Bottom-Up Forcing and the Decline of Steller Sea Lions in Alaska: Assessing the Ocean Climate Hypothesis

Andrew W. Trites[1], Arthur J. Miller[2*], Herbert D. G. Maschner[3],

Michael A. Alexander[4], Steven J. Bograd[5], John A. Calder[6], Antonietta Capotondi[4],

Kenneth O. Coyle[7], Emanuele Di Lorenzo[8], Bruce P. Finney[7], Lowell Fritz[9],

Edward J. Gregr[1], Chester E. Grosch[10], Steven R. Hare[11], George L. Hunt[12],

Jaime Jahncke[12], Nancy B. Kachel[13], Hey-Jin Kim[2], Carol Ladd[12], Nathan J. Mantua[14],

Caren Marzban[15], Wieslaw Maslowski[16], R. Mendelssohn[5], Douglas J. Neilson[2],

Stephen R. Okkonen[7], James E. Overland[13], Katherine L. Reedy-Maschner[3],

Thomas C. Royer[10], F. B. Schwing[5], Julian X. L. Wang[17] and Arliss J. Winship[1]

[1]University of British Columbia, Vancouver, BC, Canada

[2]Scripps Institution of Oceanography, La Jolla, CA

[3]Idaho State University, Pocatello, ID

[4]Climate Diagnostics Center, Boulder, CO

[5]Pacific Fisheries Environmental Laboratory, Pacific Grove, CA

[6]NOAA Oceanic and Atmospheric Research, Silver Springs, MD

[7]University of Alaska, Fairbanks, AK

[8]Georgia Institute of Technology, Atlanta, GA

[9]National Marine Fisheries Service, Seattle, WA

[10]Old Dominion University, Norfolk, VA

[11]International Pacific Halibut Commission, Seattle, WA

[12]University of California, Irvine, CA

[13]Pacific Marine Environmental Laboratory, Seattle, WA

[14]University of Washington, Seattle, WA

[15]University of Oklahoma, Norman, OK

[16]Naval Postgraduate School, Monterey, CA

[17]NOAA Air Resources Lab, Silver Spring, MD

*Correspondence. e-mail: ajmiller@ucsd.edu

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 are consistent with 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. Climate forcing, and the details of the mean and eddy oceanic response, are consistent with both the temporal aspect (populations decreased after the late 1970's) and the spatial aspect of the decline (western, but not eastern, populations decreased). The basin-wide climate variations of the North Pacific also correspond with 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. Paleontological records spanning 4000 years 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.

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 Aleutian Islands (Fig. 1). Concurrent declines also occurred farther west in the Russian coastal waters. However, population trends were reversed along the coasts of Southeast Alaska, British Columbia, Washington and Oregon where sea lions increased through the 1980s and 1990s (Loughlin, 1998; Trites and Larkin, 1996). 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). 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-1970's, with basin-wide changes noted in temperature, mixed layer depth, primary productivity, fisheries, and other variables (e.g. Beamish, 1993; Benson and Trites, 2002; Hare and Mantua, 2000; Mantua *et al.*, 1997; Miller *et al.*,

3

1994; Polovina *et al.*, 1995). 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, and paleontological evidence.

The following synthesizes the broad range of recently completed research that addressed the climate-ocean regime shift hypothesis of the Steller sea lion decline. We have two primary goals. The first is to determine whether there were any spatial and temporal patterns in the physical and biological oceanographic data that corresponded with observed differences in the diets and numbers of sea lions since the late 1950s. The second is to put the recent decline in context with similar changes that may have occurred over the past 4000 years.

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 144ºW near Prince William Sound, Alaska (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 Southeast Alaska, British Columbia and Oregon (Calkins *et al.*, 1999; Fig. 1).

Counts of Steller sea lions 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 Aleutians 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 Aleutians 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 (Call and Loughlin, 2004; Winship and Trites, 2004; Fig. 3; York *et al.*, 1996). Population data from the 1990s (Fig. 3) suggest there are two core regions of sea lion abundance (Central Aleutians and Western Gulf of Alaska) where numbers have been much higher than adjoining regions and populations generally decreased at slower rates during the 1990s, while a few were stable or increased slightly. In contrast, regions where sea lions have fared much worse are the Western Aleutians, Eastern Aleutians and Central Gulf of Alaska (Fig. 3). Three major 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 seasonal distributions (Gregr and Trites, 2004; Fig. 4) . Steller sea lions regularly haul out on shore at breeding (rookeries) and nonbreeding (haulout) sites, and typically spend one to two days at sea followed by one day resting on shore (Milette and Trites, 2003; Trites and Porter, 2002). Principle 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 centered on other major Aleutian passes (i.e. Samalga Pass and Unimak Pass during summer, and Umnak Pass during winter). Demarcation lines for summer diets are roughly in the middle of the population groupings in the Eastern Aleutians and Western Gulf of Alaska (Fig. 3).

Significant correlations between rates of population decline and the diversity of diets suggest 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 Aleutians) consumed the least diverse diets with lowest energy prey. In contrast, the increasing populations of sea lions in Southeast 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 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 to 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.

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 (Alverson, 1992; Rosen and Trites, 2000; Trites, 2003). Bioenergetic models indicate that a yearling sea lion requires about twice the relative energy compared to an adult (i.e. 14% of its body mass vs. 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.

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 (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 increase 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.

The most likely driving forces that could account for the geographic and temporal differences noted in sea lion diets, numbers and trends are spatial and temporal differences in ocean climate (Fig. 2). However, careful consideration of ocean climate data has not been undertaken to evaluate the ocean climate hypothesis.

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 temperatures (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 basinwide regime shift of the North Pacific that commenced during the winter of 1976-77 (e.g. deYoung *et al.*, 2004; Ebbesmeyer *et al.*, 1991; Hare and Mantua, 2000; Miller *et al.*, 1994). These physical changes have been linked to a number of responses within the ecosystem of the Gulf (e.g. Benson and Trites, 2002; Mantua, 2004; Mantua *et al.*, 1997).

The basic issue of the identifying regime shifts via statistical techniques is, however, 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. Rudnick and Davis (2003) showed 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.

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; Wooster and Zhang, 2004). The large-scale surface-derived indices such as the Pacific Decadal Oscillation (PDO - the first principal component of SST north of 20N 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.* (2004) 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 Trend-1 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 Trend-2 accentuated Trend-1 with a strong warming after 1972, while Trend-3 had a strong warming in the eastern Gulf of Alaska during the 1957-58 El Niño and after the 1976-77 shift. Trend-4 exhibited high interannual variability associated with El Nino/Southern Oscillation (ENSO) events with strong signatures in coastal British Columbia and in the West Wind Drift.

Overall, the nonparametric SST trends reflect important large-scale climate impacts in the Gulf of Alaska associated both with El Niño events and the 1976 regime shift. Moreover, the trends 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 trends across the region. A cluster analysis of SST time series (Bograd *et al.*, 2004) 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 component also revealed this robust east-west asymmetry.

The ocean temperature data show temporal and spatial patterns that may be 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.*, 2004). 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 temperature data is on a much coarser spatial scale than the fine scales over which sea lions forage, making it difficult to draw firm 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.*, 2004). 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 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. Fig. 5 shows the first and second nonlinear PC's (NLPC) based on these physical data. NLPC1 exhibits clear indications of a regime shift around 1976-77 when sea lions began to decline. The sharp increases in the NLPC1 scores in 1989 and 1999 also correspond with inflection points in sea lion numbers in the western population. The time series that most strongly influence NLPC1 include the PDO index, the Aleutian Low index, and coastal SST data. The explained variance in NLPC1 from this analysis is 32%, while PC1 from a linear analysis accounts for 25% of the variance in these data. NLPC2

has more interannual variability than NLPC1 with no hint of interdecadal climate regime shifts.

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 this unique temporal boundary are shown in Fig. 6 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 start of the sea lion decline. Comparing ocean climate conditions across the 1999 temporal boundary also shows similarities between the latest period 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 be a reversal to earlier conditions. Significant differences between regimes (i.e. 1970-76 and 1999-2002 shown in Fig. 6) 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 and surface fresh-water fluxes. For example, the mean Ekman pumping pattern in the Gulf (Fig. 7a) weakened appreciably after the climate shift of the mid-1970's in the northeastern basin, but strengthened in the southwestern basin (Fig.7b). 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 (Royer, 1981). Coastal discharge into the Gulf of Alaska was calculated (Fig. 8) based on Royer's (1981) model using National Weather Service temperature and precipitation data since 1980. Fig. 8 also shows the estimated discharge using precipitation from the NCEP/NCAR Reanalysis (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 Alaska Coastal Current (ACC) has increased by about 70% from the early 1970's to the late 1980's. This suggests that the strength of the coastal current increased significantly through the region designated as critical habitat for Steller sea lions in the Northeast 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; Strom *et al.*, 2004).

Royer *et al*. (2001) hypothesize that positive feedback mechanisms could occur in the Gulf of Alaska circulation. Increased freshwater 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 is consistent with the observation that increases in freshwater and coastal stratification have been occurring concurrently with increases in the water temperatures since 1970 (Royer *et al.*, 2003).

Gulf of Alaska coastal freshwater discharge shows seasonal changes in amplitude and phase (Fig. 9). The spring sub-maximum that was evident in the mid-1930s, disappeared around 1970, appeared weakly from 1978 to 1989, and reappeared again from 1994 to 2002. The timing of this freshening might be critical to the spring blooms in the Alaska Coastal Current and hence biological productivity (Brickley and Thomas, 2004). There is a long period modulation in the seasonal discharge amplitude that varies more than 30% over decadal time scales, and might also affect productivity. Wavelet analysis of the discharge (Fig. 10) reveals changes in the low frequency variations of the signal with strong 18-22 year periodicities from the 1930s-1950s. It also shows a 50-year periodicity during the middle of the record and ENSO type variations (< 10 years) in the 1970s and 1980s.

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 decipher 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 and their 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.* (2004) 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 reanalysis winds over the period 1958-1997. 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. 11). 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 (Fig. 7), which can account for a large fraction of the pycnocline depth changes as a local response (Cummins and Lagerloef, 2002).

Pycnocline depth changes are relevant for biological productivity in the Northeast 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. Second, the Northeast 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 density is controlled by salinity at high-latitudes. Thus, the depth of the top of the maximum seasonal pycnocline 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. 11) 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 reanalysis) to force a regional eddy-permitting ocean model, with a 16-km grid and 20 layers, over the 1950-1999 time period (Miller *et al.*, 2004). The model suggests that the Alaskan Stream was strengthened considerably after the shift in the northwest part of the Gulf of Alaska, and weakened in the southwestern domain. The increase in the strength of the Alaskan Stream is consistent with coarse resolution model results of Capotondi *et al.* (2004). 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.

Fig. 12 shows the 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 southeast of Kodiak Island and along the Alaskan Stream to the southwest of Kodiak. After the shift, mesoscale eddy variance increased dramatically in the northwestern Gulf of Alaska and decreased to the south and west of Kodiak Island. 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 (Okkonen *et al.*, 2003; Strom *et al.*, 2004), 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 relatively abundances of key prey species available to Steller sea lions prior to and following the 1977 regime shift.

In contrast to the eastern and western Gulf of Alaska, the mean flows of the Alaska Current in the eastern Gulf were nearly unchanged after the shift. Likewise, the surface

velocity variance was only weakly altered, being reduced slightly compared to pre-shift conditions. Hence, an east-west asymmetry occurred in the Gulf of Alaska circulation response to the strengthening 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.

While the physical ocean models can give us a sense of how the basic ocean environment might have changed after the shift, an ecosystem model is needed to understand how the physical changes can alter the food web. Towards this end, Fig. 13 shows the results of analyzing a coarse-resolution physical-ecosystem ocean model hindcast (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 Northeast Pacific. The physical component of the analysis simulated ocean temperatures, salinity, horizontal currents and upwelling, while the biological component consisted of ten 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; Chai *et al.*, 2003). The model domain extended from 45ºS to 65ºN in the Pacific, with a horizontal resolution of 2º longitude by 2º latitude (north of 20ºN) and 40 vertical levels. A simulation was performed where the model 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 1977-1998 relative to 1960-1976 (Fig. 13). 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. 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.

The 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 (although 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 physical process (e.g. upwelling) and the biological changes seen in Fig. 13, the increased mixed layer depth in late winter along the southern coast of Alaska (Fig. 14) could have reduced the light available for photosynthesis in that region during 1976-1998 relative to 1960-1976. Increased mixed layer depths could also bring nutrient-rich water up into the euphotic zone, enhancing the biological productivity.

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 employing higher resolution allow focused, regional studies of critical processes and circulation. Such an approach allows for proper representation of the complex air-sea-bottom interactions and their influence on exchanges between adjacent water masses.

A pan-Arctic coupled sea ice–ocean model provides insight into the circulation and exchanges between the sub-arctic and arctic basins (Maslowski and Lipscomb, 2003; Maslowski *et al.*, 2004b; Maslowski and Walczowski, 2002), particularly on the exchange between the North Pacific Ocean and the Bering Sea through the straits of the Aleutians. The model domain extends from about 30^oN in the North Pacific, through the Bering Sea, Arctic Ocean, into the North Atlantic to about 45^oN, on a $1/12^o$ grid with 45 levels. The model has been integrated with realistic daily-averaged 1979-1993 re-analyzed data and 1994-2001 operational products from the European Centre of Medium-range Weather Forecasts (ECMWF) to investigate interannual-to-interdecadal variations in transport through these straights.

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 (Favorite, 1974; Onishi, 2001; Reed, 1984; Reed and Stabeno, 1999; Roden, 1995;

Thompson, 1972; Warren and Owens, 1988) with those through the eastern and central passes (Reed, 1990; Reed and Stabeno, 1997; Schumacher *et al.*, 1982; Stabeno *et al.*, 1999) 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 (Crawford *et al.*, 2000; Okkonen, 1992,1996) and in field observations (Musgrave *et al.*, 1992; Reed *et al.*, 1980).

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. Fig. 15 shows depth-averaged (0-100 m) velocity snapshots and salinity differences across the 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 (Fig. 15a), 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 (Fig. 15b) — the flow of the Alaskan Stream is significantly modified down to well 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.*, 2004a; Okkonen and Maslowski, 2004).

The salinity difference between the model sections marked "Cross Slope" when the eddy is either present (Fig. 15b) or absent (Fig. 15a) in the region is shown in Fig. 15c. 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 ppt extends all the way to the surface within the Amukta Pass region when the eddy is present. 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,

16

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 for mesoscale eddy activity along the Alaskan Stream and for its contribution to circulation and hydrographic variability across Aleutian Island passes. However, long-term observations and more modeling studies of the Aleutian Island passes are needed to fully understand impacts of eddies, tides, and wind forcing on the biological environment — not only related to primary productivity — but also to higher trophic levels including Steller sea lions.

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.* (2004) applied a nonlinear 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. 16) were similar to those found by Hare and Mantua (2000), whereby the leading PC indicated a pattern with all positive scores from 1965-1979, and all negative scores from 1980-2000. However, the NLPC1 of the abiotic series shown in Fig. 5 had stronger interannual variations than the NLPC1 of the fishery/survey (biotic) data, which highlights decadal-scale changes. The time series that most strongly influenced NLPC1

included Alaska salmon landings and many rockfish recruitment records, while records for Gulf of Alaska shrimp catches acted negatively on NLPC1. The explained variance in NLPC1 from this analysis was 39%, while PC1 from a linear analysis accounted for 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 16). A closer inspection of the NLPC1 scores suggest that they preceded the overall decline of the western stock of sea lions by about 4 years, 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.* (2004) 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 nonlinearly (though monotonically). The adult sea lion data showed statistically significant negative trends in 5 of the 7 regions (Fig. 17a). 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. 17b). 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. 17c).

Research cruises to the passes of the eastern and central Aleutian Islands 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. 18) that coincided with demarcation points for sea lion diets and population dynamics (Fig. 4). 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 (Ladd *et al.*, 2004). 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 (Fig. 19a; Coyle, 2004). 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 (Fig. 19b).

In addition to zooplankton and fish, the extent of the Alaska Coastal Current also operates as a biogeographical "boundary" for seabirds around Samalga Pass (Jahncke *et al.*, 2004). 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 (Fig. 20). 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.

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 reduce the suitability of certain haulouts and rookeries, while bottom-up effects mediated through at least 3 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 (Gregr and Trites, 2004).

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. Abrupt population

increases occurred in flatfish (Wilderbuer *et al.*, 2002), gadids (Hollowed *et al.*, 2001) and salmonids (Hare and Francis, 1995). At around the same time, equally abrupt decreases occurred in shrimp and crab stocks (Orensanz *et al.*, 1998). A small mesh trawl survey conducted near Kodiak Island between 1953 and 1997 documented the wholesale change in the fish community of the Gulf of Alaska (Anderson and Piatt, 1999). The composition of trawl catches 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.

These broadscale ecological changes, across all trophic levels and generally coincident in time, are widely believed to be driven by 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. Paleontological studies have repeatedly demonstrated wide swings in abundance of fish species long before the development of large-scale fisheries (Finney *et al.*, 2002; Soutar and Isaacs, 1969). Generally, fishing impacts the adult portion of fish populations. The link between climate and population size is at the recruitment stage. 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.

Though the precise mechanisms regulating recruitment 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 increase in zooplankton production and distribution around the northern periphery of the Alaska Gyre (Brodeur and Ware, 1992; Francis and Hare, 1994). At the same time that Alaska salmon populations flourished, those off of Washington and Oregon declined. Hare *et al*. (1999) hypothesized this resulted from increased advection of zooplankton-rich subarctic water into the Alaska Gyre with a corresponding decrease into the Subarctic gyre. Another significant change that has occurred since the regime shift is a change in the developmental timing of *Neocalanus plumchrus*, the dominant

copepod in the Gulf of Alaska. Between the early 1970s and 1990s the spring bloom moved as much as one month earlier in the year (Mackas *et al.*, 1998). Such a change will impact marine fish populations favoring those with earlier hatch dates. The decline of crabs and shrimps appears to be the result both of 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.

PALEOECOLOGICAL PERSPECTIVE

Paleoecological studies provide a long-term perspective to changes seen in recent decades. Finney (2004) studied indicators of oceanic productivity in two sediment cores in the Gulf of Alaska — one from the GAK-4 site in the central Gulf shelf and one from the Bering Sea (Skan Bay). Increases in productivity are indicated by an increase in either opal content (representing diatom productivity) or delta 13C organic matter (representing all organic productivity). Results showed that considerable variability has occurred in ocean productivity over the last 300 years for each region (Fig. 21). In the Gulf of Alaska, productivity increased since the 1976-77 regime shift, while the signals are mixed in the Bering Sea. These regional differences need to be rationalized in the context of 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 years. Correlations between changes in 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 (Fig. 22). 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 impacted Steller sea lion populations as Collins *et al.* (1945) noted that, "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 were optimal non-selective foragers (i.e. harvesting species in numbers relative to their actual abundance on the landscape). Thus, changes in the proportions of phocid and otariid bones, for example, can be used as indicators of actual 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 years are identifiable using both ethno-historic 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 (Royer, private communication, 2004), 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.

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 2,000 to 3,000 years, but that the distribution patterns had changed. In particular they noted that sea lions were once numerous on Nunivak Island (along southwestern 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 of Steller sea lions are known to have undergone local extinctions in the past due to catastrophic environmental events such as earthquakes, volcanic eruptions, and tsunami (Black, 1981) — and have been documented for

Unalaska, the Sanak Islands, the Shumagin Islands, and the Attu area over the last 200 years. 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 years 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 (Trites *et al.*, 1999)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.

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.

SUMMARY

We examined the hypothesis that the decline of the Steller sea lion populations in the Aleutians and Gulf of Alaska is 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. 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) that in turn negatively affected the survival of young sea lions from 1977-1998 (Fig. 23). 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 into 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. They 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 Burek *et al.*, 2003; DeMaster and Atkinson, 2002; 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. 23).

The available data suggest that ocean climate is the most likely underlying mechanism driving 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 the most 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 climate forcing mechanism and the details of the mean and eddy oceanic response are broadly consistent with both the temporal changes (sea lion populations decreased after the late 1970's) and the spatial issue of the decline (western, but not eastern, populations decreased). Enhanced freshwater discharges could continue to increase the

water temperatures throughout the Gulf of Alaska through increases in the current speeds. The basin-wide climate changes have large-scale and regional impacts due to their effects on the biogeographic structures in the Gulf, which includes 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 paleontological record further indicates that the decline of Steller sea lions observed through the 1980s and 90s 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.

REFERENCES

Alverson, D. L. (1992) A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): the conflict arena. *Rev. Aquat. Sci.* **6**: 203-256.

Anderson, P. J. and Piatt, J. F. (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar. Ecol.-Prog. Ser.* **189**: 117-123.

Beamish, R. J. (1993) Climate and exceptional fish production off the west coast of North America. *Can. J. Fish. Aquat. Sci.* **50**: 2270-2291.

Benson, A. J. and Trites, A. W. (2002) Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. *Fish Fisher.* **3**: 95-113.

Black, L. T. (1981) Volcanism as a factor in human ecology: the Aleutian case. . *Ethnohistory* **28**: 313-340.

Bograd, S. J., Mendelssohn, R., Schwing, F. B. and Miller, A. J. (2004) Spatial heterogeneity of sea surface temperature trends in the Gulf of Alaska. *Atmos-Ocean*: *sub judice*.

Bograd, S. J., Schwing, F. B., Mendelssohn, R. and Green-Jessen, P. (2002) On the changing seasonality over the North Pacific. *Geophys. Res. Lett.* **29**: Art. No. 1333.

Bond, N. A., J. E. Overland, M. Spillane and P. Stabeno (2003) Recent shifts in the state of the North Pacific. *Geophys. Res. Lett.* **30**: Art No. 2183.

Braham, H. W., Everitt, R. D. and Rugh., D. J. (1980) Northern sea lion population decline in the eastern Aleutian Islands. *J. Wildl. Manage.* **44**: 25-33.

Brickley, P. J. and Thomas, A. C. (2004) Satellite-measured seasonal and inter-annual chlorophyll variability in the Northeast Pacific and Coastal Gulf of Alaska. *Deep-Sea Res.* **51**: 229-245.

Brodeur, R. D. and Ware, D. M. (1992) Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. *Fish. Oceanog.* **1**: 32-38.

Burek, K. A., Gulland, F. M. D., Sheffield, G., Keyes, E., Spraker, T. R., Smith, A. W., Skilling, D. E., Evermann, J., Stott, J. L. and Trites, A. W. (2003) Disease agents

in Steller sea lions in Alaska: a review and analysis of serology data from 1975-2000. *Fisheries Centre Research Reports* No. **11(4): 26pp.**

Calkins, D. G., McAllister, D. C. and Pitcher, K. W. (1999) Steller sea lions status and trend in Southeast Alaska: 1979-1997. *Mar. Mamm. Sci.* **15**: 462-477.

Call, K. A. and Loughlin, T. R. (2004) An ecological classification of Alaskan Steller sea lion (*Eumetopias jubatus*) rookeries: a tool for conservation / management. *Fish. Oceanog.*: *in press*.

Capotondi, A., M. A. Alexander, Deser, C. and A. J. Miller (2004) Low-frequency pycnocline variability in the Northeast Pacific. *J. Phys. Oceanogr.*: *sub judice*.

Chai, F., Dugdale, R. C., Peng, T.-H., Wilkerson, F. P. and Barber, R. T. (2002) One dimensional ecosystem model of the equatorial Pacific upwelling system, Part I: Model development and silicon and nitrogen cycle. *Deep-Sea Res.* **49**: 2713-2743.

Chai, F., Jiang, M., Barber, R. T., Dugdale, R. C. and Chao, Y. (2003) Interdecadal variation of the Transition Zone Chlorophyll Front, a physical-biological model simulation between 1960 and 1990. *J. Oceanogr.* **59**: 461-475.

Collins, H., Clark, A. and Walker, E. (1945) *The Aleutian Islands: Their People and Natural History*. Washington DC: Smithsonian Institution.

Coyle, K. O. (2004) Zooplankton distribution, abundance and biomass relative to water masses in eastern and central Aleutian Island passes. *Fish. Oceanog.*: *in press*.

Crawford, W. R., Cherniawsky, J. Y. and Foreman, M. G. G. (2000) Multi-year meanders and eddies in the Alaskan Stream as observed by TOPEX/Poseidon altimeter. *Geophys. Res. Lett.* **27**: 1025-1028.

Cummins, P. F. and Lagerloef, G. S. E. (2002) Low-frequency pycnocline depth variability at Ocean Weather Station P in the northeast Pacific. *J. Phys. Oceanogr.* **32**: 3207-3215.

DeMaster, D. and Atkinson, S., eds. (2002) Steller sea lion decline: is it food II? Fairbanks: University of Alaska Sea Grant, AK-SG-02-02, 80pp.

deYoung, B., Harris, R., Alheit, J., Beaugrand, G., Mantua, N. and Shannon, L. (2004) Detecting regime shifts in the ocean: data considerations. *Prog. Oceanogr.* **60**: 143-164.

Ebbesmeyer, C. C., Cayan, D. R., McLain, D. R., Nichols, F. H., Peterson, D. H. and Redmond, K. T. (1991) 1976 step in the Pacific climate: Forty environmental changes between 1968-1975 and 1977-1984. In *Interagency Ecological Study Program Report. (Proceedings of the Seventh Annual Pacific Climate (PACLIM) Workshop, Asilomar, California,April, 1990).* no. 26, California Department of Water Resources, pp. 115-126.

Favorite, F. (1974) Flow into the Bering Sea through Aleutian Island passes. In *Oceanography of the Bering Sea with emphasis on renewable resources. Occasional Publication No. 2.* D. W. Hood and E. J. Kelley (eds) Fairbanks: Institute of Marine Science, University of Alaska, pp. 59-98.

Finney, B. (2004)???

Finney, B. P., Gregory-Eaves, I., Douglas, M. S. V. and Smol, J. P. (2002) Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years. *Nature* **416**: 729-733.

Francis, R. C. and Hare, S. R. (1994) Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science. *Fish. Oceanog.* **3**: 279-291.

Freeland, H., Denman, K., Wong, C. S., Whitney, F. and Jacques, R. (1997) Evidence of change in the winter mixed layer in the Northeast Pacific Ocean. *Deep-Sea Res.* **44**: 2127-2129.

Gregr, E. and Trites, A. W. (2004) Predicting at-sea habitat use by female Steller sea lions in Alaska. *Ecol. App.* **00**: *in review*.

Hare, S. R. and Francis, R. C. (1995) Climate change and salmon production in the northeast Pacific Ocean. *Can. J. Fish. Aquat. Sci.* **121**: 357-372.

Hare, S. R. and Mantua, N. J. (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog. Oceanogr.* **47**: 103-146.

Hare, S. R., Mantua, N. J. and Francis, R. C. (1999) Inverse production regimes: Alaskan and west coast salmon. *Fisheries* **24**: 6-14.

Hermann, A. J., Haidvogel, D. B., Dobbins, E. L. and Stabeno, P. J. (2002) Coupling global and regional circulation models in the coastal Gulf of Alaska. *Prog. Oceanogr.* **53**: 335-367.

Hollowed, A. B., Hare, S. R. and Wooster, W. S. (2001) Pacific-basin climate variability and patterns of Northeast Pacific marine fish production. *Prog. Oceanogr.* **49**: 257-282.

Jahncke, J., Coyle, K. O. and Hunt, G. L., Jr (2004) Seabird distribution, abundance and diets in the central and eastern Aleutian Islands. *Fish. Oceanog.*: *sub judice*.

Jordan, J. W. and Krumhardt, A. (2003) Postglacial climate and vegetation on the western Alaska Peninsula. *Alaska J. Anthro.* **1**: 16-33.

Jordan, J. W. and Maschner, H. D. G. (2000) Coastal paleogeography and human occupation of the lower Alaska Peninsula. *Geoarchaeology* **15**: 385-414.

Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K. C., Ropelewski, C., Wang, J., Leetmaa, A., Reynolds, R., Jenne, R. and Joseph, D. (1996) The NCEP/NCAR 40-year reanalysis project. *B. Am. Meteorol. Soc.* **77**: 431-477.

Ladd, C., Hunt, G. L., Jr., Mordy, C. W., Salo, S. A. and Stabeno, P. J. (2004) Marine environments of the central and eastern Aleutian Islands: physical mechanisms, nutrient availability and primary production. *Fish. Oceanog.*: *in press*.

Lagerloef, G. S. E. (1995) Interdecadal variations in the Alaska Gyre. *J. Phys. Oceanogr.* **25**: 2242-2258.

Loughlin, T. R. (1998) The Steller sea lion: A declining species. *Bios. Cons.* **1**: 91-98.

Mackas, D. L., Goldblatt, R. and Lewis, A. G. (1998) Interdecadal variation in developmental timing of Neocalanus plumchrus populations at Ocean Station P in the subarctic North Pacific. *Can. J. Fish. Aquat. Sci.* **55**: 1878-1893.

Mantua, N. (2004) Methods for detecting regime shifts in large marine ecosystems: a review with approaches applied to North Pacific data. *Prog. Oceanogr.* **60**: 165-182.

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M. and Francis, R. C. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* **78**: 1069-1079.

Marzban, C., Mantua, N. and Hare, S. R. (2004) A nonlinear principal components analysis of North Pacific indices of climate and biological variability. *in prep.*

Maschner, H. D. G. (2000) Catastrophic change and regional interaction: the southern Bering Sea in a dynamic world system. In *Identities and Cultural Contacts in the Arctic*. M. Appelt, J. Berglund and H. C. Gulløv (eds) Copenhagen, Denmark: Proc. Conf. Danish National Museum and Danish Polar Center, Nov. 30 - Dec. 2, 1999, pp. 252-265.

Maslowski, W., J. L. Clement, S. R. Okkonen, Stabeno, P. J. and Walczowski, W. (2004a) Modeling of ocean circulation and property transport from the Alaska Stream through eastern Aleutian Island passes: 1979-2001. *Fish. Oceanog.*: *sub judice*.

Maslowski, W. and Lipscomb, W. H. (2003) High-resolution simulations of arctic sea Ice during 1979-1993. *Polar Res.* **22**: 67-74.

Maslowski, W., Marble, D., Walczowski, W., Schauer, U., Clement, J. L. and Semtner, A. J. (2004b) On climatological mass, heat and salt transports through the Barents Sea and Fram Strait from a pan-Arctic coupled ice-ocean model simulation. *J. Geophys. Res.*: *in press*.

Maslowski, W. and Walczowski, W. (2002) On the circulation of the Baltic Sea and its connection to the Pan-Arctic region - a large scale and high-resolution modeling approach. *Boreas Env. Res.* **7**: 319-325.

Mathisen, O. A., Baade, R. T. and Lopp, R. J. (1962) Breeding habits, growth and stomach contents of the Steller sea lion in Alaska. *J. Mammal.* **43**: 469-477.

Merrick, R. L., Chumbley, M. K. and Byrd, G. V. (1997) Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. *Can. J. Fish. Aquat. Sci.* **54**: 1342-1348.

Merrick, R. L. and Loughlin, T. R. (1997) Foraging behavior of adult female and young-of-year Steller sea lions in Alaskan waters. *Can. J. Zool.* **75**: 776-786.

Milette, L. L. and Trites, A. W. (2003) Maternal attendance patterns of Steller sea lions (*Eumetopias jubatus*) from a stable and a declining population in Alaska. *Can. J. Zool.* **81**: 340-348.

Miller, A. J., Cayan, D. R., Barnett, T. P., Graham, N. E. and Oberhuber, J. M. (1994) The 1976-77 climate shift of the Pacific Ocean. *Oceanogr.* **7**: 21-26.

Miller, A. J., Neilson, D. J., Lorenzo, E. D., Kim, H.-J., Capotondi, A., Alexander, M. A., Bograd, S. J., Schwing, F. B., Mendelssohn, R., Hedstrom, K. and Muscgrave, D. L. (2004) Interdecadal changes in mesoscale eddy variance in the Gulf of Alaska circulation: Implications for the Steller sea lion decline. *Atmos-Ocean*: *sub judice*.

Miller, A. J. and Schneider, N. (2000) Interdecadal climate regime dynamics in the North Pacific Ocean: theories, observations and ecosystem impacts. *Prog. Oceanogr.* **47**: 355-379.

Mueter, F. and Norcross, B. L. (2000) Changes in species composition of the demersal fish community in nearshore waters of Kodiak Island, Alaska. *Can. J. Fish. Aquat. Sci.* **57**: 1169-1180.

Musgrave, D. L., Weingartner, T. J. and Royer, T. C. (1992) Circulation and hydrography in the northwestern Gulf of Alaska. *Deep-Sea Res.* **39**: 1499-1519.

National Research Council (2003) *The decline of the Steller sea lion in Alaskan waters: untangling food webs and fishing nets.* Washington, DC: National Research Council, 216pp.

Okkonen, S. R. (1992) The shedding of an anticyclonic eddy from the Alaskan Stream as observed by the Geosat altimeter. *Geophys. Res. Lett.* **19**: 2397-2400.

Okkonen, S. R. (1996) The influence of an Alaskan Stream eddy on flow through Amchitka Pass. *J. Geophys. Res.* **101**: 8839-8851.

Okkonen, S. R. and Maslowski, W. (2004) Numerical investigations of seasonal and interannual variability of shelf break hydrography in the western Gulf of Alaska. *J. Geophys. Res.*: *sub judice*.

Okkonen, S. R., Weingartner, T. J., Danielson, S. L., Musgrave, D. L. and Schmidt, G. M. (2003) Satellite and hydrographic observations of eddy-induced shelf-slope exchange in the northwestern Gulf of Alaska. *Journal of Geophysical Research* **108**: Art. No. 3033.

Onishi, H. (2001) Spatial and temporal variability in a vertical section across the Alaskan Stream and Subarctic Current. *J. Oceanogr.* **57**: 79-91.

Orensanz, J. M., Armstrong, J., Armstrong, D. and Hilborn, R. (1998) Crustacean resources are vulnerable to serial depletion - the multifaceted decline of crab and shrimp fisheries in the greater Gulf of Alaska. *Rev. Fish Biol. Fish.* **8**: 117-176.

Peterson, W. T. and Schwing, F. B. (2003) A new climate regime in northeast Pacific ecosystems. *Geophys. Res. Lett.* **30**: Art No. 1896.

Polovina, J. J., Mitchum, G. T. and Evans, G. T. (1995) Decadal and basin-scale variation in mixed layer depth and the impact on biological production in the Central and North Pacific, 1960-88. *Deep-Sea Res.* **42**: 1701-1716.

Reed, R. K. (1984) Flow of the Alaskan Stream and its variations. *Deep-Sea Res.* **31**: 369-386.

Reed, R. K. (1990) A year-long observation of water exchange between the North Pacific and Bering Sea. *Limnol. Oceanogr.* **35**: 1604-1609.

Reed, R. K., Muench, R. D. and Schumacher, J. D. (1980) On baroclinic transport of the Alaskan Stream near Kodiak Island. *Deep-Sea Res.* **27**: 509-523.

Reed, R. K. and Stabeno, P. J. (1997) Long-term measurements of flow near the Aleutian Islands. *J. Mar. Res.* **55**: 565-575.

Reed, R. K. and Stabeno, P. J. (1999) A recent full-depth survey of the Alaskan Stream. *J. Oceanogr.* **55**: 79-85.

Roads, J., Kanamitsu, M. and Stewart, R. (2002) CSE water and energy budgets in the NCEP-DOE Reanalysis II. *J. Hydrometeorol.* **3**: 227-248.

Roden, G. I. (1995) Aleutian Basin of the Bering Sea: Thermohaline, oxygen, nutrient, and current structure in July 1993. *J. Geophys. Res.* **100**: 13539-13554.

Rosen, D. A. S. and Trites, A. W. (2000) Pollock and the decline of Steller sea lions: testing the junk food hypothesis. *Can. J. Zool.* **78**: 1243-1250.

Rosen, D. A. S. and Trites, A. W. (2004) Satiation and compensation for short-term changes in food quality and availability in young Steller sea lions (*Eumetopias jubatus*, Schreber, 1776). *Can. J. Zool.*: *in press*.

Royer, T. C. (1981) Baroclinic transport in the Gulf of Alaska. II. Freshwater driven coastal current. *J. Mar. Res.* **39**: 251-266.

Royer, T. C., Grosch, C. E. and Mysak, L. A. (2001) Interdecadal variability of Northeast Pacific coastal freshwater and its implications on biological productivity. *Prog. Oceanogr.* **49**: 95-111.

Royer, T. C., Grosch, C. E., Weingartner, T. J. and Danielson, S. (2003) Ocean climate conditions during GLOBEC Northeast Pacific Program (NEP) Long Term Observation Program (LTOP). *EOS Trans. AGU* **84**: Ocean Sci. Meeting Suppl., Abstract OS31H-03.

Rudnick, D. L. and Davis, R. E. (2003) Red noise and regime shifts. *Deep-Sea Res.* **50**: 691-699.

Savinetsky, A. B., Kiseleva, N. K. and Khassanov, B. F. (2004) Dynamics of sea mammal and bird populations of the Bering Sea region over the last several millennia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **209**: 335–352.

Schumacher, J. D., Pearson, C. A. and Overland., J. E. (1982) On exchange of water between the Gulf of Alaska and Bering Sea through Unimak Pass. *J. Geophys. Res.* **87**: 5785-5795.

Sease, J. L. and Gudmundson, C. J. (2002) Aerial and land-based surveys of Steller sea lions (*Eumetopias jubatus*) from the western stock in Alaska, June and July, 2001 and 2002. *NOAA Tech. Memorand.* NMFS-AFSC-131, 45pp.

Sinclair, E. H. and Zeppelin, T. K. (2002) Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). *J. Mammal.* **83**: 973-990.

Soutar, A. and Isaacs, J. D. (1969) A history of fish populations inferred from fish scales in anaerobic sediments off California. *Calif. Mar. Res. Comm. CalCOFI* **13**: 63-70.

Stabeno, P. J., Bond, N. A., Hermann, A. J., Kachel, N. B., Mordy, C. W. and Overland, J. E. (2004) Meteorology and oceanography of the Northern Gulf of Alaska. *Cont. Shelf Res.* **24**: 859-897.

Stabeno, P. J., Schumacher, J. D. and Ohtani, K. (1999) The physical oceanography of the Bering Sea. In *Dynamic of the Bering Sea*. T. R. Loughlin and K. Ohtani (eds) Fairbanks: University of Alaska Sea Grant Publication AK-SG-99-03, pp. 1-28.

Steele, J. H. (2004) Regime shifts in the ocean: reconciling observations and theory. *Prog. Oceanogr.* **60**: 135-141.

Strom, S. L., Olson, M. B., Maeri, E. L. and Mordy, C. W. (2004) Cross-shelf gradient in iron limitation structures in coastal Gulf of Alaska phytoplankton communities. *Mar. Ecol. Prog. Ser.*: *sub judice*.

Thompson, R. E. (1972) On the Alaskan Stream. *J. Phys. Oceanogr.* **2**: 363-371.

Thorsteinson, F. V. and Lensink, C. J. (1962) Biological observations of Steller sea lions taken during an experimental harvest. *J. Wildl. Manage.* **26**: 353-359.

Trites, A. W. (2003) Food webs in the ocean: who eats who and how much? In *Responsible Fisheries in the Marine Ecosystem*. M. Sinclair and G. Valdimarsson (eds) Wallingford: FAO, Rome and CABI Publishing, pp. 125-143.

Trites, A. W. and Donnelly, C. P. (2003) The decline of Steller sea lions in Alaska: a review of the nutritional stress hypothesis. *Mamm. Rev.* **33**: 3-28.

Trites, A. W. and Larkin, P. A. (1996) Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: how many were there? *Aquat. Mamm.* **22**: 153-166.

Trites, A. W., Livingston, P. A., Mackinson, S., Vasconcellos, M. C., Springer, A. M. and Pauly, D. (1999) Ecosystem change and the decline of marine mammals in the eastern Bering Sea: testing the ecosystem shift and commercial whaling hypotheses. Fisheries Centre Research Reports, No. **7(1):** 106pp.

Trites, A. W. and Porter, B. T. (2002) Attendance patterns of Steller sea lions (*Eumetopias jubatus*) and their young during winter. *J. Zool., Lond.* **256**: 547-556.

Warren, B. A. and Owens, W. B. (1988) Deep currents in the central Subarctic Pacific Ocean. *J. Phys. Oceanogr.* **18**: 529-551.

Wilderbuer, T. K., Hollowed, A. B., Ingraham Jr., W. J., Spencer, P. D., Connors, M. E., Bond, N. A. and Walters, G. E. (2002) Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Bering Sea. *Prog. Oceanogr.* **55**: 235-247.

Winship, A. J. and Trites, A. W. (2003) Prey consumption of Steller sea lions (*Eumetopias jubatus*) off Alaska: How much prey do they require? *Fish. Bull.* **101**: 147-167.

Winship, A. J. and Trites, A. W. (2004) Risk of extirpation of Steller sea lions in the Gulf of Alaska and Aleutian Islands: Evaluating alternative hypotheses for the population decline in western Alaska using a Bayesian population viability analysis. *Ecol. App.*: *sub judice*.

Winship, A. J., Trites, A. W. and Rosen, D. A. S. (2002) A bioenergetic model for estimating the food requirements of Steller sea lions (*Eumetopias jubatus*) in Alaska, USA. *Mar. Ecol. Prog. Ser.* **229**: 291-312.

Wooster, W. S. and Zhang, C. I. (2004) Regime shifts in the North Pacific: early indicators of the 1976-77 event. *Prog. Oceanogr.* **60**: 183-200.

York, A. E., Merrick, R. L. and Loughlin, T. R. (1996) An analysis of the Steller sea lion metapopulation in Alaska. In *Metapopulations and Wildlife Conservation*. D. R. McCullough (ed.) Washington: Island Press, pp. 259-292.

LEGENDS

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.

Figure 2. Conceptual model showing how sea lion numbers might be affected by ocean climate through bottom-up processes. 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.

Figure 3. Diets, population trends and numbers of 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 1990-2002. Trend and numbers were calculated independently for pups and non-pups. Pup and non-pup trends were then averaged and counts were summed. A population trend (λ) <1 indicates a decline. Solid vertical lines denote distinct geographic shifts in population sizes and trends by fitting loess curves. 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 the area of each circle). The frequencies sum to 100% and were calculated for the 9 principal species shown as well as for less important species not shown (grouped into 6 prey types: flatfish, forage fish, gadids, hexagrammids, other, rockfish). The zig-zag lines indicate seasonal geographic changes in diet. The demarcations for summer were determined through cluster analysis by Sinclair and Zeppelin (2002), while the winter demarcations were determined visually.

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 ≥ 0.75 are red). Regions with the highest suitability had the highest long-term average census counts from 1956 to 2002. From Gregr and Trites (2004).

Figure 5. Nonlinear principal component analysis results from a multivariate dataset of 22 physical indices representing both large-scale and local environmental processes. The error bars for the NLPC scores are obtained from a "jittering" technique that involves the introduction of small errors into the data matrix prior to computation of the NLPCs. From Marzban *et al*. (2004).

Figure 6. 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).

Figure 7. (top) Mean winter (Dec-May) Ekman pumping (CI = 0.5 x 10^{-4} cm/s) in the Gulf of Alaska for the period 1964-75 from the NCAR/NCEP reanalysis. (bottom) Change in mean winter Ekman pumping (CI = 0.1 x 10^{-4} cm/s) for the period 1977-97 relative to 1964-75. Blue indicates downward pumping. From Capotondi *et al*. (2004).

Figure 8. Modeled Gulf of Alaska coastal discharge based on National Weather Service temperature and precipitation data (blue) with glacial ablation (red) since 1980 and the same model using NCEP Reanalysis data (magenta). A 5-year Butterworth filter is applied to the data.

Figure 9. Long-term changes in the amplitude and phase of the seasonal cycle of coastal freshwater discharge in the Gulf of Alaska.

Figure 10. Wavelet analysis of the Gulf of Alaska coastal discharge, revealing changes in the low frequency variations of the signal.

Figure 11. 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*. (2004).

Figure 12. Modeled variance (CI = 100 cm^2/s^2) of the anomalous monthly mean surface currents for the 10-year epochs 1967-1976 (top) and 1979-1988 (middle), and the difference between the two epochs (bottom). Anomalies are defined with respect to the monthly mean seasonal cycle of the respective 10-year epoch. From Miller *et al.* (2004).

Figure 13. (a) Large zooplankton (mmol m^{-3}) during 1977-1998 minus 1960-1976 in a physical-ecosystem ocean model's top layer during May when the large zooplankton amount peaks. (b) The biomass of the four plankton classes (mmol m^{-3}) in each calendar month during 1960-1976 (solid lines) and 1977-98 (dashed lines) in the Gulf of Alaska region [46ºN-58ºN, 160ºW-140ºW, indicated by the box in (a)].

Figure 14. March mixed layer depth (m) in 1977-1998 minus 1960-76 from an ocean model hindcast.

Figure 15. Depth-averaged (0-100 m) model velocity (cm/s) snapshots near the Amukta Pass from the end of (a) March and (b) May of 1984 showing effect of a mesoscale eddy modeled within the Alaskan Stream on the flow across the Amukta Pass. The green solid contours represent bathymetry (m). (c) The salinity difference (ppt) along the section marked "Cross Slope" between eddy (May) and no-eddy (March) conditions. From Maslowski and Okkonen (2004a).

Figure 16. Nonlinear principal component analysis results from a multivariate dataset of 45 biotic indices (fishery and survey records) from the Bering Sea and Gulf of Alaska from 1965-2001. Error bars computed as in Figure 5. From Marzban *et al.* (2004).

Figure 17. 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. and While a "trend" often means a linear trend, Kendall's tau assesses the trend nonlinearly (though monotonically). The Z-statistic assesses the statistical significance of that trend such that if Z $\geq$ 2.575 then the hypothesis that the true tau is zero can be rejected with 99% confidence. From Marzban *et al.* (2004).

Figure 18. Underway sea surface salinity (psu) during 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*. (2004).

Figure 19. Mean abundance of zooplankton species versus station seasonal influences and water mass influences on zooplankton species composition. Pass Names: Um1 = Unimak (May), Ak1 = Akutan (May), Tng = Tananga (June), Sgm = Seguam (June), Smg = Samalga (June), Un2 = Unimak (June), Ak2 = Akutan (June). The error bars are 95% confidence intervals for power transformed mean abundance in the respective passes. The broad error bars are due to the very patchy distribution of these organisms, especially in the passes where tidally generated eddies can physically concentrate or disperse zooplankton. From Coyle (2004).

Figure 20. Seabird abundances along the Aleutian Islands from data collected in 2001 and 2002. From Jahncke *et al*. (2004).

Figure 21. Paleoproductivity indicators over the last 300 years derived from two cores in the Gulf of Alaska (GAK 4 site central gulf shelf) and Bering Sea (Skan Bay). Map in lower right shows locations. Two productivity indicators are plotted for each core: opal, which represents diatom productivity (blue) and delta 13C of organic matter (red), which represents all organic productivity. Increases in productivity would be indicated by an increase in either indicator. From Finney (2004).

Figure 22. Long term trends in the percentage of Steller Sea lions harvested by Alaska Peninsula Aleut in relation to their total sea mammal harvest. The Aleut harvested resources in proportion to their actual distribution on the landscape. This chart shows the percentage difference from the mean harvest over the last 4000 years. Climate data based pollen cores and other data of the Alaska Peninsula Project (Jordan and Krumhardt, 2003; Jordan and Maschner, 2000) and data provided by Finney.

Figure 23. 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 (see Fig. 2 for further details).