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A CRITICAL REVIEW OF THE REGIME SHIFT–"JUNK FOOD"–NUTRITIONAL STRESS HYPOTHESIS FOR THE DECLINE OF THE WESTERN STOCK OF STELLER SEA LION

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ABSTRACT

Steller sea lions (*Eumetopias jubatus*) in the central and western Gulf of Alaska, Aleutian Islands, and Bering Sea have declined by 80% in the last 30 yr. One hypothesis for the decline in this western Steller sea lion population is that a climate regime shift in 1976–1977 changed the species composition of the fish community and reduced the nutritional quality (energy density) of the sea lion prey field. This in turn led to nutritional stress and reduced individual fitness, survival, and reproduction of sea lions. Implications of this regime shift–"junk food" hypothesis are that (1) the recruitment and abundance of supposed high quality species (*e.g.*, Pacific herring, *Clupea pallasi*) decreased while those of supposed low quality (*e.g.*, species in the family Gadidae) increased following the regime shift, (2) Steller sea lion diets shifted in response to this change in fish community structure, and (3) a diet composed principally of gadids (*e.g.*, walleye pollock, *Theragra chalcogramma*) is detrimental to sea lion fitness and survival. We examine data relating to each of these implications and find little support for the hypothesis that increases in the availability and consumption of gadids following the regime shift are primarily responsible for the decline of the western population of Steller sea lion.

Key words: Steller sea lions, *Eumetopias jubatus*, regime shifts, population decline, nutritional stress, diet, prey quality, energy density.

The ongoing decline of Steller sea lions (*Eumetopias jubatus*) in western Alaska has persisted over three decades (Braham *et al.*1980, Sease and Gudmundson 2002). Steller sea lions were designated as threatened in 1990 under the U.S. Endangered Species Act (ESA) following evidence of a major decline in their abundance throughout most of their entire range, but most acutely in the core region from the Kenai Peninsula to Kiska Island (Fig. 1) (Braham *et al.* 1980, Merrick *et al.* 1987, Loughlin *et al.* 1992). The decline was first observed in the eastern Aleutian Islands in the early 1970s (Braham *et al.* 1980), but then spread eastward to Prince William

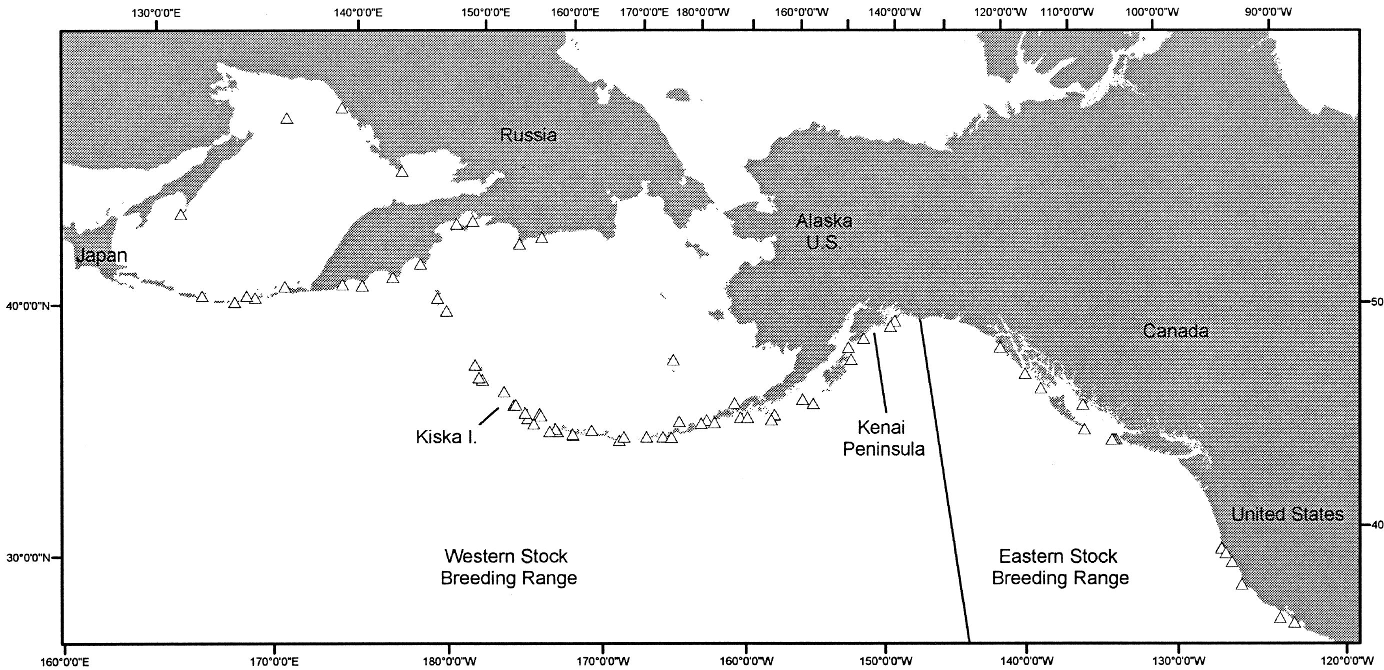

Figure 1. Locations of Steller sea lion (*Eumetopias jubatus*) rookeries within the range of the western and eastern stocks (separated at 144°W) in the North Pacific Ocean. The Kenai Peninsula–Kiska Island portion of the western stock's range is labeled.

Sound and westward through Russia (Merrick *et al.* 1987, Loughlin *et al.* 1992). Index counts of adult and juvenile Steller sea lions indicated that the population declined by over 70% from the early 1970s to 1990. The average annual rate of decline peaked between 1985 and 1989 at approximately 15% (Loughlin *et al.* 1992). From 1990 to 2000, the decline continued, but only at about 5% per year, while the survey in 2002 suggested that it may have, at least temporarily, abated in many areas (Sease and Gudmundson 2002).

What has changed so dramatically in the ecosystems of the Gulf of Alaska, Aleutian Islands, and the Bering Sea that they are able to support only 10%–20% of the Steller sea lions that they supported as recently as the 1960s and 1970s? The cause of the decline of Steller sea lions has been the subject of tens of millions of dollars worth of scientific research (Ferrero and Fritz 2002) and numerous reviews by academics (Trites and Larkin;[1] Alaska Sea Grant Program;[2,3] NRC 1996, 2003) and governmental panels (Kruse *et al.* 2001; NMFS 1996, 1998, 2000, 2001, 2003). From these reviews, similar hypotheses for the decline have been assembled, which were organized by the National Research Council (NRC 2003) into top-down and bottom-up groups of hypotheses. Top-down mechanisms kill sea lions independently of the environment's ability to support them, usually involve direct mortality and are easier to detect and, if they are human-related, solve. Potential top-down causes of increased sea lion mortality are predation, principally by killer whales (*Orcinus orca*) (Barrett-Lennard *et al.*,[4] Estes *et al.* 1998, Springer *et al.* 2003), incidental takes in fishing gear, subsistence harvest, illegal shooting, and the density-independent effects of pollution or certain diseases (see review of Burek *et al.*[5]). Bottom-up forces erode the sea lion carrying capacity and operate in a more indirect manner on individuals. In addition, they are harder to detect and considerably more difficult to ameliorate (if they are not human-related). Bottom-up hypotheses for the sea lion decline include climate-shift-induced changes in the species composition and nutritional quality of the sea lion prey community, fishery-induced reductions in the abundance and distribution of prey, and the wasting effects of pollutants or diseases. Bottom-up forces affect sea lions by "unbalancing" their energy budgets leading to nutritional stress: the energy obtained through prey consumption does not meet the energy demands of foraging, reproduction, lactation, movement, and all other aspects of normal sea lion behavior and life

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[1] Trites, A. W., and P. A. Larkin. 1992. The status of Steller sea lion populations and the development of fisheries in the Gulf of Alaska and Aleutian Islands. A report to the Pacific States Marine Fisheries Commission pursuant to NOAA Award No. NA17FD0177. Fisheries Centre, University of British Columbia, Vancouver, BC, Canada V6T 1Z4.

[2] Alaska Sea Grant Program. 1993. Is it food?: Addressing marine mammal and seabird declines. Workshop summary. University of Alaska Sea Grant Program. AK-SG-93-01, Fairbanks, AK. 59 pp.

[3] Alaska Sea Grant Program. 2002. Steller sea lion decline: Is it food? II. University of Alaska Sea Grant Program, AK-SG-02-02, Fairbanks, AK. 80 pp.

[4] Barrett-Lennard, L. G., K. Heise, E. Saulitis, G. Ellis and C. Matkin. 1995. The impact of killer whale predation on Steller sea lion populations in British Columbia and Alaska. Report for the North Pacific Universities Marine Mammal Research Consortium, Fisheries Centre, University of British Columbia, Room 18, Hut B-3, 6248 Biological Sciences Road, Vancouver, BC V6T 1Z4, Canada. 66 pp.

[5] Burek, K. A., F. M. D. Gulland, G. Sheffield, D. Calkins, E. Keyes, T. R. Spraker, A. W. Smith, D. E. Skilling, J. Evermann, J. L. Stott and A. W. Trites. 2003. Disease agents in Steller sea lions in Alaska: A review and analysis of serology data from 1975–2000. Fisheries Centre Reports, University of British Columbia 11(4). 26 pp.

history. While reducing fitness and potentially reducing rates of survival or reproduction, nutritional stress could also increase the vulnerability of individuals to top-down forces, particularly predation.

During the 30 yr of population decline, both top-down and bottom-up forces may have affected the sea lion population. From the 1960s through the 1980s, over 20,000 Steller sea lions were killed as a result of being accidentally caught during groundfish fishing operations (Loughlin and Nelson 1986, Perez and Loughlin 1991). However, between 1990 and 2001, estimated kills associated with incidental catches in the groundfish fishery have totaled less than 300 (Perez 2003). In addition, approximately 45,000 pups were harvested in the eastern Aleutian Islands and Gulf of Alaska between 1963 and 1972 (Pascual and Adkison 1994). Numbers of sea lions shot illegally may also have been high in the 1980s (Trites and Larkin[1]). However, based on modeling results, Pascual and Adkison (1994) concluded that direct mortality sources alone were not responsible for the decline experienced by the sea lion population in the 1970s and 1980s.

Bottom-up forces were also affecting western Steller sea lion populations in the 1970s and 1980s (Calkins and Goodwin;[6] Pitcher *et al.* 1998). Based on differences in size at age, sea lion growth rates (Calkins and Goodwin[6]) were likely lower in the 1980s than in the 1970s in the central Gulf of Alaska and there was an indication that pregnancy rates were lower as well (Pitcher *et al.* 1998). Consequently, during and following a period when direct sources of sea lion mortality were likely at high levels, the carrying capacity was apparently declining as well; otherwise, there would have been no density-dependent responses in the population. The reduction in carrying capacity may have continued through the 1990s, considering that the population declined by 5% per year (Sease and Gudmundson 2002) even as the rates of human-related direct mortality were greatly reduced.

The relative importance of bottom-up and top-down forces on the current western population of Steller sea lions remains an area of considerable controversy and uncertainty. The NRC (2003) concluded that top-down forces, specifically predation by killer whales, are currently more likely preventing recovery than bottom-up forces, but they could not completely eliminate nutritional stress as a factor either. They based this conclusion principally on data collected in the 1990s that suggested that sea lions were not nutritionally stressed. Data considered by the NRC, which were acknowledged to be limited in sample size, geographic range and seasonality, consisted of comparisons of birth mass, pup growth rate, body condition, field metabolic rate, foraging duration and range, diet diversity, and total levels of groundfish biomass between eastern (not declining) and western (declining) stocks of sea lions. These stocks are reproductively isolated, have genetically diverged, and inhabit different oceanographic regions (Bickham *et al.* 1996, 1998, Hare *et al.* 1999, NMFS 2000). There is no reason to assume that measures (*e.g.*, birth mass, foraging duration) from the two stocks would be the same even if both were stable or increasing in abundance. In addition, data were rarely collected on randomly chosen individuals that would represent a cross-section of the population, but more likely on "healthy" animals selected for longitudinal studies (*e.g.*, foraging studies with satellite-linked time-depth recorders). Concentration of studies at rookeries further biases results toward those successful animals that returned to give birth and mate.

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[6] Calkins, D. G., and E. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Unpublished Report, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518. 76 pp.

All of these factors could lead to the erroneous conclusion that the western stock was not nutritionally stressed in the 1990s, particularly when the non-pup population and pup production declined by 30% and 42%, respectively, in the decade (Sease and Gudmundson 2002).

Bottom-up forces leading to nutritional stress could have contributed significantly to the persistent decline of the 1990s, as well as being major impediments to recovery. Reductions in prey abundance, availability or quality, are seen as the principal causes of bottom-up nutritional stress in Steller sea lions (Alverson 1992; NRC 1996; NMFS 2000; Rosen and Trites 2000*a*, *b*; Hunt *et al.* 2002; Trites and Donnelly 2003). If sea lions are currently nutritionally stressed, what caused reductions in prey abundance, availability or quality? Several factors have been advanced, including both natural and human-related sources. One natural factor that we investigate here is a shift in the climate of the North Pacific in 1976–1977 (Trenburth and Hurrell 1994, Hare and Mantua 2000) that induced changes in the structure of the fish community that led to a change in sea lion diets to one deficient in energy (Alverson 1992; Rosen and Trites 2000*a*, *b*; Hunt *et al.* 2002; Trites and Donnelly 2003). This is called the regime shift–"junk food" hypothesis (see Rosen and Trites 2000*a*). Alternative factors that could have led to nutritional stress in Steller sea lions, including increases in fishing effort within sea lion foraging habitats (NMFS 1998, 2000, 2001), will not be discussed further.

In this paper, we review data upon which conclusions have been made in support of the regime shift–"junk food" hypothesis. We analyze the evidence for changes in fish community structure and Steller sea lion diets related to regime shifts. Our objective is not to describe the general relationship between climatic and oceanographic processes and trends in fish abundance; that is well beyond the scope of this paper. Rather, our objective is to analyze the evidence linking the regime shift of 1976–1977 with changes in abundance of sea lion prey species, specifically members of the family Gadidae (pollock, *Theragra chalcogramma*, and Pacific cod, *Gadus macrocephalus*), and those grouped together into the "forage fish" complex (Pacific herring, *Clupea pallasi*; capelin, *Mallotus villosus*; eulachon, *Thaleichthys pacificus*; and Pacific sand lance, *Ammodytes hexapterus*; Winship and Trites 2003). It is the hypothesized changes in abundance of these species (all of which are technically "forage" fish), related to the regime shift of 1976–1977, that led to suboptimal sea lion diets and decreases in their population sizes according to the regime shift–"junk food" hypothesis. In addition, we review information on the nutritional value and energy content of sea lion prey and discuss biochemical transformations that occur in fish post-mortem (particularly Gadidae) that may have affected the results of certain captive feeding trials. We conclude that, while Steller sea lions may be nutritionally stressed currently (Trites and Donnelly 2003), the existing information does not support the regime shift–"junk food" hypothesis as the primary source for that stress. We note that in the formulation of the hypothesis, some data have been overlooked, some have been used to support conclusions without considering their caveats or weaknesses, and in some cases, conclusions have gone beyond the scope of data.

Trites and Donnelly (2003) define nutritional stress as a "negative physiological and/or behavioral state resulting from sub-optimal quantity or quality of food available to an animal." As such, nutritional stress in individual animals could be caused by food (*i.e.*, energy) shortages even though the prey consumed has all required nutrients. Food shortages could stem from absolute reductions in overall biomass of prey on local or ecosystem-wide scales, or from changes in the composition of the prey community if species deficient in energy increase in abundance. Alternatively, there may be ample food resources, but because of changes in the composition of the prey field or distribution of species, the sea lion diet is deficient in one or more nutrients (rather than energy). With respect to the cause of the decline of the western Steller sea lion, food or energy shortages have largely been thought responsible for causing nutritional stress, rather than a deficiency of one or more nutrients, although the latter has not been discounted (Merrick *et al.* 1997).

In our review of the regime shift–"junk food" hypothesis, it is also important to differentiate between two types of food shortage-related nutritional stress to which Steller sea lions may be subjected. Otariid pinnipeds have traits to cope with both acute (*e.g.*, severe, short-term) and chronic (*e.g.*, moderate, long-term) nutritional stress. These include long reproductive lives (female Steller sea lions become mature at 3–8 yr of age and can live 30 yr, but pregnancy rates may drop after 20 yr of age; Pitcher and Calkins 1981), extended maternal care of the pup (up to 4 yr, but with most weaned by age 2; Pitcher and Calkins 1981, Mamaev and Burkanov,[7] Pitcher *et al.*[8]), and a diet composed of a wide variety of fish and cephalopods (Sinclair and Zeppelin 2002). Breeding male Steller sea lions face acute mass loss each summer while they fast holding territories on rookeries, which may contribute to their rather short reproductive lifespans (5–9 yr) compared to females (Thorsteinson and Lensink 1962, Pitcher and Calkins 1981). Acute nutritional stresses associated with large El Niño events in 1981–1983 and 1997–1998 in the eastern Pacific Ocean caused high rates of pup mortality in northern fur seals (*Callorhinus ursinus*, DeLong and Antonelis 1991, Melin *et al.* 2002) and California sea lions (*Zalophus californianus*, Francis and Heath 1991). However, despite these acute pup mortality events, both production and survival of northern fur seal pups in California rebounded within 3–4 yr of the 1997–1998 El Niño event (Melin *et al.* 2002) and the California sea lion population grew at an average annual rate of 8% from the mid-1970s to the early 1990s (NMFS 1995). Consequently, otariid populations can thrive despite occasionally experiencing periods of severe, short-term nutritional stress (Bowen *et al.* 2002).

Chronic nutritional stress is much harder to study in free-ranging animals. Of the several body condition and blood chemistry parameters that can be measured, almost all are non-specific indicators of nutritional stress and differences between stressed and non-stressed animals are likely to be small. Secondly, obtaining a representative cross-section of the population is difficult in Steller sea lions and other pinnipeds. The effects of small magnitude, but extended prey shortages would be hard to detect because affected individuals might die or spend less time ashore and not be observed among the sampled population (Malavear 2002). Other effects of chronic nutritional stress, such as delayed maturation, decreased fecundity or decreased growth rate, would be detected only in studies conducted on large numbers of animals over long time periods. Juvenile age classes may be particularly sensitive to chronic nutritional stress, especially if the stress were caused by decreases in food availability (Malavear

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[7] Mamaev, E. G., and V. N. Burkanov. 2004. How long do Steller sea lions drink milk? Sea Lions of the World Symposium, Alaska Sea Grant, Anchorage, AK, October 2004. Abstract available at: http://www.uaf.edu/seagrant/Conferences/sealions/abstracts.pdf

[8] Pitcher, K. W., G. W. Pendleton and T. S. Gelatt. 2004. Estimation of weaning status of juvenile Steller sea lions using mark-resight models. Sea Lions of the World Symposium, Alaska Sea Grant, Anchorage, AK, October 2004. Abstract available at: http://www.uaf.edu/seagrant/Conferences/sealions/abstracts.pdf

2002). Juveniles have proportionally less energy reserves and are more naïve foragers than adults (Loughlin *et al.* 2003). Three features of the decline of Steller sea lions that lend support for the involvement of factors (*e.g.*, food shortage) that would cause chronic nutritional stress (Trites and Donnelly 2003) are (1) smaller size at age for female Steller sea lions in the central Gulf of Alaska in the 1980s than the 1970s (Calkins and Goodwin[6]); (2) a decline in juvenile survival in the 1980s (York 1994), and (3) a reduction in adult female fecundity in the 1990s (Holmes and York 2003).

Regime Shifts and Interannual Variability

It has been commonly reported that the North Pacific Ocean underwent a regime shift in 1976–1977, from a predominately cool to a warm climate (see review by Hare and Mantua 2000). The shift itself is defined as a step change (Hare and Mantua 2000) in one or more of the following oceanographic or atmospheric indices (Benson and Trites 2002): (1) Pacific Decadal Oscillation (PDO), which is the first empirical orthogonal function of the average Pacific Ocean sea surface temperature (SST) north of 20°N from November through March (Mantua *et al.* 1997); (2) Aleutian Low Pressure Index (ALPI), which is the sum of the area in the North Pacific Ocean with average monthly sea level air pressure $<$1,000 mb in December through May (Beamish and Bouillon 1993); and (3) North Pacific Index (NPI), which is the area-weighted mean sea level air pressure from November through March in the area bounded by 30°–65°N, 140°–160°W (Trenburth and Hurrell 1994). Each of these indices is based on the integration of an oceanographic or atmospheric measurement (*e.g.*, SST or sea level air pressure) over a relatively large area over a relatively long period of time (at least 5 mo). As such, a single value serves as an index of annual atmospheric or oceanographic conditions over the North Pacific Ocean, and its value lies in the long time series of such measurements that are available.

Changes in biological communities of the North Pacific Ocean have been linked to regime shifts (Brodeur and Ware 1992, Gargett 1997, Francis *et al.* 1998, Anderson and Piatt 1999, Hare *et al.* 1999, Hare and Mantua 2000, Benson and Trites 2002, Conners *et al.* 2002). While the 1976–1977 regime shift has been the most studied (largely because of the availability of other biological time series; Hare and Mantua 2000, Benson and Trites 2002), the North Pacific Ocean is thought to have undergone similar climate shifts in the early 1920s (from cool to warm) and the mid-1940s (from warm to cool; Hare *et al.* 1999). Therefore, climatic regimes as defined by oceanic and atmospheric indices may persist for between 20 and 30 yr (Hare and Mantua 2000). Whether there are decadal-scale periods with particular physical and biological attributes in the North Pacific has recently been called into question (Rudnick and Davis 2003), but even if physical regimes are non-random, mechanisms that tightly link state changes in ocean physics to biological production have yet to be clearly described (Baumann 1998, McGowan *et al.* 1998).

Within a particular climate regime, there is considerable interannual variability in oceanic conditions. For instance, Stabeno *et al.* (2001) described the physical conditions that occurred in 1997 and 1998 in the eastern Bering Sea shelf and put the variability observed in those years into historical context. Surface water temperatures during the winter of 1997 were some of the coldest on record, but were followed by some of the warmest summer water temperatures. Furthermore, Hunt *et al.* (2002) described alternating anomalously cold (1995, 1997, and 1999) and warm years (1996, 1998, and 2000) on the southeastern Bering Sea shelf; the first two years in each of these series are in the same regime (assuming the regime shifted again in

1999; Hare and Mantua 2000). Therefore, while smoothed time-series of large time/area averages of temperature or atmospheric pressure may cycle at decadal scale frequencies, the interannual variability in thermal stratification and mixing can be greater than that between regimes (Overland *et al.* 1999, Stabeno *et al.* 2001, Hunt *et al.* 2002). Oceanographic conditions within a year are more likely to determine its biological character (*e.g.*, recruitment strength of fish species; Wespestad *et al.* 2000), not the regime to which the year may be assigned. Indeed, long-term fisheries oceanographic studies of walleye pollock (*Theragra chalcogramma*) recruitment in the Gulf of Alaska have revealed that the probability of large year-class production increases when precipitation in spring is high, wind mixing in winter is high but low in spring, and when transport through Shelikof Strait in spring is moderate (Megrey *et al.* 1996). Conditions favoring poor and good recruitment in successive years have occurred just as often as conditions favoring poor recruitment in both years (Dorn *et al.* 2002). Therefore, while certain oceanographic or atmospheric indices may generally describe general physical states, production in biological systems is more linked to environmental conditions at particular times and places.

Hypothesized Changes in Fish Community Structure

Two sources of evidence were used by Hunt *et al.* (2002) and Trites and Donnelly (2003) to conclude that the structure of the fish communities of the eastern Bering Sea and the North Pacific Ocean changed from one dominated by the "forage fish" complex to one dominated by gadids and flatfish (Pleuronectidae). The first is information about the fish communities themselves from a series of nearshore surveys conducted in the Gulf of Alaska (Anderson and Piatt 1999) and a mass-balance modeling exercise of the eastern Bering Sea ecosystem (Trites *et al.* 1999). The second is food habits information of marine piscivores, particularly Steller sea lions and northern fur seals.

Fish Communities

We analyzed trends in pollock and Pacific herring abundance and compared them with the conclusions reached by Anderson and Piatt (1999) and others in the Gulf of Alaska, and by Trites *et al.* (1999) and Hunt *et al.* (2002) in the eastern Bering Sea. Pollock and Pacific herring were chosen because considerable information is available on their abundance, age structure, and distribution (since they are commercially fished); they are eaten by Steller sea lions; and because of the considerable literature and assertions made regarding differences in their nutritional "quality" (Rosen and Trites 2000*a*, *b*; Trites and Donnelly 2003). Time series of abundance, catch and recruitment of pollock and Pacific herring that spanned at least two climatic regimes were used as indicators of the type of changes that supposedly accompanied the 1976–1977 regime shift. While it would have been preferable to also include information on osmerids, squid (primarily species in the family Gonaditae), octopus (*Octopus dofleini*), and other sea lion prey, little is known about changes in their absolute or relative abundance because of the lack of surveys and commercial fisheries that target them (Walters 1996, 2000).

Gulf of Alaska—From an analysis of nearshore shrimp trawl survey data collected by the National Marine Fisheries Service and the Alaska Department of Fish and Game from 1953 to 1997, Anderson and Piatt (1999) concluded that the 1976–1977 regime shift "triggered a reorganization of community structure in the Gulf of

Alaska ecosystem.” Shrimp trawl surveys were conducted primarily in nearshore areas on the southern and eastern sides of Kodiak Island, and along a portion of the south side of the Alaska Peninsula (Anderson and Piatt 1999). However, this was not a standardized survey in which the same areas were sampled each year, nor did it encompass the entire continental shelf, on which many of the species that Anderson and Piatt discuss range during the May through October time frame of their surveys. These two factors limit the utility of this survey time series to detect Gulf of Alaska-wide changes in fish community structure or changes in the overall abundance of individual species. Furthermore, since the surveys were conducted primarily in summer and early fall, they do not represent distributions of fish during winter and early spring, during which prey availability to sea lions is thought to be most critical for weaning juveniles and pregnant females (NMFS 1998, 2000).

Anderson and Piatt (1999) summarized the shrimp-trawl data in two ways. The first is a time series of the proportions of the total catch comprised by shrimp, gadids, flatfish and other species from 1953 to 1997 (their fig. 2). The second is smoothed (3-yr running averages) time series of catch per unit effort (CPUE) for 35 individual species or species groups from 1972 to 1997 (their fig. 3). We compared trends in pollock and Pacific herring populations as revealed by the shrimp-trawl data with those from age-structured assessments of the same populations (Williams and Quinn 2000, Dorn *et al.* 2002).

Pollock—The Gulf of Alaska (GOA) pollock stock assessment uses an age-structured model that employs fishery and survey-derived information to reconstruct the population age structure, abundance, and biomass from the mid-1960s to the present for the purposes of setting catch quotas (Dorn *et al.* 2002). The biomass time series (Fig. 2) from this assessment shows that the GOA pollock population was relatively small in the mid-1960s, increased substantially (approximately 4-fold) and leveled off in the mid-1970s (prior to the regime shift), increased again through the early 1980s, and declined over the last 20 yr. The period of greatest abundance during this 30+ yr time series was in 1981–1982 following the series of large year classes spawned in 1975–1979 (Fig. 2).

The increase in the GOA pollock population between the mid-1960s and mid-1970s occurred because strong year classes were spawned in 1967 and from 1969 to 1972 (Fig. 2). This increase in pollock prior to the regime shift was first noted by Ronholt *et al.* (1978) and later by Alton *et al.* (1987), who postulated that pollock may have been replacing the Pacific ocean perch (*Sebastes alutus*) population that was severely depleted due to overfishing. Indeed, of the 10 year classes spawned prior to the 1976–1977 regime shift, eight were larger than the mean year class size from 1967 to 1999, a proportion significantly different from random (50%) at the $P < 0.1$ level (Table 1). After the regime shift, the frequency of large year classes dropped to 46% (not significantly different from random) between 1977 and 1989, and further to 20% ($P < 0.1$) between 1990 and 1999 (Table 1). In addition, the frequency of producing smaller than average year classes increased through time along with the magnitude of the deviations below the mean (Fig. 2). This pattern suggests that conditions in 1967–1976 were the most favorable to the production of average to above-average size year classes of pollock in the GOA in the last 30 yr. While some of the decline between 1977 and 1989 may have been a density-dependent response, this does not seem likely between 1990 and 1999 given the similarity in biomass levels to those observed prior to the regime shift (Fig. 2). Other factors, such as the abundance of groundfish predators in the ecosystem (Bailey 2000) or fishery effects on spawning aggregations (NMFS 2000), could be having a greater impact on

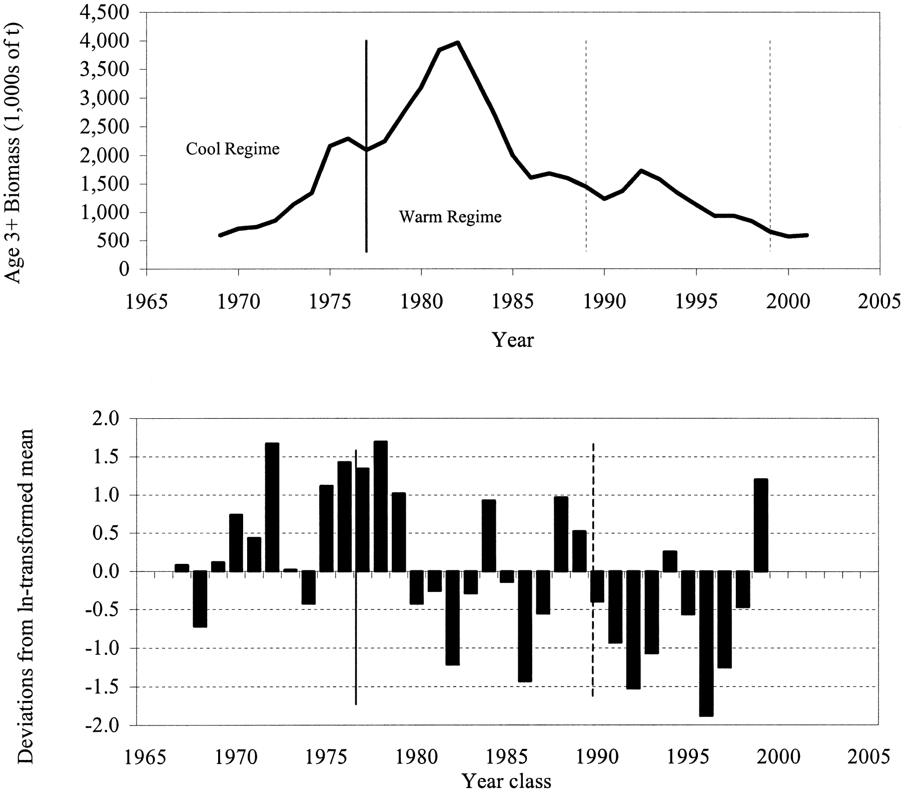

Figure 2. Gulf of Alaska pollock biomass (top: age 3+) and deviations of ln-transformed recruitment (numbers at age 3) from the 1967–1999 mean (bottom). Data from Dorn *et al.* 2002. Vertical lines separate climate regimes with strong (solid line) and moderate (dashed line) signal strength (Hare and Mantua 2000).

recruitment strength in the 1990s rather than the oceanographic factors which may have predominated in the 1970s and 1980s.

The patterns of pollock abundance in the Gulf of Alaska, as revealed by stock assessments (Dorn *et al.* 2002) and shelf-wide bottom trawl surveys (Mueter and Norcross 2002), do not agree with the nearshore shrimp trawl survey data discussed

Table 1. Number of large year classes of Gulf of Alaska pollock by period (Dorn *et al.* 2002). # > mean = number of cohorts in period that were larger than the ln-transformed mean from 1967 to 1999 assessed as 3-yr-olds. Regime descriptions follow Hare and Mantua (2000). $P = \chi^2$ probability that number of cohorts greater than the mean is not different than random.

Period	Regime	Number of cohorts	# > mean	Percent	*P*
1967–1976	Cool	10	8	80%	<0.1
1977–1989	Warm	13	6	46%	>0.5
1990–1999	?	10	2	20%	<0.1

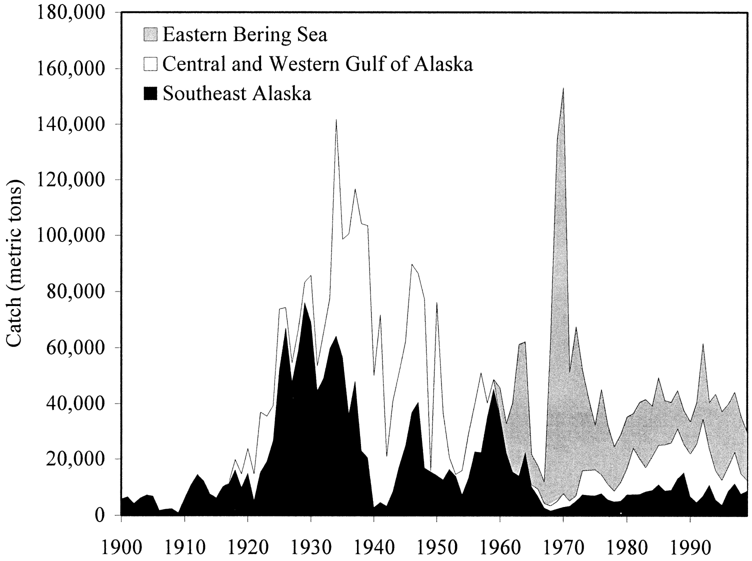

Figure 3. Pacific herring catch in Alaska by area, 1900–1999 (Alaska Department of Fish and Game website: http://www.cf.adfg.state.ak.us/geninfo/finfish/herring/overview/overview.htm; viewed October 2002.

by Anderson and Piatt (1999). Anderson and Piatt (1999) first suggest that the gadid complex was moderately abundant in the 1960s, small in the 1970s, and then increased monotonically through the 1980s and 1990s. Stock assessments for Gulf of Alaska pollock (Dorn *et al.* 2002) and Pacific cod (Thompson *et al.* 2002) indicate quite a different pattern of abundance for the two species, both of which peaked in the early or mid-1980s and have since declined. Analyses of shelf-wide bottom trawl survey data collected from the 1960s through 1996 revealed a similar pattern (Mueter and Norcross 2002). Anderson and Piatt (1999) also show that pollock CPUE in the shrimp trawl surveys was relatively constant from 1973 to 1990, and then increased 3-fold in a stepwise manner in 1991, more than a decade after the regime shift. Neither of the two gadid or pollock trends discussed by Anderson and Piatt (1999) reflect the gulf-wide patterns described by Ronholt *et al.* (1978), Alton *et al.* (1987), Dorn *et al.* (2002), Mueter and Norcross (2002), or Thompson *et al.* (2002), and more likely reflect changes in species distribution (see Shima *et al.* 2002*a*). The regime shift from cool to warm conditions in 1976–1977 was not associated with an increase in the likelihood of producing a large year class of pollock; quite the contrary, the probability declined but any relationship to the regime shift may be coincidental (Table 1).

Pacific herring—There have been three phases to the Pacific herring fishery in Alaska from 1900 to the present (Fig. 3) (Wespestad 1991, Alaska Department of Fish and Game web site[9]). The first phase was the reduction fishery that started in southeast Alaska in the late 1890s and grew to between 50,000 and 75,000 metric tons (t) per year by the late 1920s. As the fishery in this area declined in the mid-1930s, the reduction fishery in the central and western Gulf of Alaska (Prince

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[9] http://www.cf.adfg.state.ak.us/geninfo/finfish/herring/overview/overview.htm; October 2002.

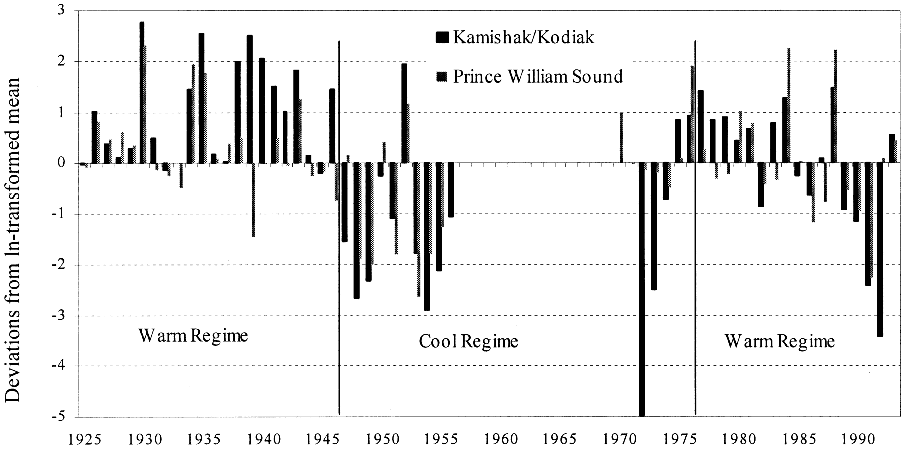

Figure 4. Annual deviations of ln-transformed recruitment of Pacific herring from their 1925–1993 means for two stocks in the central Gulf of Alaska: Kamishak Bay/Kodiak and Prince William Sound (both numbers at age 3). Data from Williams and Quinn (2000). Vertical lines separate climate regimes (Hare and Mantua 2000).

William Sound through the eastern Aleutian Islands) increased in size through the late 1940s, and then declined through the 1950s. Peak state-wide catches of 100,000–140,000 t per year occurred in the mid-1930s. The second phase consisted of foreign fisheries that caught herring offshore, primarily in the eastern Bering Sea from 1960 to 1980. Foreign harvests were eliminated under provisions of the U.S. Magnuson Fishery Conservation and Management Act passed in 1976, and the Alaska herring fishery became an entirely domestic enterprise. The third phase of the Alaskan herring fishery began in 1970 and has targeted roe-bearing females (or harvested roe on kelp directly) in late winter and early spring.

Williams and Quinn (2000) assembled recruitment time series of Pacific herring from 14 stocks in the Bering Sea and northeast Pacific Ocean for the years 1917–1993. Four of these herring stocks are within the range of the western Steller sea lion, two in the Gulf of Alaska (Prince William Sound and Kodiak/Kamishak), and two in the Bering Sea (Norton Sound and Togiak). Both Gulf of Alaska stocks tend to produce larger year classes during warm regimes (Fig. 4). For instance, during the warm regimes of 1925–1946 and 1977–1989, the Kodiak/Kamishak herring stock produced above average year classes during 82% and 69% of the years, respectively (Table 2). During the intervening cool regime from 1947 to 1976, this stock produced an above-average year class during only 20% of the 15 yr for which data were available. During both warm and cool regimes, the percentages of above average year classes were significantly different from random (50%; Table 2). The Prince William Sound stock had a similar pattern of year-class strength variability, but none was statistically different from random (Fig. 4; Table 2).

The pattern of CPUE for herring shown in figure 3 of Anderson and Piatt (1999) does not agree with the recruitment time series of Williams and Quinn (2000). Herring CPUE in the shrimp trawl survey increased almost 5-fold between 1973 and 1980, then declined 5-fold by 1985 and remained low through 1997. While herring abundance appeared to increase in the shrimp trawl survey data following

Table 2. Number of large year classes of Pacific herring in two stocks in the central Gulf of Alaska by period (Williams and Quinn 2000). # > mean = number of cohorts in period that were larger than the ln-transformed mean from 1925 to 1993 in each stock (Kamishak Bay-Kodiak and Prince William Sound). Period from 1990 to 1993 not included in summary because of small sample size. Regime descriptions follow Hare and Mantua (2000). $P = \chi^2$ probability that number of cohorts greater than the mean is not different than random.

			Kamishak/Kodiak			Prince William Sound		
Period	Regime	Number of cohorts	# > mean	Percent	*P*	# > mean	Percent	*P*
1925–1946	Warm	22	18	82%	<0.005	12	55%	>0.5
1947–1976	Cool	15	3	20%	<0.025			
1947–1976	Cool	16				6	38%	>0.1
1977–1989	Warm	13	9	69%	<0.025	6	46%	>0.5

the regime shift, it was not sustained through the 1980s as suggested by the recruitment data (Fig. 4). Consequently, gross Pacific herring abundance in the Gulf of Alaska (and general availability to Steller sea lions) was likely greater, rather than less, following the regime shift of 1976–1977. This is contrary to the hypotheses of Alverson (1992) and Trites and Donnelly (2003).

In summary, the shrimp trawl data analyzed by Anderson and Piatt (1999) does not reflect abundance trends for the entire fish community of the Gulf of Alaska, and as such, may not be appropriate to use as evidence of system-wide reorganization following the 1976–1977 regime shift. Their data on historical pollock and herring abundances are not in agreement with the trends of independent assessments of GOA-wide pollock (Dorn *et al.* 2002) or local herring stocks (Williams and Quinn 2000). In addition, osmerid production in the GOA may not have declined as suggested by Anderson and Piatt (1999) considering the large size of the arrowtooth flounder population in the GOA and the high proportion of capelin in their diet in the 1990s (Yang and Nelson 2000). Thus, decreases in the catch rates of capelin in the shrimp trawl survey data may reflect a more offshore distribution of the species in the summer, but not necessarily a decrease in their total abundance or production. Offshore movement after spawning could have affected their availability to Steller sea lions during this portion of the year, but not necessarily when they are aggregated nearshore prior to or during spawning (Calkins and Goodwin,[6] Merrick and Calkins 1996, Sinclair and Zeppelin 2002, Sigler *et al.* 2004). While the shrimp trawl surveys were conducted in areas near shore where juvenile (<2 yr old) sea lions are most often found, they may not accurately describe prey distributions or abundances in the foraging habitats of adult and weaned individuals. This is because sea lions target dense prey patches, particularly when they are aggregated for spawning (Sinclair and Zeppelin 2002, Sigler *et al.* 2004). On the other hand, trawls are poor survey instruments for patchily distributed prey (Walters 1996, 2000). Trawl survey data, while useful as indices for stock assessments (*e.g.*, Dorn *et al.* 2002, Ianelli *et al.* 2002), are not collected at the fine spatial and temporal scales necessary to describe sea lion prey distributions.

Instead of the monotonically increasing pollock (gadid) population in the Gulf of Alaska through the 1990s portrayed by Anderson and Piatt (1999), this population has done just the opposite: declined monotonically. In addition, the only representative of the "forage" fish complex for which abundance and recruitment data exist, Pacific herring, increased in abundance following the regime shift. Therefore, we see no evidence of a switch from a "cool" community dominated by "forage" fish to a "warm" community dominated by gadids after 1976. On the contrary, gadid recruitment and abundance patterns in particular appear to be related to changes in environmental conditions that occur more frequently than multidecadal regime shifts (Hollowed and Wooster 1992, 1995), to the abundance of piscivores (Bailey 2000), or to possible fishing effects (NMFS 2000). Changes in the sizes of shrimp and other crustacean populations that the surveys targeted may have also been affected by the distribution and intensity of local fisheries, especially considering many began to decline prior to the 1976–1977 regime shift (Orensanz *et al.* 1998).

Eastern Bering Sea—Ecosystem models, by necessity, include many assumptions and by themselves, should not be used as evidence that something has or has not occurred. However, one of the primary sources used by Hunt *et al.* (2002) and Trites and Donnelly (2003) to support the hypothesis that the structure of the eastern Bering Sea ecosystem switched from one dominated by "forage" fish to one dominated by gadids and flatfish following the regime shift is an ecosystem modeling exercise conducted by Trites *et al.* (1999). In this study two food-web models were constructed of the eastern Bering Sea: one that attempted to represent the structure in the 1950s before large-scale commercial whale and fish fisheries were established, and another in the 1980s. The principal hypothesis investigated by Trites *et al.* (1999) involved the effects that commercial whaling in particular had on the food web dynamics of the eastern Bering Sea, but other hypotheses involved how natural cycles of climate change may have interacted with patterns of human exploitation to "shift the ecosystem into a new domain." The authors acknowledge that because of the paucity of data on which to base the structure of the 1950s version of the model, they are less certain about the actual state of the 1950s ecosystem than in the 1980s. For the size of the 1950s pollock population, for instance, the authors cite a personal communication from V. Wespestad, who had obtained data collected by Russian scientific fisheries in the eastern Bering Sea in the late 1950s, data which were not of similar scope or quality as those upon which the 1980s ecosystem structure was based. The 1950s Russian data formed the primary basis for the model input that pollock biomass in the 1950s was 16% of that in the 1980s, an input assumption that drives the model result that pelagic "forage" fish were more abundant in the 1950s. In order to balance the model, pelagic "forage" fish (for which no abundance data existed for the 1950s) had to be much more abundant in the 1950s than in the 1980s to satisfy the foraging demands of the larger marine mammal populations at that time. If the eastern Bering Sea in the 1950s is assumed to have a lower abundance of pollock and the pinniped populations consume a larger biomass of prey than in the 1980s, then the model, by necessity, will estimate larger biomasses of other consumed species (*e.g.*, "forage" fish) in the 1950s than the 1980s. As will be discussed in more detail in the next section, diet estimates of Steller sea lions and northern fur seals were also used to support the model input assumption that pollock biomass was much lower in the 1950s than in the 1980s. While at some point in the 1950s the pollock population may have been smaller than what it was at its peaks in 1971, 1985, or the early 1990s, this does not imply that it remained low for an extended period of time and was part of a stable, preregime shift ecosystem structure. Indeed, pollock biomass in the eastern Bering Sea has varied in magnitude in response to tremendous variation in recruitment, similar to other gadid populations the world over (Myers 2001).

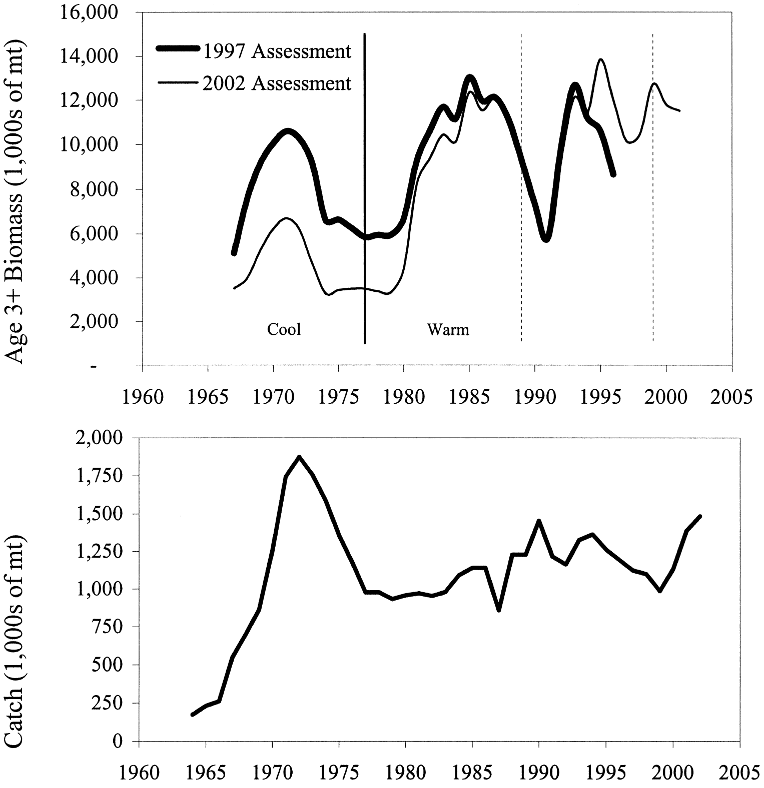

Figure 5. Eastern Bering Sea pollock population and fishery catch data, 1964–2001. Top: Age 3+ biomass of pollock from assessments conducted in 1997 (Wespestad *et al.* 1997) and 2002 (Ianelli *et al.* 2002). Bottom: Catch of pollock on the eastern Bering Sea shelf. Vertical lines separate climate regimes with strong (solid line) and moderate (dashed line) signal strength (Hare and Mantua 2000).

Pollock—The eastern Bering Sea (EBS) pollock stock assessment also uses an age-structured model that employs fishery- and survey-derived information to reconstruct the population age structure, abundance, and biomass from the mid-1960s to the present for the purposes of setting catch quotas (Wespestad 1997, Ianelli *et al.* 2002). Biomass time series (Fig. 5) from these assessments show that the EBS pollock population was relatively large in the early 1970s, was smaller in the mid-1970s, increased through the early 1980s to an early peak in 1985, and has varied between 6 million and 14 million t since. In the 34- and 38-yr time series shown in Fig. 5 (top), there have been at least three peaks in abundance that are separated by 8, 10, or 14 yr, and one peak occurred prior to 1976. Catches from the EBS shelf population increased rapidly from the inception of the fishery in 1964 to over 1.8 million t in 1971, followed by a decline and a stabilization at between 1 million and 1.5 million t since then (Fig. 5, bottom). The largest catches of pollock on the eastern Bering Sea shelf occurred in the early 1970s prior to the regime shift of 1976–1977. Large foreign-based fisheries moved into the eastern Bering Sea during the mid-1960s because earlier exploratory surveys revealed that the pollock stock was large and virtually unfished (Alverson 1992).

Table 3. Number of large year classes of eastern Bering Sea pollock by period (Ianelli *et al.* 2002). # > mean = number of cohorts in period that were larger than the ln-transformed mean from 1964 to 1999 assessed as 3-yr-olds. Regime descriptions follow Hare and Mantua (2000). $P = \chi^2$ probability that number of cohorts greater than the mean is not different than random.

Period	Regime	Number of cohorts	# > mean	Percent	*P*
1964–1976	Cool	13	6	46%	>0.5
1977–1989	Warm	13	7	54%	>0.5
1990–1999	?	10	6	60%	>0.5

Bakkala (1993) reviewed survey and fishery data from the eastern Bering Sea in his description of the structure and historical changes in the groundfish complex, and concluded that pollock had peaks in abundance both before and after the 1976–1977 regime shift. Based on scattered survey information and fishery data, he concluded that EBS pollock probably increased in abundance between the mid-1960s and early 1970s, prior to the 1976–1977 regime shift, but the sizes of the population before and after the increase are highly uncertain. Estimates of the abundance of pollock prior to the regime shift are based largely on fishery data, and few fishery independent sources (*e.g.*, surveys) are available. Also, assumptions regarding constancy of natural mortality tend to decrease estimates of cohort strength early in an assessment time series if fishery-independent data are not available (Bakkala 1993). This leads to the often-observed increase in abundance of a fished species shortly after the fishery starts, or in the case of EBS pollock, from the early to late 1960s. Therefore, Bakkala (1993) concluded that the early cohort analyses likely underestimated the size of the pollock population in the early 1960s, thus exaggerating the apparent increase later in the decade. Uncertainty in the size of the EBS pollock population prior to the regime shift is also reflected in two recent stock assessments, Wespestad (1997) and Ianelli *et al.* (2002) (Fig. 5, top). Both show a peak in biomass in 1971, but the 1997 estimate (10.6 million t) is 40% larger than that of 2002 (6.7 million t). Therefore, while there are data to support the conclusion that pollock increased in abundance between the mid-1960s and early 1970s, the levels from and to which it increased are highly uncertain.

There is evidence that the abundance of another gadid species, Pacific cod, varies on decadal scales in the eastern Bering Sea (Bakkala 1993). Survey data collected from the 1960s to the present suggest that Pacific cod biomass levels were similar in the mid-1960s to those observed in the mid 1980s, but they were much lower in the 1970s (Bakkala 1993). Consequently, both pollock and Pacific cod had peaks in abundance prior to the regime shift, and there is little to suggest that gadids increased to unprecedented levels following the regime shift. Besides, the historical record, which goes back to the mid-1960s, shows only one previous peak in abundance for both species. We have no evidence that this level of variation did not exist prior to the beginning of the assessment time series, or to what levels the populations may or may not have risen.

Contrary to the GOA pollock population that produced fewer large year classes with time (Table 1), the EBS pollock population has had similar rates of large year class production in each regime that were also not significantly different from random (Ianelli *et al.* 2002; Table 3). In other words, large year classes were produced at nearly identical frequencies regardless of the regime type.

Table 4. Number of large year classes of Pacific herring in two stocks in the eastern Bering Sea by period (Williams and Quinn 2000). # > mean = number of cohorts in period that were larger than the ln-transformed mean from 1972 to 1993 (Norton Sound stock) or from 1969 to 1993 (Togiak stock). Period from 1990 to 1993 was not included in summary because of its small sample size. Regime descriptions follow Hare and Mantua (2000). $P = \chi^2$ probability that number of cohorts greater than the mean is different than random.

			Norton Sound			Togiak		
Period	Regime	Number of Cohorts	# > Mean	Percent	*P*	# > Mean	Percent	*P*
1972–1976	Cool	5	1	20%	<0.5			
1969–1976	Cool	8				2	25%	<0.25
1977–1989	Warm	13	10	77%	0.05	9	69%	<0.25

Analyses of changes in CPUE of species caught in bottom trawl surveys have been used as evidence in support of ecosystem reorganization in the eastern Bering Sea following the regime shift of 1976–1977 (Conners *et al.* 2002). Data analyzed were collected in summer from three sites on the shelf that totaled approximately one-fourth of the standard area surveyed each year by NMFS (Walters 1996, 2000). Much like the results of Anderson and Piatt (1999) for the Gulf of Alaska, the time series of pollock CPUE in each of the three sites shown by Conners *et al.* (2002) bears little resemblance to the historical abundance reconstructed by Ianelli *et al.* (2002) or Wespestad (1997), particularly in the Unimak and Pribilof sites. The conclusion of Conners *et al.* (2002) that groundfish, and in particular gadids were in low abundance from 1972 to 1976 is also in conflict with the assessments of Wespestad (1997) and Quinn and Collie (1990), as well as the large pollock fishery catches that occurred at that time (an average of 1.55 million t per year from 1972 to 1976; Fig. 5). Instead, the analyses of Conners *et al.* (2002) may indicate annual differences in distribution of pollock on the shelf in a manner similar to Wyllie-Echeverria (1996), Wespestad *et al.* (2000), and Hunt *et al.* (2002).

Pacific herring—There are two principal stocks of Pacific herring in the EBS: one that spawns in nearshore areas of Norton Sound and another in the Togiak region of northern Bristol Bay (Williams and Quinn 2000). Williams and Quinn (1997) assessed the Norton Sound stock and reconstructed the population dynamics from 1981 to 1995. The Norton Sound stock increased in size during the 1980s and peaked in the early 1990s at approximately 50,000 t total biomass due to years with above average recruitment in the late 1970s and early 1980s (Table 4; Fig. 6). The Togiak stock is larger than the Norton Sound stock, and has ranged in size from 70,000 t to 200,000 t between 1980 and 1999. Similar to the GOA Pacific herring stocks, years with below average recruitment for both these EBS stocks were more common prior to the 1976–1977 regime shift than after (Table 4; Fig. 6).

Wespestad (1991) assessed the entire eastern Bering Sea population of Pacific herring (both stocks) for the period 1959–1988 using both fishery and survey information. His population reconstruction revealed a total herring biomass of over 1 million t in the early to mid-1960s, followed by a steep decline and low population levels throughout the 1970s (Fig. 7). This decline preceded the regime shift by approximately 10 yr, and may have been the result of heavy fishing pressure (Wespestad 1991). In the early 1980s (after the regime shift), the population increased (Wespestad 1991), which is in agreement with the assessments of Williams

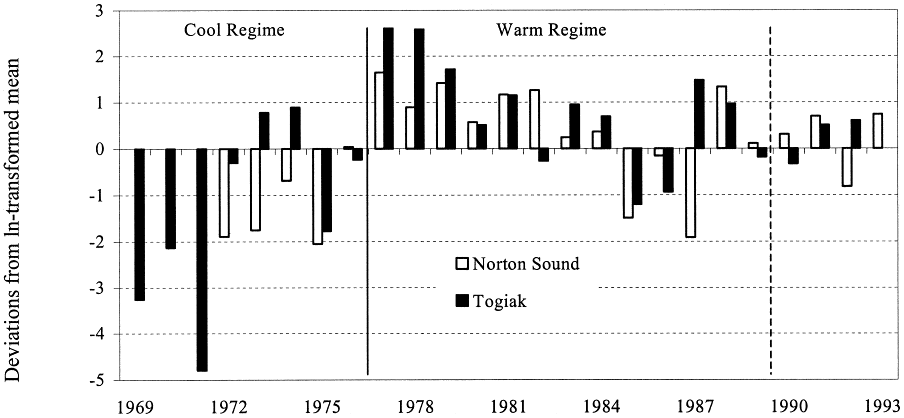

Figure 6. Annual deviations of ln-transformed recruitment of Pacific herring from their 1969–1993 means for two stocks in the Eastern Bering Sea: Norton Sound (numbers at age 3) and Togiak (numbers at age 4). Data from Williams and Quinn (2000). Vertical lines separate climate regimes with strong (solid line) and moderate (dashed line) signal strength (Hare and Mantua 2000).

and Quinn (1997, 2000). Even at its peak in the early 1960s, the abundance of herring was not greater than that of pollock prior to the regime shift (Fig. 7).

Hunt *et al.* (2002) conclude from analyses of summer groundfish survey data that the abundance of juvenile pollock and other "forage" fish declined considerably after the 1976–1977 regime shift in the eastern Bering Sea. The "forage" fish complex definition used by Hunt *et al.* (2002) is different than that used by Winship and Trites (2003), and is based on the combined overall mean catch per unit effort (CPUE = kg/ha) of age 1 pollock, age 1 Pacific cod, Pacific herring, eulachon, and capelin in the summer groundfish surveys. However, there are several issues associated with the forage fish abundance index proposed by Hunt *et al.* (2002) that limit its utility.

First, the gear (bottom trawl) used in the groundfish surveys is not designed to sample the age classes and species used in Hunt *et al.*'s (2002) forage fish abundance index (Ianelli *et al.* (2002) for age 1 pollock, Thompson and Dorn (2002) for age 1 Pacific cod, and Walters (1996, 2000) for herring, eulachon, and capelin). As a result, differences in catch per unit effort between years may not reflect annual differences in relative abundance, but instead relative availability to the gear or simply noise. Thus, an index based on the combined means of variable and noisy data has questionable validity. Second, Hunt *et al.*'s (2002) fig. 11C shows the variability of the index: the annual time series varies between about 0.5 and 4.5 kg/ha with little or no temporal trend. Furthermore, without confidence bounds on the annual means, it is not possible to determine if annual indices are significantly different from one other.

In addition, Hunt *et al.* (2002) state that the biomass of age 1 pollock declined from 1975 to 1999. They base this on analyses of age 1 pollock abundance estimates in subareas of the eastern Bering Sea from bottom trawl surveys. This conclusion is inconsistent with pollock stock assessment information which shows that above average year classes were produced with similar frequencies regardless of the regime (Table 3) and pollock biomass varied between about 6 million and 14 million t

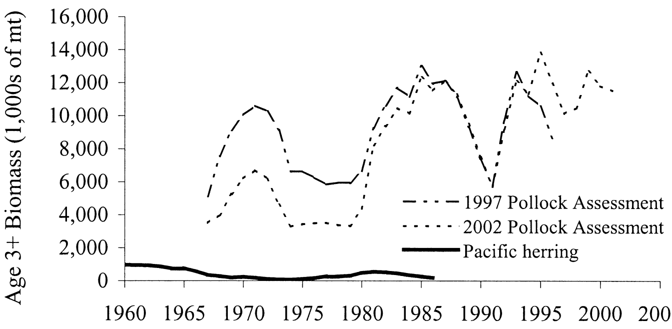

Figure 7. Biomass (age 3+) of pollock (Wespestad 1997; Ianelli *et al.* 2002) and Pacific herring (Wespestad 1991) in the eastern Bering Sea.

between the early 1970s and 2001 (Fig. 5). Although Hunt *et al.* (2002) report that age 1 pollock abundance dropped considerably in the 1980s and 1990s, adult pollock abundance increased (Hunt *et al.* 2002; Ianelli *et al.* 2002). It is difficult to understand how adult pollock biomass increased over a 20-yr period, while at the same time, the number and biomass of recruits declined. Their conclusion might be possible, however, if the age 1 pollock biomass time series they analyzed were poorly correlated with adult biomass, because of poor and possibly variable age 1 selectivity by the survey bottom trawls.

The summer distribution of capelin may have changed in the eastern Bering Sea. Naumenko (1996) described a capelin concentration near the Pribilof Islands from surveys conducted in the early 1970s that may have moved northward to the mainland Alaskan coastline in the 1980s and 1990s (Walters 1996, 2000). This could affect osmerid availability to Steller sea lions during the summer and fall, but not during the rest of the year if they continue to aggregate for spawning in similar locations (Sinclair and Zeppelin 2002).

In summary, we find little empirical evidence to support the conclusion that the biological community of the eastern Bering Sea shelf switched from one dominated by "forage" fish to one dominated by gadids following the regime shift of 1976–1977. On the contrary, herring recruitment strength actually increased after 1976, while variations in the abundance of gadid species were related to changes in recruitment strength which appear to be unrelated to multidecadal regime shifts (Hare and Mantua 2000).

Diets of Steller Sea Lions and Northern Fur Seals

Alverson (1992), Trites and Donnelly (2003), and Hunt *et al.* (2002) hypothesized that declining proportions of energy-rich osmerids and clupeids, along with increasing proportions of energy-poor gadids in sea lion diets led to nutritional stress in the western stock of Steller sea lions. The perceived changes in the sea lion diet were supposedly due to changes in the fish community structure of the North Pacific Ocean and the eastern Bering Sea caused by shifts in the climate from a cool to a warm regime in 1976–1977. As just discussed, evidence for decreases in osmerid and clupeid abundance and increases in gadid abundance following the regime shift is weak or contradictory. We now examine the data on Steller sea lion diets before and after the 1976–1977 regime shift for evidence of a shift from a clupeid-osmerid dominant diet to a gadid-dominant diet. In addition, the abundant diet data on northern fur seals, much of which was collected prior to the regime shift, is also examined.

Steller sea lions—There are seven published reports of Steller sea lion food habits collected in the range of the western stock prior to 1977 (Table 5A). Of these, only Mathisen *et al.* (1962) and Thorsteinson and Lensink (1962) were part of dedicated sea lion studies, all others were opportunistic collections. Merrick and Calkins (1996) concluded that there were insufficient data for interdecadal comparisons of the western sea lion diet because early studies had small sample sizes (Imler and Sarber 1947, Wilke and Kenyon 1952, Fiscus and Baines 1966), focused on a single site in one season (Mathisen *et al.* 1962), or considered only territorial males (Thorsteinson and Lensink 1962). The latter two studies also did not completely identify prey remains (Merrick and Calkins 1996).

Sea lion diet data collected by Mathisen *et al.* (1962) and Thorsteinson and Lensink (1962) are the largest samples of preregime shift sea lion diets, yet revealed only limited smelt and no herring consumption; diets were dominated by cephalopods, most likely octopus (Table 5B). The species in their samples suggested that sea lions were foraging near shore. This would be the likely result in a sample collected in summer at rookeries and primarily composed of adult males and perinatal females.

Osmerids or clupeids were the dominant prey species in only one of the pre-1977 diet studies, Fiscus and Baines (1966). Looking further into their collections, capelin were found in 9 of 16 western sea lion stomachs examined, and were dominant in 7 collected in spring and early summer. Consumption of smelt primarily during these seasons has been observed in subsequent studies (Calkins and Goodwin,[6] Merrick and Calkins 1996, Sinclair and Zeppelin 2002). In the remaining six preregime shift studies of western sea lions, dominant prey items were cephalopods (two studies), salmon (*Oncorhynchus* spp.; one study; tied with pollock), flatfish (one study), herring (one study), or pollock (two studies; Table 5). A preregime shift sea lion diet dominated by osmerids and clupeids and low in gadids, as suggested by Hunt *et al.* (2002) and Trites and Donnelly (2003), was thus based on only seven sea lions collected opportunistically in two different years and at three locations in the north Pacific Ocean (Fiscus and Baines 1966). Regardless of the inappropriateness of making this conclusion from such a small sample, it ignores data from other diet studies from the time period. Because of limitations associated with location, seasonality, and sample sizes, data collected prior to the mid-1970s appear to be inadequate to characterize the diet of the entire western Steller sea lion population prior to the regime shift.

Beginning in the mid-1970s, however, diet data were collected in more systematic ways that permit a more accurate description of the sea lion diet throughout the year (Merrick and Calkins 1996). Collections were made at a wider variety of locations throughout the range of the western population, including haul outs, than had been done previously, and throughout the year rather than primarily at rookeries during the breeding season (Table 5). Although there are 10 studies listed in Table 5, three of these are the most complete collections and analyses to date: Pitcher (1981; same as Calkins and Pitcher 1982), Calkins and Goodwin,[6] and Sinclair and Zeppelin (2002; includes samples analyzed by Merrick *et al.* 1997). In each of these studies, pollock, cod, flatfish, and Atka mackerel (*Pleurogrammus monopterygius*) were the most commonly consumed species by western Steller sea lions. As more samples

Table 5. Food habits information for Steller sea lions collected in the range of the western stock, 1945–1998.

		Months				Region						
Reference	Years	Jan–Mar	Apr–Jun	Jul–Sep	Oct–Dec	CGOA	WGOA	EBS	EAI	CAI	WAI	Russia
A. Sample sizes and characteristics												
Imler and Sarber (1947)	1945			7		7						
Wilke and Kenyon (1952)	1949, 1951			3				3				
Mathisen *et al.* (1962)	1958		94				94					
Thorsteinson and Lensink (1962)	1959		56			9	27		20			
Tikhomirov (1968)	1962	X	X					X				
Fiscus and Baines (1966)	1960, 1962		16			4	2	1	9			
Perlov (1975)	1966–1969			?								
Lowry *et al.* (1982)	1976	4						4				X
Pitcher (1981)	1975–1978	43	54	9	47	136	17					
Calkins (1998)	1981	60										60
Calkins (1998)	1981	32						32				
Frost and Lowry (1987)	1985	13						13				
Gearin[13]	1985, 1986			3	8			11				
Calkins and Goodwin[6]	1985, 1986		X		X	74						
Merrick *et al.* (1997)	1990–1993			76		76						
Merrick *et al.* (1997)	1990–1993			67					67			
Merrick *et al.* (1997)	1990–1993			167						167		
Merrick *et al.* (1997)	1990–1993			28							28	
Goto and Shimazaki (1998)	1994–1996	62										62
Sinclair and Zeppelin (2002)	1990–1998	X	X	X	X	574						
Sinclair and Zeppelin (2002)	1990–1998	X	X	X	X		929					
Sinclair and Zeppelin (2002)	1990–1998	X	X	X	X				889			
Sinclair and Zeppelin (2002)	1990–1998	X	X	X	X					1370		

Table 5. Continued.

Reference	Sample type	Sample location	Data type	Percent of sample with prey item (x = present)												
				Pollock	Cod	Flatfish	Greenling	Rockfish	Smelts	Sandlance	Herring	Salmon	Sculpin	Shrimp/Crab	Squid	Octopus
B. Food habits data																
Imler and Sarber (1947)	Stomach	Land	FO	57		71						28				43
Wilke and Kenyon (1952)	Stomach	Land	PW	7	10	49				32			<1			2
Mathisen *et al.* (1962)	Stomach	Land	FO				13	9	14	1		1	6	10		44
Thorsteinson and Lensink (1962)	Stomach	Land	FO			6	4	11		25			4	2		20
Tikhomirov (1968)	Visual	At-sea									D					
Fiscus and Baines (1966)	Stomach	At-sea	FO	6		12	6	6	56	25			19			
Perlov (1975)	Stomach	At-sea	FO	63			10						1		>30	25
Lowry *et al.* (1982)	Stomach	At-sea	PV	97		1									1	1
Pitcher (1981)	Stomach	Land	FO	67	12	5		3	11		11	4	4	7	23	13
Calkins (1998)	Stomach	At-sea	FO	83	43	3					17		>12	2	2	18
Calkins (1998)	Stomach	At-sea	FO	100	28	>19		3			6		6	>10	19	19
Frost and Lowry (1987)	Stomach	At-sea	PV	48							48					
Gearin[13]	Stomach	Land	FO	>36	>45	54								18		45
Calkins and Goodwin[6]	Stomach	Land	FO	58	7	14				7	3	3	1	>1	4	32
Merrick *et al.* (1997)	Scat	Land	FOSS	66		4	<1		6			20	0		3	
Merrick *et al.* (1997)	Scat	Land	FOSS	33		2	31		8			17	7		2	

Table 5. Continued.

Reference	Sample type	Sample location	Data type	Percent of sample with prey item (x = present)												
				Pollock	Cod	Flatfish	Greenling	Rockfish	Smelts	Sandlance	Herring	Salmon	Sculpin	Shrimp/Crab	Squid	Octopus
Merrick *et al.* (1997)	Scat	Land	FOSS	13		0	69		1			6	4		8	
Merrick *et al.* (1997)	Scat	Land	FOSS	7		0	77					5	5		7	
Goto and Shimazaki (1998)	Stomach	At-sea	FO	89	76	24									69	11
Sinclair and Zeppelin (2002)	Scat	Land	FO	>50	>5	>20	<5	x	x	>10	>10	>10	<10		<10	<10
Sinclair and Zeppelin (2002)	Scat	Land	FO	>70	>10	>10	<5	x	x	>10	<10	>10	>10		<5	<5
Sinclair and Zeppelin (2002)	Scat	Land	FO	>50	>10	<5	>20	x	x	<5	>5	>20	>10		<10	<10
Sinclair and Zeppelin (2002)	Scat	Land	FO	<10	>10	<5	>60	x		<5	<5	>20	>10		<20	<20

Abbreviations: CGOA = central Gulf of Alaska; WGOA = western Gulf of Alaska; EBS = eastern Bering Sea; EAI = eastern Aleutian Islands; CAI = central Aleutian Islands; WAI = western Aleutian Islands; X = number for cell is unknown; ? = season of sample collection is unknown but likely to be as indicated; FO = frequency of occurrence; PW = percent by weight; PV = percent by volume; FOSS = Split sample FO.

[13] Gearin, P. J. Unpublished report. Stomach contents, age, and sex of northern sea lions collected from St. Paul Island, Alaska, in 1985 and 1986. Available Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

throughout the range and year have been taken, it has become more apparent that changes in the consumption of prey species reflect seasonal and geographic differences in their distributions and availability (Sinclair and Zeppelin 2002).

The first of these collections, summarized by Pitcher (1981) and Calkins and Pitcher (1982), consisted of 153 stomachs collected throughout the year from 1975 to 1978 from Prince William Sound through the Kodiak archipelago. These collections span the regime shift, with some collected before and some after; pollock was the dominant prey item (Table 5). A similar, but smaller collection ($n = 74$) from the same area was made in 1985–1986 (Calkins and Goodwin[6]). Trites and Donnelly (2003) place considerable emphasis on the lack of capelin in the mid-1980s data in concluding that the diet had changed. Because of seasonal differences in the collection dates between these and the 1975–1978 collections, Calkins and Goodwin[6] and Merrick and Calkins (1996) previously indicated that such a conclusion was not supported by the data. Based on a comprehensive study (over 3,700 scats collected throughout the U.S. range of the western stock), Sinclair and Zeppelin (2002) concluded that sea lions feed on aggregated fish species, particularly when the fish are near shore for spawning. Species consistently appearing in the diet were schooling species that live on the shelf (*e.g.*, pollock, Atka mackerel) or are nearshore residents (*e.g.*, octopus, flatfish). Species that have considerable variability in their seasonal representation (*e.g.*, Pacific cod, Pacific salmon, osmerids, clupeids) are ones that aggregate for spawning in nearshore areas and then disperse. For these species to appear in the diet, the timing and size of collections were very important, and their absence or presence should not be overemphasized in the analysis.

Northern fur seals—Based on comparisons of data collected before and after the regime shift of 1976–1977, Sinclair *et al.* (1994) and Hunt *et al.* (2002) concluded that changes in the northern fur seal diet in the eastern Bering Sea were the result of climate-mediated shifts in fish community composition. They compared the prevalence of walleye pollock and capelin in the stomachs of 73 fur seals (with food in their stomachs) collected in the early 1980s (Sinclair *et al.* 1994) with those of 3,927 fur seals collected from 1960 to 1974 (Kajimura 1984). The basis of this conclusion, however, should be examined in detail, specifically with respect to sample size and location.

Fur seal stomach content data summarized by Kajimura (1984) were obtained from the pelagic collection of 3,927 fur seals in the southeastern Bering Sea in 7 yr: 1960, 1962–1964, 1968, 1973 and 1974. Collections were made throughout the southeastern Bering Sea, in shelf, slope and basin waters from Unimak Pass and the Krenitzen Islands in the south to well beyond the Pribilof Islands in the north, during June–October (when fur seals inhabit the area). In the Bering Sea, Kajimura (1984) noted the strong correlation between location and the species of prey ingested by fur seals. Atka mackerel and capelin were the principal prey near the Aleutian Islands. On the Bering Sea shelf, the most commonly eaten prey were walleye pollock, Pacific herring, and Greenland turbot, while off the shelf, fur seals ate gonatid squids and deep-sea bathylagid smelts. Pollock was the number one ranked prey (based on percentage of total stomach content volume) in the months of July ($n = 1{,}288$ fur seals), August ($n = 2{,}001$) and September ($n = 510$), when fur seals were primarily coming and going from the rookeries and haul-outs on the Pribilof Islands. Fewer fur seals were collected in June ($n = 86$) and October ($n = 32$) when fur seals were entering and leaving the Bering Sea, respectively, through the Aleutian passes; capelin was the number one ranked prey in these two months.

The fur seal stomachs with contents discussed by Sinclair *et al.* (1994) were collected in October 1981 ($n = 7$), September–October 1982 ($n = 23$), and August 1985 ($n = 43$). Of these 73 animals, 60 (17 of 23 collected in 1982 and all 43 collected in 1985) were collected near the Pribilof Islands in waters of 200 m depth or less where Kajimura (1984) found pollock to be the most common prey; these collections comprised over 80% of the 1981–1985 sample analyzed by Sinclair *et al.* (1994). The remaining 13 animals were collected 30–40 nmi north or northwest of Unimak Pass. It was near the Aleutian Islands and in the passes themselves where Kajimura (1984) found most of the capelin consumption to occur, and capelin was not generally among the principal prey species around the Pribilof Islands listed by either Kajimura (1984) or Sinclair *et al.* (1994). Therefore, Sinclair *et al.* (1994) and Hunt *et al.* (2002) conclude that capelin were much less abundant after the 1976–1977 regime shift based on the food habits of only 73 animals (less than 2% of the size of the Kajimura (1984) samples), of which more than 80% were collected in times and areas where capelin consumption was not expected. Since there is no reliable time series of total capelin or smelt biomass for the eastern Bering Sea (Bakkala 1993; Walters 1996, 2000), Hunt *et al.* (2002) rely on the fur seal food habits data of Sinclair *et al.* (1994), as well as their analysis of forage fish abundance in the bottom trawl survey time series (their fig. 11C) as indicators of system-wide change in fish community structure. This reliance may be misplaced given the sample size and location issues associated with these fur seal diet comparisons. Instead, rather than system-wide structural changes, their findings may only suggest changes in the summer-time distribution of capelin following spawning (Naumenko 1996).

Recent observations on sea lion and northern fur seal food habits, as well as the fish communities of the Bering Sea and Gulf of Alaska, must also be put into historical context. Although there were no scientific surveys or collections from 100 yr ago that are strictly comparable with those of the last 25 yr, the observations and conclusions of some of the first naturalists and scientists to visit Alaska are worthy of note (Jordon *et al.* 1896, 1898; Alexander 1898*a*, *b*; Jordon and Evermann 1902). In reports from numerous expeditions to the Pribilof and Aleutian islands, researchers found Alaskan pollock in the Bering Sea and neighboring waters south to Sitka and the Kurils to be “excessively abundant, swimming near the surface and furnishing the great part of the food of the fur seal” (Jordon and Evermann 1902). Likewise, both Pacific cod and Atka mackerel were described as being very abundant in the Bering Sea and Aleutian Islands in much the same locations as today. Therefore, while no biomass estimates of pollock or herring exist from the 1890s and early 1900s, observations at the time suggest that pollock and Pacific cod were abundant, not rare, and that fur seals and Steller sea lions commonly ate them.

Variability in gadid abundance is related to variability in the size of year classes that recruit to the populations (Dorn *et al.* 2002, Ianelli *et al.* 2002). There appears to be little connection between recent changes in gadid abundance in the North Pacific Ocean and recent regime shifts (Hare and Mantua 2002, Benson and Trites 2002). Over the last 30 yr, the rate at which large year classes of pollock were produced in the Gulf of Alaska has declined, while in the eastern Bering Sea it has remained relatively constant. Furthermore, recent peaks in gadid abundance are likely not unprecedented in size, nor did the regime shift of 1976–1977 result in increases in the frequency of production of large gadid year classes. For Pacific herring, the frequency with which strong year classes were produced increased after 1976, which increased their abundance and may have increased their availability to sea lions. Although there is no evidence that “forage” fish dominated the North Pacific and eastern Bering Sea ecosystems prior to 1976, changes in their nonspawning distributions to more northerly or offshore habitats may have occurred. In addition, there is little within the information on diets to support the hypothesis that the proportion of the sea lion diet comprised of "forage" fish decreased and of gadids increased following the regime shift. On each of these points, these findings do not support the regime shift–"junk food" hypothesis for nutritional stress in the western stock of Steller sea lions. This hypothesis will now be examined with respect to the issue of prey quality, both in terms of total energy density and other factors that could affect individual sea lion health.

Nutritional Value of Steller Sea Lion Prey

Several lines of reasoning have been used to conclude that pollock and other gadid fish are nutritionally inferior prey for Steller sea lions. First, pollock and other gadids generally have lower energy densities, containing fewer calories per unit weight than herring and other fish with high lipid content (Alverson 1992, Rosen and Trites 2000*b*, Trites and Donnelly 2003). Consequently sea lions would have to eat more biomass of gadids to survive and maintain weight and body fat in cold environments with variable food supplies (Kirsch *et al.* 2000, Rosen and Trites 2000*b*, Trites and Donnelly 2003). Along these lines, juvenile Steller sea lions may not be able to physically ingest enough pollock to survive (Trites and Donnelly 2003). Second, pollock and other gadids are less digestible than high fat fish (Lawson *et al.* 1997, Rosen and Trites 2000*a*) and they take more energy to digest (Rosen and Trites 1997). Third, consumption of pollock may be responsible for a syndrome in pinnipeds and other mammals called "gadoid anemia," wherein ingestion of gadid fishes causes iron depletion (Thompson *et al.* 1997, Rosen and Trites 2000*b*, Trites and Donnelly 2003). These and other results of captive feeding experiments and proximate prey analyses have been extrapolated to the wild population with few reservations or caveats. We address each of these statements in an attempt to conclude whether the preponderance of the evidence supports the hypothesis that sea lion diets high in gadids are likely, by themselves, to cause nutritional stress.

It has been known for many decades that prey species differ in energy and lipid density. It has also been recognized that there is considerable within-species variability in these due to season, age, location, and reproductive status. Pollock generally have lower energy densities and lipid contents than herring. However, there is a large amount of overlap in these among the various species of fish eaten by free-ranging Steller sea lions (Fig. 8). Many non-gadid prey species are very similar to pollock and other gadids in caloric density and lipid content. These include various flatfish species, smelt, sand lance (*Ammodytes hexapterus*), capelin, squid, and salmon. Smelts (except eulachon), sand lance and capelin in particular are often grouped into the "fatty forage fish" category, even though their caloric density is similar to that of pollock. By contrast, Atka mackerel, a principal food of Steller sea lions in the Aleutian Islands (Sinclair and Zeppelin 2002), has caloric densities that overlap greatly with herring (Logerwell and Schaufler, in press). It is therefore inappropriate to refer to prey as "fatty" or "lean" without reference to time of year, reproductive status, or the like.

The lipid content and energy density of pollock, herring, and other forage fish vary considerably between seasons and are related to feeding and reproductive cycles (Jangaard *et al.* 1967; Stansby 1976; Anthony *et al.* 2000; Logerwell and Schaufler, in press). Proximate composition and caloric density varies with age, size, and sex of

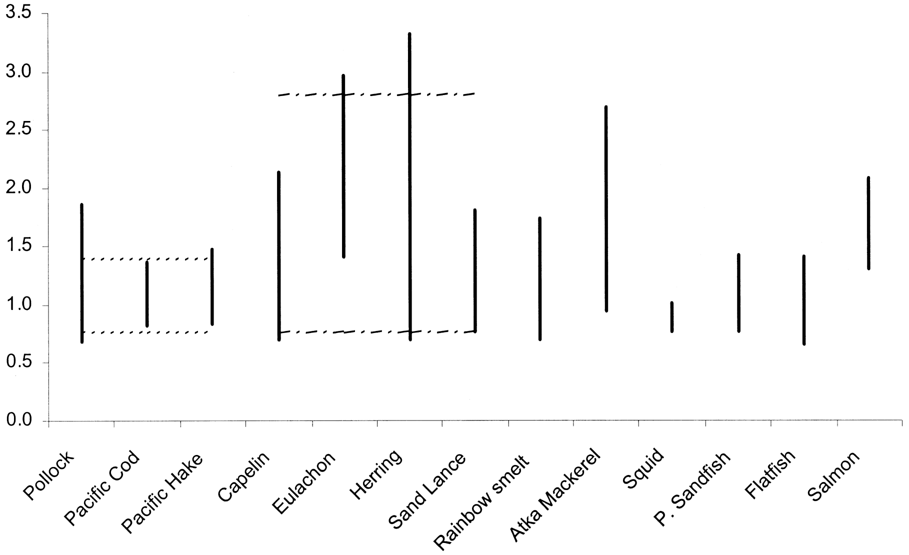

Figure 8. Range of caloric densities for different Steller sea lion prey species from the literature. Pacific sandfish is *Trichodon trichodon*, Pacific hake is *Merluccius productus*, and rainbow smelt is *Osmerus mordax*. Horizontal lines spanning the gadid (dashed) and forage (dash-dot) species show the range used by Winship and Trites (2003) in modeling sea lion bioenergetics. (Sources: McBride *et al.* 1959; Kizevetter *et al.* 1965; Jangaard *et al.* 1967; Stoddard 1968; McCallum *et al.* 1969; Kizevetter 1971; Jangaard 1974; Geraci 1975, 1986; Stansby 1976; Miller 1978; Ashwell-Erickson and Elsner 1981; Sidwell 1981; Croxall and Prince 1982; Brett 1983; Holdway and Beamish 1984; Harris 1985; Harris *et al.* 1986; Smith *et al.* 1986, 1988; Paul *et al.* 1990; Steward and Ibarra 1991; Buckley and Livingston 1994; Perez 1994; Paul and Paul 1998; Hendry and Berg 1999; Payne *et al.* 1999; Robards *et al.* 1999; Anthony *et al.* 2000; Logerwell and Schaufler, in press.)

fish, as well as with environmental and nutritional influences. Seasonal variation in the lipid content of herring ranges from 0.5% to 6% during early summer to around 20% later in the year (Stoddard 1968; Logerwell and Schaufler, in press; Iverson *et al.* 2002). Lipid content in pollock varies from a low of ~1.0% (spring) to a high of 8%–10% (between late summer and late winter). The caloric difference between a herring with 7.5% lipid and one with 19.4% lipid is nearly 100% (Geraci 1975). This variability must be considered when assessing the nutritional quality of any species of fish as Steller sea lion prey (Fadely *et al.*[10]).

Captive studies showing weight losses or body composition changes in Steller sea lions on lower calorie diets (Rosen and Trites 1999, 2000*a*, *b*) have used fish that did not represent the full range in energy density and proximate composition for fish in the wild. For example, the energy density of pollock used by Rosen and Trites (2000*a*, *b*) ranged from 1.04 to 1.13 kcal/g (Fig. 8), while pollock have energy densities as high as 1.85 kcal/g (Logerwell and Schaufler, in press) (Fig. 8). In the

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[10] Fadely, B. S., J. A. Zeligs and D. P. Costa. 1994. Assimilation efficiency and maintenance requirements of California sea lion (*Zalophus californianus*) fed walleye pollock (*Theragra chalcogramma*) and herring (*Clupea harengus*). Report to the National Marine Mammal Laboratory. National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115.

experiment conducted by Rosen and Trites (2000*a*), the energy densities of herring, pollock, and salmon were 10%, 19%, and 40% (respectively) lower than the highest reported values of these species in the wild (Fig. 8). Furthermore, the lowest energy density of herring fed to sea lions (1.74 kcal/g, Rosen and Trites 2000*a*) was 150% higher than the lowest reported value (0.7 kcal/g, Fig. 8). Considering the much wider range of energy densities and lipid contents seen in prey species in the wild, it is misleading to generalize the effect on sea lions of the more restricted caloric range of the samples used in captive feeding studies.

Incorporating results based on energy density ranges that are smaller than those in the wild has important consequences for the results of modeling studies that have examined the prey abundances required to support sea lion populations (Winship and Trites 2003). For example, Winship and Trites (2003) used a single annual value for the energy density of gadids, which ignored their seasonal variability in energy density (Jangaard *et al.* 1967). In addition, the single annual value for gadid energy density is drawn from a distribution (0.8–1.4 kcal/g) that does not extend high enough to encompass the range observed, at least for pollock, in nature (Fig. 8). The consequence of underestimating the energy density of gadids is an overestimation of prey biomass needed to sustain Steller sea lion individuals and populations in the Gulf of Alaska and eastern Aleutian Islands, where pollock and other gadids constitute a large fraction of the sea lion diet. The range of values for "forage fish" in Winship and Trites (2003) is mainly representative of herring and eulachon. This range is too high for other osmerids and sand lance (Fig. 8), which may constitute significant fractions of the sea lion diet. This leads to an underestimation of the food biomass necessary to sustain sea lions in Southeast Alaska and other parts of the Gulf of Alaska where forage fish forms a large part of sea lion diets at certain times of year. In addition, Atka mackerel has a much broader range of energy densities than the values used by Winship and Trites (2003), including a measured maximum (Logerwell and Schaufler, in press) that is twice as high as that used in Winship and Trites (2003). The use of more realistic values for Atka mackerel energy density in the model would reduce the biomass of fish consumed by sea lions in the Aleutian Islands. If similar corrections were applied to all prey species throughout the Alaska range of Steller sea lions, the longitudinal trend in per capita biomass requirements discussed by Winship and Trites (2003) may disappear.

Much of the discussion about the "quality" of a prey species has focused on the amount of lipid the prey contains which, for the most part, determines its energy density (Rosen and Trites 2000*a*, *b*; Winship and Trites 2003). Protein content may be equally important as lipid in defining nutritious food sources, particularly for young or working animals (Geraci 1975). Goodman-Lowe *et al.* (1999) fed Hawaiian monk seals diets composed of a variety of prey types and found that diets high in protein and low in lipid provided more metabolizable energy. All test diets, which were composed of herring and other prey species higher in protein and lower in lipid, provided significantly more metabolizable energy than did herring diets alone. There also appears to be limits to the ability of some pinnipeds to extract lipids and their energy from diets very high in fat. In Pacific harbor seals (*Phoca vitulina*), lipid digestibility declined with lipid intake and excess lipid in the diet was excreted in the feces (Trumble *et al.* 2003), a finding also applicable to ringed seals (Lawson *et al.* 1997). Harbor seals also had greater protein and total digestible energy intake when fed pollock than herring (Trumble *et al.* 2003).

Other support for pollock's junk food status comes from claims that it is less "digestible" (*i.e.*, yields a lower percent of consumed energy to the animal after all losses are accounted for) than fish with a higher fat content (Rosen and Trites 1999, 2000*a*, *b*). Digestibility, however, varies with the proximate composition of the prey, and with nutritional status, age, size, and sex of the test animal, as well as the meal size, frequency, and acclimation to the diet (Lavigne *et al.* 1982, Goodman-Lowe *et al.* 1999). Short-term, single-species studies on Steller sea lions have not adequately controlled for these sources of variability, and though useful to study some aspects of nutritional physiology, do not encompass the diversity found in the wild. Studies combining natural prey types can determine how diet composition affects the amount of metabolizable energy and an animal's assimilation efficiency (AE, the proportion of ingested nutrients absorbed from the gastrointestinal tract and available for maintenance functions) (Goodman-Lowe *et al.* 1999).

Differences in AE and other measures of digestive efficiency have been used to characterize prey quality despite the fact that digestive efficiencies measured for pollock, herring, and other pinniped prey species are all high (mostly greater than 85%; Rosen and Trites 2000*a*) and probably not significantly different. Measures of digestibility of pollock and other gadids were either similar to herring (Fadely *et al.*[10] using California sea lions, and Trumble *et al.* 2003 using Pacific harbor seals) or greater than herring (Miller 1978 using northern fur seals and Ashwell-Erickson and Elsner 1981 using Pacific harbor seals). In addition, results have been mixed in studies that have looked at the relationship between multispecies diets of different quality (defined as lipid content or energy density) and AE. One study on ringed seals (Lawson *et al.* 1997) found only weak relationships between AE and lipid content ($r^2 = 0.38$) or energy density ($r^2 = 0.267$) while another (Parson 1977) and one on Pacific walrus (Fisher *et al.* 1992) found none. Interestingly, AE in ringed seals was lower than expected when they were fed high-fat capelin (Lawson *et al.* 1997). This was also true for harbor seals fed high-fat herring (Trumble *et al.* 2003).

The heat increment of feeding (HIF; the energy cost of digesting a meal) may be higher for squid and pollock than for herring, thus making these species more costly to consume (Rosen and Trites 1999, 2000*b*). However, Markussen *et al.* (1994) reported a higher HIF (9.0% of gross energy intake) in juvenile harbor seals fed high-energy herring than those fed low-energy herring (5.1%). The effect of caloric density on HIF can vary (Costa and Kooyman 1984) and sometimes does not seem to be significant (Barbour 1993). Differences in lipid and protein content of herring-only diets did not appear to affect HIF (Rosen and Trites 1997), but did affect HIF in mixed diets of squid and herring (Rosen and Trites 1999). If HIF varies with prey composition of the diet, then seasonal differences in prey proximate composition may also be significant. Furthermore, the energy in HIF may not be wasted, but instead used in maintaining constant body temperature by decreasing the amount of energy needed for homeothermy (Kleiber 1975, Lavigne *et al.* 1982) in areas of cold ambient air and water temperatures.

As well as being nutritionally inferior foods, it has also been suggested that gadid fish may have negative health consequences on free-ranging Steller sea lions beyond those associated with their energy or lipid content (Rosen and Trites 2000*a*, *b*; Trites and Donnelly 2003). "Gadoid anemia" is a condition observed in captive mink, rats, and harbor porpoise that were fed diets either high in, or entirely composed of, gadids (Stout *et al.* 1960, Andersen 1966, Costley 1970, Rouvinen *et al.* 1997). Thompson *et al.* (1997) mention this as a possible cause of anemia in harbor seals. The factor responsible for the anemia is thought to be the post-mortem breakdown products of trimethylamine oxide (TMAO), one of which is formaldehyde. TMAO is a normal, physiologically important constituent found in many marine fish, and gadids are relatively high in TMAO. Post-mortem breakdown of TMAO can occur *via* exogenous bacterial enzymes or endogenous enzymes in fish. Endogenous enzymes which reduce TMAO are present in many species, but their breakdown products have been noted especially in gadid fish (Heberd *et al.* 1982) and squid (Amano and Yamada 1964, Yamada 1968, Stanley and Hultin 1984). The amount of TMAO breakdown products can be increased by physical damage to the fish prior to freezing, by frozen storage at temperatures above −30°C (or above −6°C in the case of bacterially aided breakdown), and by temperature fluctuations during freezing or during the thawing process. Symptoms of formaldehyde action were microcytic-hypochromic anemia, decreased body weights, changes in hematocrit levels, and pigmentation problems in the fur (the "cotton-fur" syndrome in mink; Stout *et al.* 1960). Formaldehyde may cause decreased intestinal motility (Smith 1968, cited in Costley 1970) and permeability, which would reduce iron absorption and lead to microcytic-hypochromic anemia (Fozzard and Dominguez 1969).

The negative effect of formaldehyde in the diet has been documented in captive mink, rats, and harbor porpoise fed previously frozen gadid fishes (Stout *et al.* 1960, Andersen 1966, Costley 1970, Rouvinen *et al.* 1997). However, anemia symptoms did not appear when raw, unfrozen gadid fishes were consumed (Costley 1970, Rouvinen *et al.* 1997). Thus, "gadoid anemia" is not likely to be found in marine mammals in the wild and seems to affect only captive animals fed previously frozen fish (Geraci 1981). Furthermore, the "gadoid anemia" identified by Thompson *et al.* (1997) in wild harbor seals was macrocytic, not microcytic anemia, which results from some vitamin deficiencies and loss of red blood cells due to hemorrhage or exposure to toxic chemicals (Wallach 1996). Thompson *et al.* (1997) however, note that a local source of toxins, perhaps from a sewage outfall within the area inhabited by the seals may be the cause of the anemia seen in their study. Little is known about how possible effects of TMAO breakdown caused by post-mortem changes in fish due to handling or storage problems may affect dietary studies of captive pinnipeds. Further studies should be done to quantify this effect.

Despite inconsistent or conflicting outcomes, the results of many captive feeding studies have been inappropriately extrapolated to wild populations of Steller sea lions. Data from previous captive Steller sea lion feeding studies indicating mass loss due to a "low energy" diet were collected from trials lasting only a few weeks (Rosen and Trites 1999, 2000*b*). If these studies were too short, results could be due to inadequate acclimatization of the digestive systems in the captive animals (Lawson *et al.* 1997). The sample size in these studies was very small (n = 4–6). Results of these studies could also be attributed to refusal of food due to palatability. Animals on a new diet are apt to eat less if not adequately acclimated to it (Hediger 1960, Wackernagel 1960). We know little about natural feeding rhythms and flexibility, and these, as well as the attractiveness of certain foods, can be affected by age and sex (Kear 1976; all of the captive sea lions used in the Rosen and Trites studies were juveniles). The manner of presentation, time of day, percent of day spent feeding, as well as the type of food itself, are all important in feeding behaviors of captive animals (Kear 1976). Also, endogenous cycles of reproductive age animals can cause seasonal difference in lipid deposition (Beck *et al.* 2003). Conclusions drawn from these studies, therefore, should not be applied to wild sea lions uncritically.

The considerations discussed above do not support the hypothesis that pollock (or other low energy density prey) are inherently less nutritious than herring or other "fatty" fishes. First, there is a large amount of seasonal variation in the energy density of all of the fish species that sea lions eat. Indeed, many of the species categorized as "fatty forage fishes" have energy densities similar to that of pollock for most of the year. The natural ranges of energy densities of fish have not been adequately represented in captive feeding studies done to date. Second, digestibility of both pollock and herring is high, and few if any statistically significant differences have been found. Third, there is no evidence that "gadoid anemia" exists in animals that eat raw, unfrozen fish, so it is unlikely to be found in wild sea lions. Due to some contradictory findings, the potential sources of variability that have not been adequately controlled for, and possible problems associated with single species diet studies, results of captive feeding studies should not be simplistically extrapolated to the sea lions in the wild. Pinnipeds are confronted with an ever-changing suite of prey species and apparently possess a flexible digestive system that, within limits, can compensate for periods when only low-energy density prey may be available by increasing protein and lipid assimilation efficiencies to maintain energy input (Trumble *et al.* 2003).

Conclusions

While western Steller sea lions may have been subjected to chronic nutritional stress (Trites and Donnelly 2003), it does not appear to be the result of regime-shift mediated increases in the proportion of low-energy prey species in their diet because: (1) gadid sea lion prey species fluctuate in abundance, and changes in the 1970s and 1980s in the North Pacific Ocean and Bering Sea were neither abnormal in their magnitude, nor were they particularly linked with the regime shift of 1976–1977 or cycles that are multiple decades in length. In particular, neither the Bering Sea nor the North Pacific Ocean was likely dominated by "forage" fish prior to the regime shift, and by gadids and flatfish after (Anderson and Piatt 1999, Hunt *et al.* 2002); (2) evidence supporting significant changes in sea lion diets coincident with the 1976–1977 regime shift is weak or non-existent; (3) prey energy density varies seasonally and is only one of many factors in the energy budget of a sea lion; reliance on "average" energy densities ignores the seasonal and spatial differences in energy content and the costs associated with foraging; (4) detrimental health effects associated with high gadid diets in captivity may have resulted from biochemical changes occurring in frozen/thawed fish, and have not been observed with certainty in the wild; and (5) extrapolation of the results of captive feeding experiments directly to sea lions in the wild may not be appropriate.

In addition, and perhaps most importantly, gadid fish species have been and continue to be principal components of the diets of other pinnipeds in the North Pacific and elsewhere (Table 6). Of particular note is the high frequency of occurrence of gadids in the diets of increasing populations of eastern stock Steller sea lions, harbor seals (*Phoca vitulina*), and California sea lions (*Zalophus californianus*) along the west coast of North America from Southeast Alaska to northern California (Bailey

Table 6. Gadid consumption by increasing populations of pinnipeds in the Atlantic and Pacific Oceans. All diet samples were scats or spewings and the data are reported as frequency of occurrence, except Bowen *et al.* (1993) for gray seals (*Halichoerus grypus*) and Alonso *et al.* (2000) for South American sea lions (*Otaria flavescens*), which are percent of total wet weight consumed; and Punt *et al.* (1995) for Cape fur seals, which is estimated proportion of the diet. Population status and trend refer to time period when data were collected.

Pinniped species or stock	Population status and trend	Location	% gadid in food habits samples (season or sex)	Source
California sea lion	High and increasing	California	~90% (summer)	Bailey and Ainley (1982)
		California	30%–50% (winter)	Bailey and Ainley (1982)
		Oregon	14%–74% (fall, winter)	Riemer and Brown[11]
		Washington	81%–83% (summer)	Gearin *et al.* (1999)
Eastern Steller sea lions	High and increasing	Oregon	62%–100% (summer)	Riemer and Brown[11]
		SE Alaska	55%–90% (all year)	Trites *et al.*[12]
		British Columbia	62% (all year)	Olesiuk (1993)
Harbor seals	High and increasing	NW Atlantic	71% (all year)	Williams (1999)
Cape fur seals	High and increasing	South Africa	Up to 60% (all year)	Punt *et al.* (1995)
S. American sea lion	High and increasing	Argentina	52% (males)	Alonso *et al.* 2000
Gray seals	Average and increasing	NW Atlantic	35% (all year) 16% (all year)	Bowen *et al.* (1993)

and Ainley 1982, Olesiuk 1993, Riemer and Brown,[11] Gearin *et al.* 1999, Williams 1999, Trites *et al.*[12]). These similar (or nearly identical in the case of eastern stock Steller sea lions) species have population trajectories opposite that of western Steller sea lions yet have diets rich in gadids year-round. Indeed, in a comparative analysis of food habits and population status of western Steller sea lions (declining), harp seals in the Barents Sea (declining), California sea lions along the U.S. west coast (increasing) and Cape fur seals (*Arctocephalus pusillus pusillus*) along the southwest

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[11] Riemer, S. D., and R. F. Brown. 1996. Marine mammal (Pinniped) food habits in Oregon. Contract No. 95–97 Report to the Pacific States Marine Fisheries Commission. Oregon Department of Fish and Wildlife, Newport, Oregon 97365. 26 pp. Riemer, S. D., and R. F. Brown. 1997. Prey of pinnipeds at selected sites in Oregon identified by scat (fecal) analysis, 1983–1996. Technical Report 97-6-02, Oregon Department of Fish and Wildlife, Newport, Oregon 97365. 34 pp.

[12] Trites, A. W., D. G. Calkins and A. Winship. 2003. Diets of Steller sea lions in southeast Alaska. Abstract of talk presented at Scientific Symposium, Marine science in the northeast Pacific: Science for resource dependent communities. Abstract available April 2004 at Exxon Valdez Trustee Council website, http://www.evostc.state.ak.us/pdf/2003%20Abstract%20Book.pdf, p. 212.

African coast (increasing), Shima *et al.* (2000*b*) found that, independent of their population trend, gadids were prominent in the diet of each pinniped (see also Punt *et al.* 1995). These observations alone argue strongly that diets rich in gadids do not have negative health consequences for pinnipeds nor do they cause their populations to decline.

Whether the recovery of the Steller sea lion population is currently affected by nutritional stress remains a subject of considerable debate (NMFS 2001, Alaska Sea Grant Program,[3] Trites and Donnelly 2003, NRC 2003). To ultimately address this uncertainty, we must better understand the energy budgets of sea lions, in particular adult females and juveniles. For instance, how do adult females partition energy between the developing fetus, lactation for their current pup, and their own requirements? How is the weaning process affected by prey availability, as well as maternal and juvenile condition? And ultimately, what are minimal and optimal threshold densities of prey for recovering and recovered Steller sea lion populations? In addition, just as there was not likely a single cause of the population decline, there may not be a single factor that leads to recovery. At low population sizes, the effects of some factors that may not have been involved in the decline (*e.g.*, predation) may become magnified. The development of successful strategies to facilitate the recovery of the Steller sea lion will hinge on an objective evaluation of the suite of factors that affect the population.

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