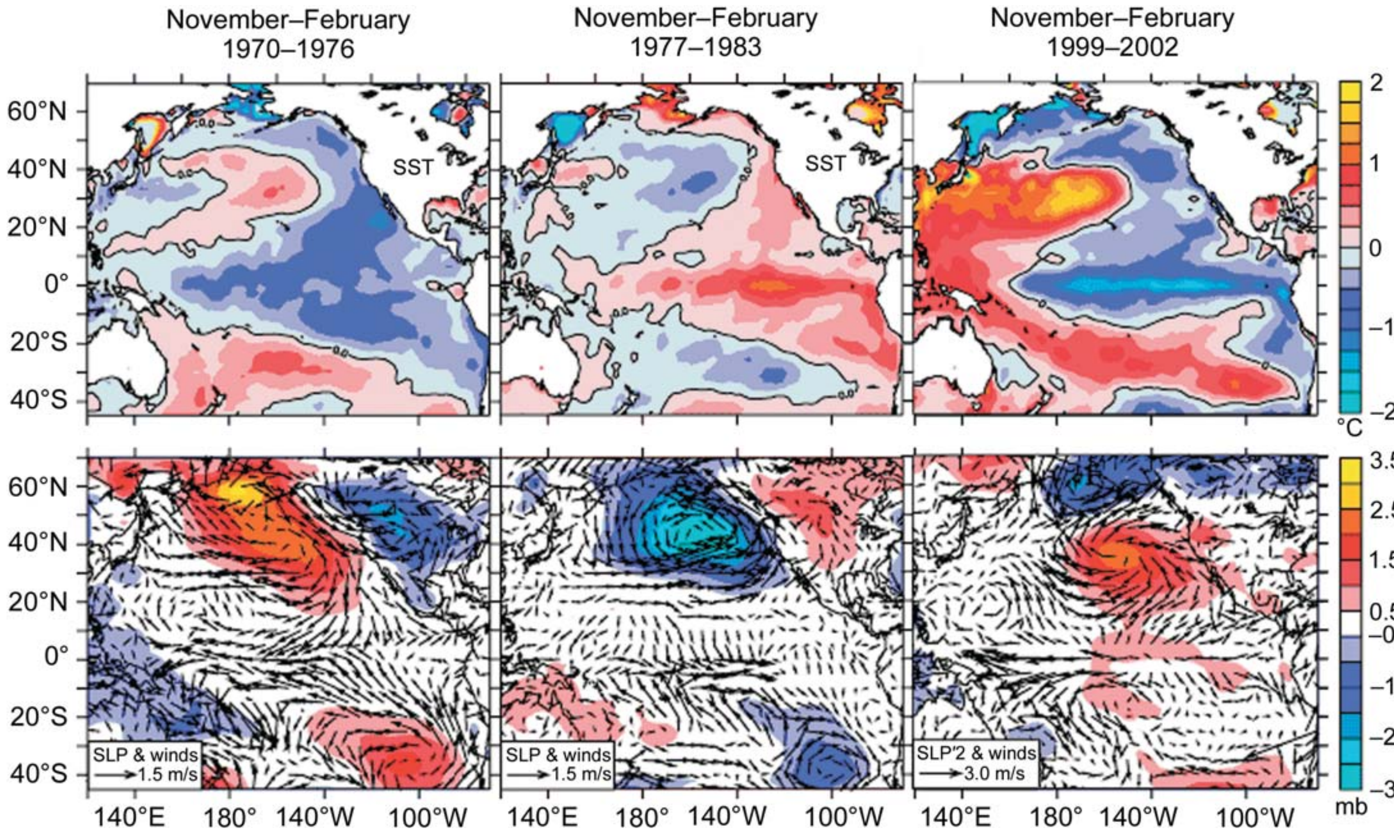
Physical oceanographic data for the North Pacific are generally sparse in time and space, and this is especially true in the Gulf of Alaska. Broad-scale changes over recent decades have been identified in sea surface temperature (SST), which is the most complete set of oceanographic data available. The 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. These physical changes have been linked to a number of responses within the ecosystem of the Gulf. For some variables, especially biological ones, the mid-70s transition was not a sharp change, and the duration of the stable time periods before and after the shift may have ranged from six years to more than twenty years.

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. Some detailed mechanisms have been proposed, 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, 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.

Regional and depth-dependent differences in the timing and amplitude of important ocean climate events in the eastern subarctic Pacific could have caused local differences in ecosystem response. 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 productivity and structure. But there is also significant spatial heterogeneity in long-term SST patterns across the region. An analysis of SST time series reveals five distinct regions, with common variability within the eastern Gulf of Alaska and the western Gulf of Alaska, as well as the transitional zone to the south. Other analyses 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. 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. 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.

Important changes were observed across the unique mid-70s temporal boundary for winter SST, sea level pressure, and surface wind anomalies before and after 1976-77. The timing of this major regime shift corresponds to the 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 (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 be a reversal to earlier conditions. Significant differences between regimes (1970–1976 and 1999–2002) are evident, such as a strong, displaced Aleutian Low with a strengthened North Pacific High. This suggests that more than two stable



Sea surface temperature anomalies (top panels) and sea level pressure anomalies and surface wind anomalies (bottom panels) for winter periods (November–February) before and after the 1976-77 regime shift and for the most recent period.

climate states may exist, and it adds support to the arguments that a second SST pattern has become more important than the PDO in recent years.

The east–west patterns of sea lion population dynamics are therefore 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 the populations decreased significantly in the western Gulf. 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. Numerical simulations can be used to gain further insight into how these physical changes may have influenced the sea lions and other species.

Ocean Modeling

Because of the sparseness of oceanographic observations in space and time (especially before the 1976-77 climate shift), a number of modeling studies were designed to decipher the physical processes that may have led to changes in the sea lion 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.

A coarse-resolution hindcast of the Gulf of Alaska over the period 1958–1997 showed a shoaling of the pycnocline in the central part of the Gulf of Alaska after the mid-1970s and a deepening in a broad band that follows the coast. The deepening was particularly pronounced in the northern and western part of the Gulf of Alaska, to the southwest 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.

Changes in the distribution of mesoscale eddies in the Gulf of Alaska after the 1976-77 regime shift were studied in a regional eddy-permitting ocean model over the 1950–1999 time period. After the shift, mesoscale eddy variance changed dramatically in the western Gulf of Alaska. The consequences of this change included altering the cross-shelf/slope mixing of water masses of the open-ocean and shelf regions. Since mesoscale eddies provide a mechanism for transporting nutrient-rich open-ocean waters to the productive near-shore shelf region, the fundamental flow of energy through the food web may have been altered by this physical oceanographic change. This mechanism may have altered the relatively abundances of key prey species available to Steller sea lions prior to and following the 1977 regime shift.

In contrast to the western Gulf of Alaska, the model surface velocity variance in the eastern Gulf was only weakly altered. 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 southeast Alaska continuing their steady increase across the temporal boundary of the 1976-77 climate shift.

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 subarctic and Arctic basins, 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. Model-simulated eddies along the Alaskan Stream have significant influence on both the circulation and the water mass properties across the eastern and central Aleutian Island passes. Eddy-related upwelling of salty water along the southern slope affects the water column down to about 1000 m. 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. Since 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 in which mesoscale eddies frequently propagate along the Alaskan Stream.

There is therefore 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-70s climate regime shift. These changes are strongest in the western Gulf, where sea lion populations experienced precipitous declines during the same period. 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 may have been fundamentally altered by changes in these basic physical oceanographic changes. There are also other 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.

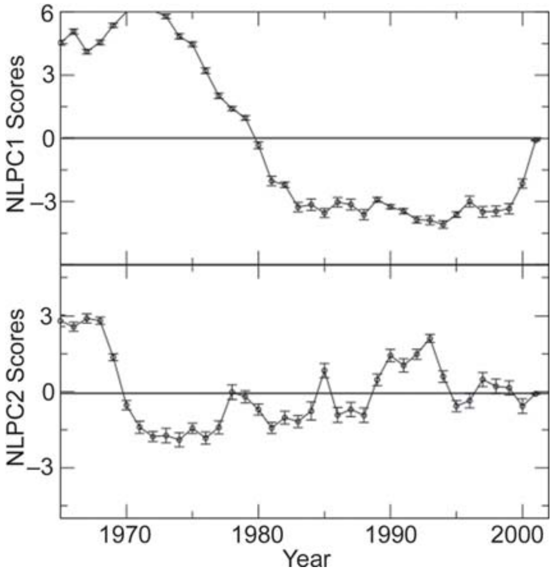
Ecosystem and Biogeographic Links

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.

A nonlinear analysis of a multivariate data set also captures the pattern of decline of Steller sea lions. The 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 main result is a pattern with all positive scores from 1965–1979 and all negative scores from 1980–2000.

Research cruises to the passes of the eastern and central Aleutian Islands revealed a number of

Nonlinear principal component (NLPC) analysis results from a multivariate data set of 45 biotic indices (fishery and survey records) that span broad regions over the Bering Sea, Gulf of Alaska, and North Pacific Ocean from 1965 to 2001. The top panel shows the first (and dominant) characteristic time series that emulates the pattern of sea lion decline and the 1976-77 climate shift. The bottom panel shows the second characteristic time series that exhibits interannual variability.



intriguing biogeographic features of the region that correspond to the population and dietary divisions of sea lions. Sharp fronts in surface salinity were found at Unimak and Samalga Passes that coincided with demarcation points for sea lion diets and population dynamics. Samalga Pass appears to be a boundary between shelf waters to the east and open-ocean waters to the west, with the Alaska Coastal Current influencing the waters east of the pass and the Alaskan Stream water influencing the waters farther west. The difference in source waters in the two regions likely affects the distributions of nutrients and biota around the different passes.

Changes in the abundance and composition of zooplankton species are associated with seasonal changes in water mass and other physical properties along the island chain. Declines in the abundance of *Neocalanus plumchrus* and *N. flemingeri* at Akutan and Unimak Passes in June resulted as these species left the surface waters and migrated down to depths over 300 m. Elevated abundances of *Calanus marshallae* and *Acartia* spp. at Umnak, Akutan, and Unimak Passes were due to their preference for warmer neretic conditions. Abundances of two species of euphausiid along the islands showed a preference by *Thysanoessa inermis* for the neretic waters 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 Alaska Coastal Current also operates as a biogeographical "boundary" for seabirds around Samalga Pass. Seabirds depending on coastal food webs (shearwaters and puffins) are more abundant east of Samalga, whereas seabirds depending on oceanic food webs (fulmars and auklets) are more abundant west of Samalga. Fulmars and shearwaters consume oceanic copepods and shelf-break species of euphausiids west of Samalga, while both of these seabirds consume shelf species of euphausiids east of Samalga.

At-sea surveys of seabirds during cruises in 2001 and 2002 showed large-scale patterns of avifauna that suggest that the central and western Aleutian Islands support the vast majority of breeding seabirds dependent on oceanic zooplankton, whereas the eastern Aleutian Islands support the majority of piscivorous seabirds. 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 points of much seabird foraging activity.

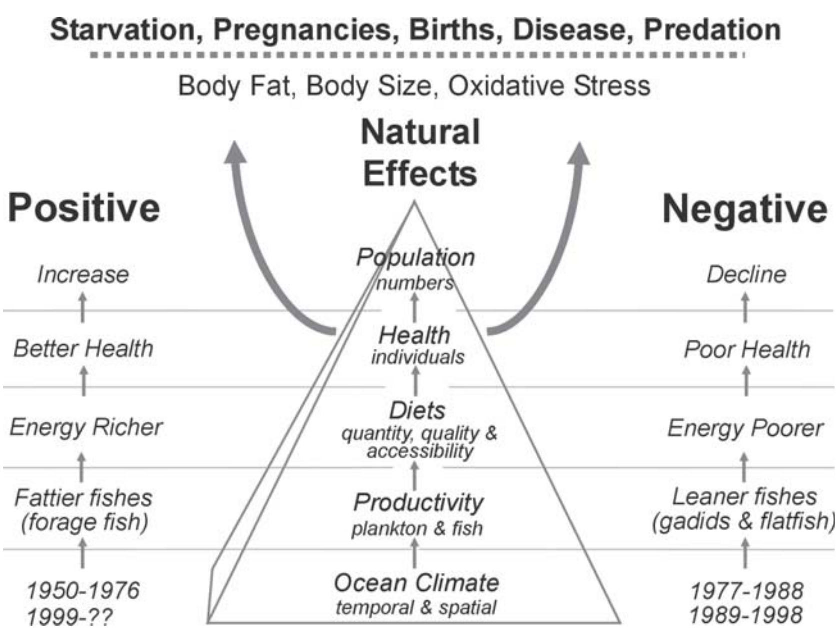
Changes in the benthic and pelagic fish communities within the Gulf of Alaska and Aleutian Islands in response to the regime shift of 1976 were dramatic. Population increases occurred in flatfish, gadids, and salmonids as a result of an increase in the frequency of strong year classes after 1976. At around the same time, decreases occurred in shrimp and crab stocks. Small-mesh trawl surveys conducted near Kodiak Island between 1953 and 1997 documented the "community reorganization" in the Gulf of Alaska. 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 less than 20% of its peak abundance by the mid-1980s. Steller sea lions numbers at the nearby rookery on Chowiet Island also fell rapidly through the 1980s. Similarly the Pribilof Islands population of northern fur seals, which accounts for about 80% of the world population, also declined unexpectedly from the late 1970s to mid-1980s. All three populations of pinniped species appear to have declined at about the same time, 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 (fishing) is without impact. Fishing can, and does, affect community dynamics. The effect of fishing is added to natural sources of variability. Archaeological studies have repeatedly demonstrated wide swings in the abundance of fish species long before the development of large-scale fisheries. 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 abruptly.

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 might have reduced the suitability of certain haulouts and rookeries, while bottom-up effects mediated through at least three trophic levels (such as phytoplankton, zooplankton, and 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, 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.

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



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 correlate 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-70s, 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 on changes seen in recent decades. Indicators of oceanic productivity in two sediment cores, one from the central Gulf of Alaska shelf and one from the Bering Sea (Skan Bay), showed that considerable variability has occurred in ocean productivity over the last 150 years for each region. In the Gulf of Alaska, two productivity proxies increased since the 1976-77 regime shift, while the two proxy signals were mixed in the Bering Sea. 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 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 the 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. The archaeological data indicate that significant variations occurred in the distributions of key species over the last 5000 years. Correlations between changes in the relative abundances of species such as Steller sea lions and regional 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. Notably, the greatest abundance of Steller sea lions occurred during the Little Ice Age, which may be significant. The end of the Little Ice Age also appears to have coincided with a reduction in Steller sea lion populations.

Decadal-scale changes in the marine ecosystem spanning nearly 150 years are identifiable using both ethnohistoric data and traditional ecological knowledge of local Aleut fishermen. Based on Russian and early American accounts of the region, there have been two periods in the last 250 years—one in the 1870s, coinciding with a warming period as observed in the Sitka air temperatures, and another in the 1790s—when there were few or no Steller sea lions in many areas of the North Pacific, leading to widespread starvation for the indigenous peoples who depended on them. These depressions in the population levels cannot be correlated with any human-based harvesting of either the sea lions or their food sources.

Traditional knowledge of local fishermen indicates that the North Pacific ecosystem underwent a series of disruptions over the last 100 years that may or may not have been caused by 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, during which time shrimp and crab were dominant components of the ecosystem. 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 that the Aleut term for codfish can be rendered into English as “the fish that stops,” meaning that it disappears periodically. 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 manifest 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 Aleutians Islands and Gulf of Alaska is a consequence of physical oceanographic changes caused by 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. It is therefore conceivable that a change in climatic conditions following the 1976-77 regime shift may have enhanced the survivorship and distribution of leaner species of prey (such as pollock, flatfish, and Atka mackerel), which in turn negatively affected the survival of young sea lions from 1977 to 1998. 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 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, the fishing hypothesis, the disease hypothesis, and the killer whale predation hypothesis. Instead, the ocean climate hypothesis provides a holistic framework within which each of the alternative hypotheses can be aligned.

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