The sequential megafaunal collapse hypothesis: Testing with existing data

Douglas P. DeMaster [a,*], Andrew W. Trites [b], Phillip Clapham [a], Sally Mizroch [a], Paul Wade [a], Robert J. Small [c], Jay Ver Hoef [a]

[a] *NOAA Fisheries, 7600 Sand Point Way, NE, Seattle, WA 98115, USA*
[b] *Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, Vancouver, BC, Canada V6T 1Z4*
[c] *Alaska Department of Fish and Game, 1255 West 8th Street, Juneau, AK 99802, USA*

Abstract

Springer et al. [Springer, A.M., Estes, J.A., van Vliet, G.B., Williams, T.M., Doak, D.F., Danner, E.M., Forney, K.A., Pfister, B., 2003. Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? Proceedings of the National Academy of Sciences 100 (21), 12,223–12,228] hypothesized that great whales were an important prey resource for killer whales, and that the removal of fin and sperm whales by commercial whaling in the region of the Bering Sea/Aleutian Islands (BSAI) in the late 1960s and 1970s led to cascading trophic interactions that caused the sequential decline of populations of harbor seal, northern fur seal, Steller sea lion and northern sea otter. This hypothesis, referred to as the Sequential Megafaunal Collapse (SMC), has stirred considerable interest because of its implication for ecosystem-based management. The SMC has the following assumptions: (1) fin whales and sperm whales were important as prey species in the Bering Sea; (2) the biomass of all large whale species (i.e., North Pacific right, fin, humpback, gray, sperm, minke and bowhead whales) was in decline in the Bering Sea in the 1960s and early 1970s; and (3) pinniped declines in the 1970s and 1980s were sequential. We concluded that the available data are not consistent with the first two assumptions of the SMC. Statistical tests of the timing of the declines do not support the assumption that pinniped declines were sequential. We propose two alternative hypotheses for the declines that are more consistent with the available data. While it is plausible, from energetic arguments, for predation by killer whales to have been an important factor in the declines of one or more of the three populations of pinnipeds and the sea otter population in the BSAI region over the last 30 years, we hypothesize that the declines in pinniped populations in the BSAI can best be understood by invoking a multiple factor hypothesis that includes both bottom–up forcing (as indicated by evidence of nutritional stress in the western Steller sea lion population) and top–down forcing (e.g., predation by killer whales, mortality incidental to commercial fishing, directed harvests). Our second hypothesis is a modification of the top–down forcing mechanism (i.e., killer whale predation on one or more of the pinniped populations and the sea otter population is mediated via the recovery of the eastern North Pacific population of the gray whale). We remain skeptical about the proposed link between commercial whaling on fin and sperm whales, which ended in the mid-1960s, and the observed decline of populations of northern fur seal, harbor seal, and Steller sea lion some 15 years later.
© 2006 Published by Elsevier Ltd.

---

* Corresponding author. Tel.: +1 206 526 4000; fax: +1 206 526 4004.
 E-mail address: Douglas.DeMaster@noaa.gov (D.P. DeMaster).

1. Introduction

"Apex predators often initiate forces that cascade across successively lower trophic levels" (Estes et al., 1998).

The Sequential Megafaunal Collapse (SMC) hypothesis (Springer et al., 2003) is based on the premise that the depletion of large whale populations by commercial whaling in the 1960s and 1970s in the North Pacific (primarily fin (*Balaenoptera physalus*) and sperm whale (*Physeter macrocephalus*) populations in the Bering Sea and Aleutian Islands (BSAI) region) deprived mammal-eating ("transient-type") killer whales (*Orcinus orca*) of an important prey resource and thus forced them to switch from preying upon fin and sperm whales to preying upon populations of pinnipeds and sea otters (*Enhydra lutris*), precipitating sequential declines in those populations. This hypothesis was developed based on the timing and spatial pattern of large whale removals in the North Pacific and the timing of observed declines in four marine mammal populations using count data collected at different sites across the BSAI and Gulf of Alaska (GOA): harbor seals (*Phoca vitulina richardii*) at Tugidak Island (western GOA), northern fur seals (*Callorhinus ursinus*) at St. George and St. Paul Islands (southwest Bering Sea), Steller sea lions (*Eumetopius jubatus*) across the BSAI and GOA, and sea otters in the Aleutians (Fig. 1A).

There is no argument among scientists that the number of Steller sea lions in the BSAI and GOA has declined dramatically over the last 30 years (Braham et al., 1980; Kenyon and Rice, 1961; Loughlin et al., 1984; Loughlin et al., 1992; Merrick et al., 1987; Trites and Larkin, 1996). Large declines occurred in the eastern Aleutian Islands (AI) and western GOA between the 1960s and the mid-1970s, while numbers increased in the central AI. The number of sea lions throughout the BSAI and GOA began to decrease in the late 1970s, followed by a reduction in the rate of decline in the late 1990s. The overall abundance of the western population likely did not change appreciably from when the earliest counts were obtained (1956–1960) through 1980 (Loughlin et al., 1984), or perhaps increased slightly (Trites and Larkin, 1996). Whereas the peak population abundance in the late 1970s was approximately 250,000 animals, the most recent information (including non-pup counts through 2004) indicates that the population may have stabilized or is now in an increasing phase (Eberhardt et al., 2005; Winship and Trites, 2006) at approximately 40,000 animals.

Despite the general agreement about the patterns of sea lion population change, there is considerable argument regarding the factors responsible for the divergent population trajectories observed across regions over the last 40 years. Some authors have proposed that a multitude of factors together produced this unusual trajectory (e.g., Loughlin and York, 2000; NMFS, 2001; NRC, 2003). Others have proposed that a series of different factors, acting sequentially, may have produced the decline (e.g., Fritz et al., 1995; Matkin et al., 2002; NMFS, 2001). Another view is that a single underlying factor best explains the available data (Trites and Donnelly, 2003; Springer et al., 2003; Trites et al., 2006a).

There has been far less discussion of factors responsible for declines in the other three species (i.e., Pribilof Islands northern fur seal, western Alaska harbor seal, and southwestern Alaska sea otter) that are the subject of the SMC hypothesis (Springer et al., 2003). As was the case for the western population of Steller sea lion, there is no argument that the southwestern Alaska population of sea otter (Estes et al., 1998) and the Pribilof Islands population of northern fur seal have declined (Trites, 1992). Although some have argued that the decline in the northern fur seal population in the BSAI has been continuous since the 1970s (Springer et al., 2003), others have pointed out that the trajectory of the fur seal population in the BSAI has been complex and is best characterized as having increased throughout most of the 1970s, declined from the late 1970s to the early 1980s, remained relatively constant from the mid-1980s to the mid-1990s, and declined again beginning in the mid-1990s (Trites, 1992; Angliss and Lodge, 2004; Fig.1b). Data are inconclusive regarding trends in the BSAI and GOA populations of harbor seal, although clear declines were reported in harbor seal abundance at Tugidak Island in the 1970s (Pitcher, 1990) and in Prince William Sound from at least 1984 (Frost et al., 1999). Regarding the decline in sea otter abundance, only Estes et al. (1998), have proposed that
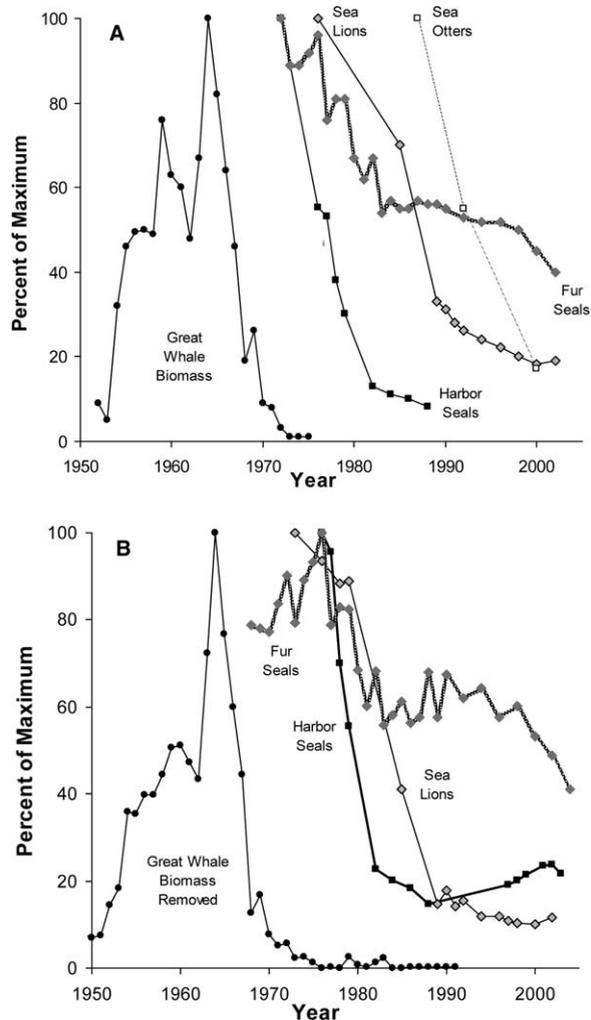
Fig. 1. Biomass of large whales removed and changes in abundance of harbor seals, Steller sea lions, northern fur seals and northern sea otters at select sites in the Gulf of Alaska and Aleutian Islands. Panel A shows the data compiled by Springer et al. (2003) to conclude that declines of pinnipeds were sequential. Panel B shows harbor seal counts from the southwest beach of Tugidak Island, non pup Steller sea lion counts from the nearby Chowiet Island, and northern fur seal pup counts from St. Paul Island. These data suggest that all three populations began declining at about the same time. The biomass of large whales removed shown in Panel B is the annual catch in the Bering Sea, Aleutian Islands and Gulf of Alaska (i.e., catches from 50° N latitude and above) (from Mizroch and Rice, 2006) and differs from that calculated by Springer et al. in Panel A. Note that catch is not an index of numbers or biomass of whales present. See text for further details.

killer whale predation is the primary factor. The declines in abundance of Tugidak Island harbor seals and Pribilof Island northern fur seals (since 1975) are unexplained (Pitcher, 1990; Trites, 1992). Other than the SMC hypothesis, no comprehensive explanations have been published. The purpose of our study was to test whether the SMC hypothesis is consistent with available information on these prey populations. Here, we take an inductive approach in evaluating the merits of the SMC hypothesis and two other hypotheses that we have developed.

2. The sequential megafaunal collapse hypothesis

Springer et al. (2003) reported that "Populations of seals, sea lions, and sea otters have sequentially collapsed over large areas of the northern North Pacific Ocean and southern Bering Sea during the last several

decades. A bottom–up nutritional limitation mechanism induced by physical oceanographic change or competition with fisheries was long thought to be largely responsible for these declines. The current weight of evidence is more consistent with top–down forcing. Increased predation by killer whales probably drove the sea otter collapse and may have been responsible for the earlier pinniped declines as well. We propose that decimation of the great whales by post-World War II industrial whaling caused the great whales' foremost natural predators, killer whales, to begin feeding more intensively on the smaller marine mammals, thus ''fishing-down'' this element of the marine food web. The timing of these events, information on the abundance, diet, and foraging behavior of both predators and prey, and feasibility analyses based on demographic and energetic modeling are all consistent with this hypothesis.''

The premise of our paper is that the SMC hypothesis is not consistent with available information. In particular, it is our contention that: (1) large whales (other than minke whales [*Balaenoptera acutorostrata*] and gray whale [*Eschrichtius robustus*] calves) were never an important prey item in the diet of mammal-eating killer whales, (2) there was not a declining trend in the net biomass of all large whales in the BSAI in the 1960s and 1970s, and (3) the decline in the abundance of pinnipeds in the BSAI is best characterized as spatially heterogeneous, but within a given region approximately concurrent (and not sequential over the range of the three pinniped populations under consideration between the western Gulf of Alaska and the western Aleutian Islands). We suggest that the two alternative hypotheses, described herein, are more consistent with the available data than is the SMC hypothesis.

3. Assumptions of the sequential megafaunal collapse hypothesis

Springer et al. (2003) speculated that predation by killer whales resulted in the sequential declines in abundance of three populations of pinnipeds in the BSAI and the southwestern Alaska population of sea otter. While they are not arguing that bottom–up interactions have no influence on the dynamics of these four populations, they suggest that the dominant interaction in this ecosystem for these four marine mammal populations is top–down forcing (i.e., predation by killer whales). In this paper, we are not arguing that top–down forcing has no influence on the dynamics of these four populations. Rather, we are proposing that both top–down and bottom–up forcing mechanisms are important but it is not possible to determine with existing data which mechanism predominates for at least the three pinniped populations that are the subject of the SMC. We remain skeptical of the proposed link between commercial whaling on fin and sperm whales, which ended in the mid-1960s, and the declines of populations of northern fur seal, harbor seal, and Steller sea lion that occurred some 15 years later.

We evaluated the following three assumptions that are necessary for the mechanism proposed in the SMC hypothesis to function:

1. Killer whales were dependent on fin and sperm whales as prey in the Bering Sea;
2. The biomass of all large whales was in decline in the 1960s and 1970s in the Bering Sea;
3. Pinniped declines in the 1970s and 1980s in the BSAI were sequential.

4. Testing the assumptions

Assumptions #1 and #2: Killer whales were dependent on fin and sperm whales as prey in the Bering Sea and the biomass of large whales was in decline in the 1960s and 1970s.

The SMC hypothesis supposes that great whales were an important prey for killer whales and, furthermore, is based on expectations that fin, sei (*Balaenoptera borealis*), and sperm whale numbers in the vicinity of the Aleutian Islands declined in the 1960s through the early 1970s due to commercial whaling and that other large whales were not available as prey to killer whales because of prior over-exploitation and a lack of recovery (Springer et al., 2003). Springer et al. likely assumed that fin and sperm whales were an important part of the diet of mammal-eating killer whales because these were the predominant species of large whale harvested in the vicinity of the Aleutian Islands in the 1950s and 1960s (Mizroch and Rice, 2006; Wade et al., 2006). However, there is nothing in the published literature to indicate that fin and sperm whales were ever an impor-

tant prey resource for killer whales in the vicinity of the Aleutian Islands (Mizroch and Rice, 2006; Wade et al., 2006; Trites et al., 2006b). Although equivocal, the best available data indicate that mammal-eating killer whales in this area and elsewhere prey primarily on pinnipeds, minke whales, gray whale calves and small odontocetes (Mizroch and Rice, 2006; Wade et al., 2006; Trites et al., 2006b).

Furthermore, the SMC hypothesis relies in part upon the biomass of landed large whales being positively correlated with the total biomass of all large whales. However, it appears that the pattern of commercial landings of large whale biomass (primarily from fin and sperm whales) in the BSAI in the 1950s and 1960s (Springer et al., 2003; Fig. 1) was not well correlated with the trajectory of large whale biomass (i.e., total abundance of all large whale species) in this same area during this same time period (Mizroch and Rice, 2006; Pfister, 2004; Pfister and DeMaster, 2006; Wade et al., 2006; Whitehead and Reeves, 2005). Unfortunately, it is not possible to derive a reliable time series of total large whale biomass because data for several of the key species (e.g., sperm and fin whale) are lacking. There is no doubt that large whale biomass in the North Pacific has significantly declined (Pfister, 2004) since commercial whaling commenced in the 19th Century for gray, northern right (*Eubalaena japonicus*), and bowhead (*Balaena mysticetus*) whales, and in the 20th Century for other species of baleen whales and sperm whale. However, the SMC hypothesis is concerned with the net change in large whale biomass in the 1960s.

Quantitative data are not available to allow for the construction of the appropriate time series of abundance (hence biomass) for fin and sperm whales – the two species predominantly killed by commercial whalers in the 1960s (Mizroch and Rice, 2006). The available qualitative data indicate that, while sperm whale and fin whale biomass likely declined in the Bering Sea in the 1960s, these declines were likely offset by increasing abundances of other large whale species in the 1960s and 1970s (see below and see Pfister, 2004; Pfister and DeMaster, 2006: Fig. 4b; Wade et al., 2006: Figs. 6 and 7). This conclusion is also consistent with findings reported by Whitehead and Reeves (2005): ''there was no sudden global decline in either numbers or biomass of living whales during the 1970s'' (although it should be noted that the conclusions of White & Reeves were not specific to the North Pacific Ocean). Therefore, if the SMC hypothesis was correct regarding the link between commercial whaling and the importance of large whales in the killer whale diet, we would have expected mammal-eating killer whales to have shifted from preying on fin and sperm whales to preying on other species of large whales in the BSAI, rather than shifting their focus to pinnipeds and sea otters.

At least one species of large whale was not significantly impacted by commercial whaling. Minke whales are a known prey species of killer whales and were never a target of commercial whaling. They are thought to be abundant throughout the area (Pfister, 2004). Therefore, minke whale biomass in the 1950s and 1960s was likely constant throughout the period.

Humpback whale (*Megaptera novaeangliae*) abundance has increased since the early 1980s, which is consistent with an hypothesis that humpback abundance likely started to increase after whaling ceased in the late 1960s (Pfister and DeMaster, 2006). Mizroch et al. (2004) estimated that the central North Pacific population of humpback whale increased by 10% per year (1.10, 95% CI 1.03–1.16) with a basin wide population on the order of 6000 animals in the early 1990s (Calambokidis et al., 1997). In addition, it appears that the biomass of the eastern North Pacific gray whale population and the western Arctic bowhead whale population increased throughout the 1950s and 1960s (Eberhardt and Breiwick, 1992; Hobbs et al., 2004; IWC, 2004). The gray whale population was estimated to have increased from 1968 to the 1990s at a rate of approximately 3% per year to a level of 17,000–28,000 animals between 1998 and 2002 (IWC, 2004). The bowhead whale population increased at a rate of approximately 3% per year to approximately 10,000 animals in 2002 (IWC, 2004). It should be noted that the presence of bowhead whales in the Bering Sea is only relevant to this argument if the assumption made by Williams et al. (2004) is correct that mammal-eating killer whales remain in the vicinity of the Bering Sea/Aleutian Islands on a year round basis. Lacking the necessary information on seasonal movements of mammal-eating killer whales known to be present in the Bering Sea during the summer months, it is not possible to verify this assumption at this time.

Based on the information presented herein and information reported in Pfister and DeMaster (2006, Fig 4b), Wade et al. (2006); Mizroch and Rice (2006); and Whitehead and Reeves (2005, Fig. 2), it appears unlikely that killer whales in the Bering Sea depended upon large whales prior to commercial whaling, or that a shift occurred in their diets, or the overall biomass of all large whales was in decline in the 1960s and 1970s in the Bering Sea.

Assumption #3: Pinniped declines in the 1970s and 1980s in the BSAI were sequential.

An important component of the SMC hypothesis is the sequential declines in the BSAI and GOA Alaska populations of harbor seal (ca 1972), the Pribilof Island population of northern fur seal (ca 1974), and the western population of Steller sea lion (ca 1976: Fig. 1a). Further, the SMC hypothesis suggests that all three declines started prior to the regime shift in the North Pacific in 1977. We agree with Springer et al. (2003) that the declines in sea otter abundance in the vicinity of the Aleutian Islands occurred after the declines in the three populations of pinnipeds. However, there are several problems in determining whether the declines in abundance of the three pinniped species were sequential or concurrent and whether these declines occurred before or after the regime change in 1977.

Springer et al. (2003) cite Pitcher (1990) as the source of the harbor seal counts used to derive their population trajectory. These were annual mean counts of animals between 1976 and 1988, conducted during the molting period from a single haulout on southwestern Tugidak Island. No counts are available prior to 1976, although Pitcher (1990) estimated the abundance for the entire island (including animals feeding at sea) from 1964 to 1988 based on a simulated population trajectory using the number of pups killed on the island in 1964 and 1965. Springer et al. (2003) apparently combined the estimated total population size (from Pitcher's model) in 1972 with the partial island counts of animals on shore from 1976 to 1996 in their population trajectory (Fig. 1A). Combining these disparate data sets is misleading and creates the false impression that a dramatic decline in harbor seal numbers occurred between 1972 and 1976 (Fig. 1A). The decline in abundance could have begun earlier than the first count, but the data are not available to test this hypothesis.

Springer et al. (2003) suggested that the decline in counts of harbor seals at Otter Island (one of the Pribilof Islands and isolated from the remaining seal populations) was further evidence that the trajectory of harbor seal numbers at the Tugidak Island haulout was representative of trends in harbor seal abundance from the much larger BSAI and GOA regions. However, the haulout on Tugidak Island is not representative of the larger regions. Counts of several large haulouts in the southeast Bering Sea were relatively stable from 1966 to 1990, while counts at other large haulouts increased during the mid-1970s (Hoover-Miller, 1994).

Springer et al. (2003) computed an average number of northern fur seal pups born on St. Paul and St. George Islands (Fig. 1A). Such an approach fails to account for the years when pups were not counted on St. George Island and places too much weight on the count data from St. George Island relative to its small contribution to overall fur seal numbers (i.e., approximately 10% of total pup production). By averaging the pup counts from the two islands, it appears in Fig. 1A that pup production was in a slow decline from the early 1980s to the mid-1990s and then declined at a more rapid rate after ~1995 (Fig. 1A). Plotting only pup counts from St. Paul Island (Fig. 1B) indicates that the population was stable from approximately 1984 to 1996. Our interpretation of these data (as shown in Fig. 1B) is that they are not consistent with the SMC hypothesis, as the decline was not monotonic as predicted. A more important problem, however, is that the data for the initial year of the time series of fur seal pup counts, which indicates a decline in abundance starting between 1974 and 1976 (Springer et al., 2003), does not correspond with published counts. After correcting these two problems, our interpretation of the time series of northern fur seal pup counts up until 1980 is that the Pribilof Islands population declined following a period of increasing pup production in the early to mid-1970s and (2) the decline started to occur sometime between 1978 and 1980.

Comparisons of pinniped population dynamics for the purpose of evaluating whether observed declines in abundance were concurrent or sequential should be from common geographical regions, where trajectories of count data have similar patterns. Furthermore, given the data reported in Loughlin et al. (1984), York (1994), Eberhardt et al. (2005), Winship and Trites (2006), Frost et al. (1999) and Hoover-Miller (1994), it is neither possible nor meaningful to conclude that the western population of Steller sea lion and the southwestern population of harbor seal had population trajectories that were uniform over their entire distribution. Rather, where the data exist, it appears that different portions of a population's range had very different population trajectories. We have attempted a comparison of population trajectories from a common region by examining the change in abundance of harbor seals at the southwestern haulout on Tugidak Island with Steller sea lion abundance at the nearby Chowiet Island rookery and northern fur seals from St. Paul Island. Chowiet Island sea lion counts are a more appropriate unit of comparison with Tugidak harbor seal counts than the index counts drawn from the entire sea lion range by Springer et al. (2003). In part, this is because of the known heterogeneity in the nature and magnitude of population trajectories by sub-areas for the western Steller sea lion population

(Loughlin et al., 1984; York, 1994; Trites et al., 2006a; Winship and Trites, 2006) and GOA harbor seals (Frost et al., 1999; Small et al., 2003). Including the counts of northern fur seals from St. Paul Island is appropriate because this is the subpopulation with the most complete census data, and because these animals migrate south into the Gulf of Alaska in the fall and return to St. Paul Island via the Gulf of Alaska in the spring.

A statistical analysis of the temporal pattern of declines in numbers of Steller sea lion, harbor seal, and northern fur seal from a common geographical region is presented in Appendix 1. Unfortunately, Springer et al. (2003) did not include a statistical analysis to support their conclusion that the observed declines in abundance of the three pinniped populations and the one sea otter population were sequential; therefore, we can not compare analyses. It should also be noted that such an analysis is complicated because the census data for two of the three populations begin with maximum counts (i.e., Steller sea lion and harbor seal). Therefore, it is not possible to tell if the observed declines started at the time of the first census or prior to the first census. To avoid this problem, we fit sigmoid curves to the three population trajectories for pinnipeds and tested a series of hypotheses regarding the relationship among the timing of the inflection points for the three time series (Appendix 1). We made the reasonable assumption that the temporal relationship among the three time series (i.e., sequential versus concurrent declines) could be inferred from the relationship among the timing of the three inflection points (rather than testing hypotheses regarding the onset of the declines). We used general likelihood ratio tests to evaluate which hypotheses could be rejected. Based on this analysis, it appears that harbor seals at Tugidak Island and northern fur seals at St. Paul Island had their steepest decline (i.e., the time of the inflection point) at approximately the same time, around 1979, while Steller sea lions from the Chowiet Island rookery had their steepest decline about 4 years later, around 1983, according to the model where $\mu_1 = \mu_3$. We recognize that this test is not quite the same as testing whether the declines in abundance for the three pinniped populations were sequential in onset or even whether the declines in abundance from a common geographical region began in sequence. However, we conclude from our analysis that in a common geographic region (1) the timing of declines in abundance for harbor seals and northern fur seals was concurrent and preceded the decline in Steller sea lions by about 4 years and (2) most of the declines in pinniped abundance were likely to have followed the regime shift in 1977.

Estimated dates of maximum rate of decline (i.e., the estimated year in which the inflection point occurred) were 1967.9 for whale catches, 1978.5 for harbor seals, 1979.8 for northern fur seals, and 1983.3 for Steller sea lions. For sea otters, we used the midpoint of the decline, 1993.5, as the decline appears linear in the published data. The Cramer–von Mises test statistic for these 5 dates with 4 inter-event intervals was 0.061, which was less than the critical value of 0.177 for $\alpha = 0.10$. Hence, we cannot reject the hypothesis that the timing of the declines occurred at random. That is, our test for random occurrence of declines does not support the SMC hypothesis, which predicts a regular pattern in the onset of the declines for the three pinniped and one sea otter population. Interestingly, the test does not support a pattern of decline that was highly clumped, which would be the case if the regime shift in 1977 were the only factor driving the declines in at least the pinniped species.

Based on the information summarized above, we conclude that the available data do not support the assumption that the declines of populations of northern fur seal, Steller sea lion, and harbor seal in the vicinity of the BSAI were sequential as predicted by the SMC hypothesis. Further, we suggest that a parsimonious application of the SMC hypothesis is not consistent with the complex trajectory of the Pribilof Island population of northern fur seal (i.e., declining population between 1978 and 1983; stable population between 1983 and 1995; and a declining population between 1995 and 2004).

5. Discussion

The purported link between commercial whaling in the vicinity of the Aleutian Islands in the 1960s and the subsequent decline in the abundance of several pinniped and one sea otter population is not supported by the available data or by a number of recent studies. Wade et al. (2006) reviewed a broad range of data and concluded that the hypothesis that killer whale predation switched from primarily large whale prey to other marine mammals species and induced declines in populations of pinnipeds and sea otters was based upon a selective and simplistic analysis of trend data. They also concluded that the prey-switching hypothesis rests upon a poorly supported assumption regarding the importance of (non-calf) large whales as primary prey items for killer whales.

Mizroch and Rice (2006) reviewed the historical information on stomach contents of sampled killer whales in the North Pacific and found that less than 3% of the mammal-eating killer whale ecotype examined prior to 1968 contained large or mid-sized whale prey items (based on stomachs with food items present). Mizroch and Rice also concluded that the primary pulse of commercial whaling in the vicinity of the Aleutian Islands and Gulf of Alaska (i.e., north of 50° North latitude) was between 1963 and 1965 and primarily targeted sperm and fin whales (by order of biomass removed in the 1950s and 1960s). For the most part, legal commercial whaling in this area ended in 1967, after which most catches were made south of the Aleutian Islands (i.e., south of 50° North latitude, Mizroch and Rice, 2006; Figs. 4, 5, and 11).

Although killer whales are known to prey sometimes upon calves, evidence from scarification studies and from direct observations of predation attempts strongly suggests that most such attacks occur before calves reach the high-latitude waters that are the focus of the SMC hypothesis (Mehta, 2004). Thus, the idea that, prior to commercial whaling, killer whales were sustained primarily by a diet of whale calves in high latitudes is not supported by the available evidence. It is also worth noting that while attacks on sperm whales have been documented on rare occasions, fin whales do not appear to be targeted as prey by killer whales, as evidenced by the lack of reported attacks and very low rates of scarring (Mehta, 2004).

In addition, Trites et al. (2006b) examined the population increases of sea otters, harbor seals and Steller sea lions that followed cessation of commercial whaling in British Columbia. They found no evidence that killer whales had impeded growth of the British Columbia populations of pinnipeds, and concluded that the responses were inconsistent with the SMC hypothesis. They also concluded that the hypothesis was not supported by what is known about the ecology of killer whales and the biology of large whales.

In contrast to our conclusions and those of Wade et al. (2006) and Trites et al. (2006b), Williams et al. (2004) concluded there was evidence supporting the SMC hypothesis based on theoretical bioenergetic calculations. They show that as few as 40 killer whales could have caused the decline in abundance of western Steller sea lions, and as few as 5 killer whales could have caused the observed decline in the southwestern Alaska population of sea otters. The changes in mortality needed to account for the observed declines in these two species by a minimum number of killer whales was based on the assumption that all of the caloric needs were derived from a single species of prey, which is not supported by dietary studies on killer whales. Williams et al. (2004) also determined that "relatively minor changes in killer whale feeding habits could easily account for the recent changes in sea otter and Steller sea lion populations observed for the Aleutian Islands".

The authors of the SMC hypothesis speculated that predation by killer whales on three populations of pinnipeds and one population of sea otter caused the observed declines and that the sudden onset of the sequential dietary shifts of mammal-eating killer whales from harbor seals to northern fur seals to Steller sea lions and lastly to sea otters was the result of the severe reduction in biomass of the preferred prey of killer whales – large whales in the 1950s and 1960s. In our opinion, the information reported above is not consistent with the SMC. In particular, the proposed link between the impact of commercial whaling in the vicinity of the Aleutian Islands in the 1960s and 1970s and the subsequent decline of the three pinniped populations and one sea otter population is not supported by the available data.

Whereas it is possible that killer whale predation contributed to the decline in the western population of Steller sea lion (particularly when sea lion numbers were low), a parsimonious candidate for the most significant factor, or at least one of several key factors, is nutritional stress. Many studies have supported the conclusion that western Steller sea lions were nutritionally stressed in the 1980s relative to the 1970s (e.g., Calkins et al., 1998; Pitcher et al., 1998; Benson and Trites, 2003; and Trites and Donnelly, 2003). In particular, a number of studies reported changes in diets, body size, survival rates, and reproductive rates that are consistent with Steller sea lions having experienced a nutritional insult in the western portion of their range between the 1970s and 1980s (Trites and Donnelly, 2003). Most notably, Steller sea lions were smaller in length, girth, and weight in the 1980s compared to animals prior to the population decline (Calkins et al., 1998). They also appeared to have incurred an increase in juvenile mortality (York, 1994) and a decrease in productivity as measured by pup counts, the incidence of failed pregnancies, and reduced pregnancy rates among lactating females (Pitcher et al., 1998). Finally, Hennen (2006) reported that the population trajectories of individual rookeries of western Steller sea lions were positively correlated with commercial fishing effort in the 1980s, but were not correlated with commercial fishing effort in the 1990s. He suggested that conservation measures imposed on the fishery in the 1990s were responsible for this change. His findings are also consistent with the

hypothesis that nutritional stress (which in this case was associated with commercial fishing effort) was an important factor in causing the observed decline of western Steller sea lions. Most of these changes in life history reported in this paragraph are not consistent with top–down (i.e., predation) forcing mechanisms alone.

Evidence of nutritional stress having occurred during the 1990s is much less conclusive than for the 1980s due to changes in data collection protocols (Trites and Donnelly, 2003). However, the conclusion drawn by the National Research Council (NRC) panel on the decline of the western population of Steller sea lion (NRC, 2003), that there is no evidence for nutritional stress in the 1990s in this population, appears to have been premature. The data that exist on diets and blood chemistries indicate that the nutritional challenges faced by sea lions in the 1980s may have continued for another decade (Zenteno-Savin et al., 1997; Sinclair and Zeppelin, 2002; Merrick et al., 1997; Winship and Trites, 2003). Sea lions at rookeries that consumed diets of low diversity and low energy prey were also noted to have declined more rapidly than regions where diets were more diverse and richer (Merrick et al., 1997; Winship and Trites, 2003). Finally, population modeling also indicated a drop in birth rates at some sea lion rookeries during the 1990s (Holmes and York, 2003; Winship and Trites, 2006). Again, the changes in life history reported in this paragraph are not consistent with top–down (i.e., predation) forcing mechanisms alone.

We suggest two alternative hypotheses to explain the observed decline in pinnipeds in the vicinity of the Aleutian Islands in the 1970s to date:

(1) Both bottom–up and top–down forcing were instrumental in driving the dynamics of harbor seal, sea lion, and fur seal populations in the vicinity of the Aleutian Islands.
(2) Regarding the mechanism for top–down forcing, the recovery of the eastern North Pacific gray whale population and their associated seasonal abundance in the eastern Aleutian Islands in spring (during migration) may have produced a localized increase in the number of mammal-eating killer whales in that region that then remained and switched to feed on other marine mammal prey in other seasons.

Neither of these hypotheses is linked to the removal of large whales by commercial whaling. The second hypothesis should be considered a subset of the first, as there is irrefutable evidence (see above) that nutritional stress was an important factor affecting Steller sea lions during the 1980s and to a lesser extent in the 1990s.

Whitehead and Reeves (2005) recently proposed a third alternate hypothesis. They have suggested that killer whales did not utilize free-ranging large whales as prey, but did scavenge intensely on large whale carcasses produced by the commercial whaling fleet in the mid-20th Century. Therefore, with the cessation of commercial whaling, "diet shifts may have triggered declines in other prey species". As noted above, this hypothesis would not be consistent with the available evidence for nutritional stress affecting Steller sea lions during the 1980s.

Based on the available data, it appears reasonable to infer that multiple factors have influenced the population dynamics of Steller sea lions (Loughlin and York, 2000), including legal and illegal shooting, mortality incidental to commercial fisheries, predation by killer whales and nutritional stress. Trites et al. (2006a) have also postulated that multiple factors such as reduced rates of pregnancy, increased incidence of disease, and greater susceptibility to predation likely contributed to the Steller sea lion decline. They further noted that all of these factors could have been induced by a major change in ocean climate in the late 1970s that negatively altered the quantity, quality and accessibility of prey. In contrast, Fritz and Hinckley (2005) dispute the hypothesis that changes in climatic conditions in the late 1970s negatively affected sea lions. Unfortunately, published data on changes in condition indices, indicative of nutritional stress, are not available for the three populations of harbor seal currently recognized in Alaska or for the Pribilof Islands population of northern fur seal.

Hypothesis 2 was proposed by John Durban (pers. comm., National Marine Mammal Laboratory, 7600 Sand Point Way, Seattle, WA 98115). Under this scenario, the recovery of the eastern North Pacific population of gray whale and their migration by all age classes, including calves, through Unimak Pass in the eastern Aleutian Islands could have attracted large numbers of mammal eating killer whales to this region in the spring. Gray whale numbers rose from 10,000–12,000 in the late 1960s to approximately 17,000–28,000 between 1998 and 2002 (IWC, 2004). Recent observations, as well as traditional knowledge, indicate that killer whales feed extensively on gray whales during their northbound migration in the spring (Matkin and

Barrett-Lennard, North Gulf Oceanic Society and Vancouver Aquarium Marine Science Center, unpublished data), and that at least some individual killer whales can be found in the area over the subsequent summer months (NMML, unpublished data). In months when gray whales migrate out of this area, killer whales would have been forced to prey on other species of marine mammals. As noted above, however, the notion that predation alone, without any contribution from other factors (e.g., nutritional stress), has driven the observed decline of the western population of Steller sea lion is not consistent with the available data.

As noted by Matkin et al. (2002), it appears unlikely that killer whale predation on western Steller sea lions was the only or primary cause of the decline in abundance observed in the 1980s and 1990s. The line of inductive reasoning reported in this paper is consistent with the conclusion reported by Matkin et al. (2002). Additional studies and analyses may yet reveal merits of the SMC hypothesis; however, the information that is available at present to test this hypothesis fails to support the contentions that have been put forward. Our opinion is that multiple factors were ultimately responsible for the decline of the three pinniped populations reported by Springer et al. (2003). Further, it seems unlikely that the commercial harvest on fin and sperm whales, which for the most part ended in the mid-1960s, unleashed prey switching by mammal eating killer whales that dramatically affected the dynamics of three pinniped populations a minimum of 15 years later.

Appendix 1

Data for these analyses are presented in Fig. 1B of the main paper and are available on request from the corresponding author (DeMaster).

1.1. Statistical methods

1.1.1. Statistical model for estimating date of maximum decline
The class of statistical models we assumed for the data is given by

$$Y_{ij} = f_i(x_{ij}) + \varepsilon_{ij}, \tag{A.1}$$

where Y_{ij} is the response (percent of maximum) for the jth time period for the ith species, x_{ij} is the year of the jth time period for the ith species, $f_i(x_{ij})$ is a function of time (year) for the ith species, and ε_{ij} is independently distributed from a normal distribution for the jth time period for the ith species; $\varepsilon_{ij} \sim N(0, \pi_i f_i(x_{ij}))$. Here, year (x_{ij}) is between 1968 and 2004, and $i = 1, 2, 3$, or 4 for harbor seal abundance, Steller sea lion abundance, northern fur seal abundance, and great whales biomass removed, respectively. It is also common for errors to increase as the response increases, so we let the variance be proportional to the mean with parameter π_i for each species.

Because the responses have shown declines, with some showing stability either before or after the decline, we need a flexible nonlinear model for $f_i(x_{ij})$. Such a curve is given by

$$f_i(x_{ij}) \equiv \alpha_i + \eta_i \exp(\beta_i(x_{ij} - \mu_i))/(1 + \exp(\beta_i(x_{ij} - \mu_i))), \tag{A.2}$$

which is just a logistic (sigmoid) curve, scaled so that the lower asymptote is α_i, the upper asymptote is η_i, and it is parameterized so that β_i controls the steepness of the curve, and μ_i is the inflection point (time of steepest ascent or descent, depending on the sign of β_i). Other models are possible, but we chose this particular nonlinear model because the single parameter μ_i locates the inflection point, so we can test whether curves are "shifted" by setting some $\mu_i = \mu_k$; $i \neq k$. We can then use likelihood ratio tests and Cramer-von Mises tests on the timing of the inflection points, μ_i; $i = 1, 2, 3, 4$.

1.1.2. Fitting the model using maximum likelihood
Using Eqs. (A.1) and (A.2), for any species data, two times the negative log-likelihood is

$$l_i(\boldsymbol{\theta}_i; \mathbf{y}) = -\log[p(\mathbf{y}_i; \boldsymbol{\theta}_i)] \propto \sum_{j=1}^{n_i} \log\left(\sqrt{\pi_i f_i(x_{ij})}\right) + \frac{1}{2\pi_i f_i(x_{ij})}(y_{ij} - f_i(x_{ij}))^2,$$

where $\boldsymbol{\theta}_i = (\alpha_i, \eta_i, \beta_i, \mu_i, \pi_i)'$. Minimizing $l(\boldsymbol{\theta}; \mathbf{y})$ for $\boldsymbol{\theta}$ yields the maximum likelihood estimates. We programmed $l(\boldsymbol{\theta}_i; \mathbf{y}_i)$ using the computer language R and minimized it using the BFGS method (a quasi-Newton method),

published simultaneously in 1970 by Broyden, Fletcher, Goldfarb and Shanno, which yields the maximum likelihood estimates.

1.1.3. Likelihood ratio tests

We initially want to test whether we can reject the null hypothesis that the 3 pinniped species: harbor seals, fur seals, and sea lions, declined at the same time. First, we form the joint log-likelihood for the 3 species,

$$l(\boldsymbol{\theta}; \mathbf{y}) = \sum_{i=1}^{3} l_i(\boldsymbol{\theta}_i; \mathbf{y}),$$

where $\boldsymbol{\theta} = (\boldsymbol{\theta}_1', \boldsymbol{\theta}_2', \boldsymbol{\theta}_3')'$. The most general model we can build is to have all free parameters that have separate estimates for each species. This gives completely separate curves for the 3 species. However, we can consider simpler models (fewer estimated parameters) where we set some elements in $\boldsymbol{\theta}$ equal; for example, by assuming $\mu_1 = \mu_2 = \mu_3$, which would indicate that mid-points of declines in all 3 species occurred at the same time, although the rates may have been different (which is controlled by β_i). The simpler model is always a subset of the most general model, and we wish to test whether some of the μ_i parameters can be set equal. *F*-tests and *t*-tests have been developed for linear models such as regression and ANOVA. For the nonlinear model that we are considering, we used the more general likelihood ratio test. The general theory of likelihood ratio tests can be found in most introductory texts on mathematical statistics (e.g., Bain and Engelhardt, 1987, pg. 395).

1.1.4. A test for the random occurrence of declines

As a null hypothesis, we do not expect all species to decline at the same time. A more appropriate null hypothesis is that declines occurred independently of each other. If events occur randomly in time, then for any time segment, the number of events follows a Poisson distribution, and the distribution of all events is called a homogeneous Poisson process (HPP, Bain and Englehardt, 1987, pg. 462). Under the HPP model, the distribution of the times between events follows an exponential distribution (Bain and Englehardt, 1987, pg. 465). Thus, we can test the null hypothesis that declines occurred at random, versus the alternatives that they were clustered in time, or regular in time (the sequential hypothesis of Springer et al.), by using a goodness-of-fit test for times between declines, under the null hypothesis that these times follow an exponential distribution. The Cramer–von Mises goodness-of-fit is such a test (Bain and Englehardt, 1987, pg. 423), which is

$$CM = \frac{1}{12n} + \sum_{i=1}^{n} \left[[1 - \exp(t_{i:n}/\bar{t})] - \frac{i - 0.5}{n} \right]^2,$$

where $t_{i:n}$ is the *i*th ordered value of the time intervals between declines. Critical values for CM, under the null hypothesis, are given in Bain and Englehardt (1987, pg. 536).

1.2. Results

1.2.1. Likelihood ratio tests

A series of 3 fitted models is given in Table 1. The model with all free parameters (15 of them) is given in the first column, and the fitted models are shown in Fig. A.1. The second column shows the model where we set $\mu_1 = \mu_3$. Notice that the difference in $l(\hat{\boldsymbol{\theta}} \mid \mathbf{y})$ for the two models is $110.65 - 108.35 = 2.30$, and because this is less than 3.84 ($P = 0.05$ for a chi-square with 1 degree of freedom), we cannot reject the null hypothesis that the two parameters are equal (i.e., that the curves have equal inflection points) with $\alpha = 0.05$. However, notice the third column for the model, $\mu_1 = \mu_2 = \mu_3$. Here, the difference in $l(\hat{\boldsymbol{\theta}} \mid \mathbf{y})$ for the two models is $128.64 - 110.65 = 17.99$, and because this is more than 6.635 ($P = 0.01$ for a chi-square with 1 degree of freedom), we reject the null hypothesis that all three parameters are equal. Thus, it appears that harbor seals and fur seals had their steepest decline at approximately the same time, around 1979, and sea lions had their steepest decline about 4 years later, around 1983, according to the model where $\mu_1 = \mu_3$.

Table 1
Parameter estimates for various models

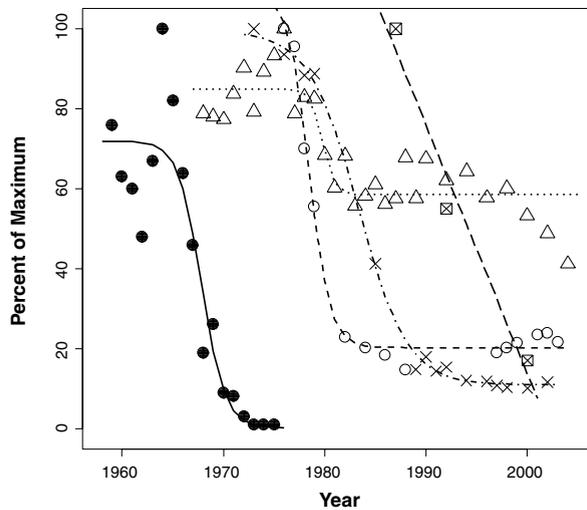| Parameter	Models		
	All Parameters free	$\mu_1 = \mu_3$	$\mu_1 = \mu_2 = \mu_3$
$\hat{\alpha}_1$	20.25	19.72	19.72
$\hat{\eta}_1$	89.40	72.63	72.63
$\hat{\beta}_1$	−0.953	−1.028	−1.028
$\hat{\mu}_1$	1978.4	1979.6	1979.6
$\hat{\pi}_1$	0.262	0.273	0.600
$\hat{\alpha}_2$	10.90	10.90	10.43
$\hat{\eta}_2$	88.49	88.46	109.57
$\hat{\beta}_2$	−0.414	−0.414	−0.270
$\hat{\mu}_2$	1983.3	1983.3	1979.6
$\hat{\pi}_2$	0.117	0.117	0.816
$\hat{\alpha}_3$	58.49	59.11	58.83
$\hat{\eta}_3$	26.51	27.56	26.48
$\hat{\beta}_3$	−1.66	−1.05	−1.73
$\hat{\mu}_3$	1979.8	1979.6	1979.6
$\hat{\pi}_3$	0.648	0.741	0.659
$l(\hat{\boldsymbol{\theta}} \mid \mathbf{y})$	108.35	110.65	128.64

Fig. A.1. Model fits to all species and whale catch data. Solid line and solid circles are whale catch data, short dashed line and open circles are harbor seal data, dotted line and triangles are for northern fur seal data, dash-dot line and x's are Steller sea lion data, and the long dashed line and squares filled with x's are for sea otter data.

1.2.2. The Cramer–von Mises Test

A separate fitted logistic curve for the whale catch data is also given in Fig. A.1. There were not enough data to fit a nonlinear curve to sea otters, so we used simple regression, and we used the midpoint of the decline, 1993.5, as it appears linear. The estimated times of maximum decline for whale catches, harbor seals, fur seals, and sea lions were 1967.9, 1978.4, 1979.8, and 1983.3, respectively. The Cramer-von Mises test statistic for these 5 dates, with 4 inter-event intervals, was CM = 0.061, which was less than the critical value of 0.177 for $\alpha = 0.10$. Hence, there is little evidence that we can reject the notion that declines occurred at random. Of course, we only had 5 time events, and hence 4 intervals, so this test lacks power. However, even with these small sample sizes, it is possible to detect extreme regularity or clustering. For example, if declines had been very regular, occurring in 1968, 1974, 1980, 1986, and 1992, then CM = 0.403, which is larger than the critical value of 0.337 for $\alpha = 0.01$, so we could have rejected this set of dates as occurring randomly. On the

other hand, if declines had been strongly clustered, and had occurred in 1968, 1969, 1970, 1971, and 1992, then CM = 0.302, which is larger than the critical value of 0.273 for α = 0.025, so we also could have rejected this set of dates as occurring randomly.

References

Angliss, R.P., Lodge, K.L., 2004. Alaska Marine Mammal Stock Assessments, 2003. NOAA Technical Memorandum NMFS-AFSC-144, 230pp.

Benson, A.J., Trites, A.W., 2003. Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. Fish and Fisheries 3, 95–113.

Braham, H.W., Everitt, R.D., Rugh, D.J., 1980. Northern sea lion population decline in the eastern Aleutian Islands. Journal of Wildlife Management 44, 25–33.

Calambokidis, J., Steiger, G.H., Straley, J.M., Quinn II, T.J., Herman, L.M., Cerchio, S., et al., 1997. Abundance and population structure of humpback whales in the North Pacific Basin. Report to Southwest Fisheries Science Center, National Marine Fisheries Service, La Jolla, California, 71pp.

Calkins, D.G., Becker, E.F., Pitcher, K.W., 1998. Reduced body size of female Steller sea lions from a declining population in the Gulf of Alaska. Marine Mammal Science 14 (2), 232–244.

Eberhardt, L.L., Breiwick, J., 1992. Impact of recent population data on historical population levels of bowhead whales inferred from simulation studies. Report of the International Whaling Commission 42, 485–489.

Eberhardt, L.L., DeMaster, D.P., Sease, J., 2005. Projecting the trend of Steller sea lion populations in western Alaska. Marine Mammal Science 21 (4), 728–738.

Estes, J.A., Tinker, M.T., Williams, T.M., Doak, D.F., 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282, 473–476.

Fritz, L.W., Ferrero, R.C., Berg, R.J., 1995. The threatened status of Steller sea lion, *Eumetopias jubatus*, under the Endangered Species Act: effects on Alaska groundfish management. Marine Fisheries Review 57 (2), 14–27.

Fritz, L.W., Hinckley, S., 2005. A critical review of the regime shift- junk food – nutritional stress hypothesis for the decline of the western stock of Steller sea lion. Marine Mammal Science 21, 476–518.

Frost, K.J., Lowry, L.F., Ver Hoef, J.M., 1999. Monitoring the trend of harbor seals in Prince William Sound, Alaska, after the *Exxon Valdez* oil spill. Marine Mammal Science 15, 494–506.

Hennen, D.R., 2006. Associations between the Steller sea lion decline and the Gulf of Alaska and Bering Sea commercial fisheries. Ecological Applications, in press.

Hobbs, R.C., Rugh, D.J., Waite, J.M, Breiwick, J.M., DeMaster, D.P., 2004. Abundance of eastern North Pacific gray whales on the 1995/96 southbound migration. Journal of Cetacean Research and Management 6 (2), 115–120.

Holmes, E.E., York, A.E., 2003. Using age structure to detect impacts on threatened populations: a case study with Steller sea lions. Conservation Biology 17 (6), 1794–1806.

Hoover-Miller, A.A., 1994. Harbor seal (*Phoca vitulina*) biology and management in Alaska. Marine Mammal Commission, Washington, D.C, 45 pp.

International Whaling Commission, 2004. Report of the Scientific Committee. Journal of Cetacean Research and Management 6, 211–217.

Kenyon, K.W., Rice, D.W., 1961. Abundance and distribution of the Steller sea lion. Journal of Mammalogy 42, 223–234.

Loughlin, T., Rugh, D., Fiscus, C., 1984. Northern sea lion distribution and abundance: 1956–1980. Journal of Wildlife Management 48, 729–740.

Loughlin, T.R., Perlov, A.S., Vladimirov, V.A., 1992. Range wide survey and estimate of total number of Steller sea lions in 1989. Marine Mammal Science 8, 220–239.

Loughlin, T.R., York, A.E., 2000. An accounting of the sources of Steller sea lion, *Eumetopias jubatus*, mortality. Marine Fisheries Review 62 (4), 40–45.

Matkin, C.O., Barrett-Lennard, L., Ellis, G., 2002. Killer whales and predation on Steller sea lions. In: DeMaster, D., Atkinson, S. (Eds.), Steller sea lion decline: Is it food II. University of Alaska Sea Grant Program, AK-SG-02-02, Fairbanks.

Mehta, A.V., 2004. How important are baleen whales as prey for killer whales (*Orcinus orca*) in high latitudes? Unpublished Master's thesis, Boston University, Boston, MA, 87pp.

Merrick, R.L., Loughlin, T.R., Calkins, D.G., 1987. Decline in abundance of the northern sea lion, *Eumetopias jubatus*, in Alaska, 1956–86. Fishery Bulletin 85, 351–365.

Merrick, R.L., Chumbley, M.K., Byrd, G.V., 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. Canadian Journal of Fisheries and Aquatic Sciences 54 (6), 1342–1348.

Mizroch, S.A., Herman, L.M., Straley, J.M., Glockner-Ferrari, D., Jurasz, C., Darling, J.D., Cerchio, S., Gabriele, C.M., Salden, D.R., von Ziegesar, O., 2004. Estimating the adult survival rate of Central North Pacific humpback whales. Journal of Mammalogy 85 (5), 963–972.

Mizroch, S.A., Rice, D.W., 2006. Have North Pacific killer whales switched prey species in response to depletion of the great whale populations? Marine Ecology Progress Series, in press.

National Research Council, 2003. Decline of the Steller sea lion in Alaskan waters: Untangling food webs and fishing nets. National Academies Press, Washington, D.C., 204pp.

National Marine Fisheries Service, 2001. Endangered Species Act – Section 7 Consultation- Biological Opinion. October 2001. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Juneau, Alaska.

Pfister, B., 2004. Computations of historic and current biomass estimates of marine mammals in the Bering Sea. AFSC Processed Report 2004–05. Alaska Fisheries Science Center, Seattle, WA, 41pp.

Pfister, B., DeMaster, D.P., 2006. Changes in marine mammal biomass in the Bering Sea/Aleutian Island region before and after the period of industrial whaling. In: Estes, J., Williams, T., Doak, D., DeMaster, D.P., Brownell, Jr. R. (Eds.), Whales, Whaling, and the Marine Ecosystem. Berkeley, CA: University of California Press, in press.

Pitcher, K.W., 1990. Major decline in number of harbor seals, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. Marine Mammal Science 6, 121–134.

Pitcher, K.W., Calkins, D.G., Pendleton, G.W., 1998. Reproductive performance of female Steller sea lions: an energetics-based reproductive strategy? Canadian Journal of Zoology 76, 2075–2083.

Sinclair, E.H., Zeppelin, T.K., 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). Journal of Mammalogy 83 (4), 973–990.

Small, R.J., Pendleton, G.W., Pitcher, K.W., 2003. Trends in abundance of Alaska harbor seals, 1983–2001. Marine Mammal Science 19, 96–114.

Springer, A.M., Estes, J.A., van Vliet, G.B., Williams, T.M., Doak, D.F., Danner, E.M., Forney, K.A., Pfister, B., 2003. Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? Proceedings of the National Academy of Sciences 100 (21), 12,223–12,228.

Trites, A.W., 1992. Northern fur seals: why have they declined? Aquatic Mammals 18, 3–18.

Trites, A.W., Donnelly, C.P., 2003. The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. Mammal Review 33, 3–28.

Trites, A.W., Larkin, P.A., 1996. Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: how many were there? Aquatic Mammals 22.3, 153–166.

Trites, A.W., Miller, A.J., Maschner, H.D.G., Alexander, M.A., Bograd, S.J., Calder, J.A., Capotondi, A., Coyle, K.O., Lorenzo, E.D., Finney, B.P., Gregr, E.J., Grosch, C.E., Hare, S.R., Hunt, G.L., Jahncke, J., Kachel, N.B., Kim, H.J., Ladd, C., Mantua, N.J., Marzban, C., Maslowski, W., Mendelssohn, R., Neilson, D.J., Okkonen, S.R., Overland, J.E., Reedy-Maschner, K. L., Royer, T.C., Schwing, F.B., Wang, J.X.L., Winship, A.J., 2006a. Bottom-up forcing and the decline of Steller sea lions in Alaska: assessing the ocean climate hypothesis. Fisheries Oceanography, in press.

Trites, A.W., Deecke, V.B., Gregr, E.J., Ford, J.K.B., Olesiuk, P.F., 2006b. Killer whales, whaling and sequential megafaunal collapse in the North Pacific: a comparative analysis of the dynamics of marine mammals in Alaska and British Columbia following commercial whaling. Marine Mammal Science, in press.

Wade, P., Barrett-Lennard, L., Black, N., Brownell, R. L. Jr., Burkanov, V., Burdin, A., Calambokidis, J., Cerchio, S., Dahlheim, M., Ford, J., Friday, N., Fritz, L., Jacobsen, J., Loughlin, T., Lowry, M., Matkin, C., Matkin, D., Mehta, A., Mizroch, S., Muto, M., Rice, D., Siniff, D., Small, R., Steiger, G., Straley, J., Van Blaricom, G., Clapham, P. 2006. Marine mammal abundance, biomass, and trends in the eastern North Pacific – a reanalysis of evidence for sequential megafauna collapse. Marine Mammal Science, in press.

Whitehead, H., Reeves, R., 2005. Killer whales and whaling: the scavenging hypothesis. Royal Society Biology Letters 11 (July), 1–5.

Williams, T.M., Estes, J.A., Doak, D.F., Springer, A.M., 2004. Killer appetites: Assessing the role of predators in ecological communities. Ecology 85 (12), 3373–3384.

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

Winship, A.J., Trites, A.W., 2006. Risk of extirpation of Steller sea lions in the Gulf of Alaska and Aleutian Islands: A population viability analysis based on alternative hypotheses for why sea lions declined in western Alaska. Marine Mammal Science 22 (1), 124–155.

York, A.E., 1994. The population dynamics of northern sea lions, 1975–1985. Marine Mammal Science 10 (1), 38–51.

Zenteno-Savin, T., Castellini, M.A., Rea, L.D., Fadely, B.S., 1997. Plasma haptoglobin levels in threatened Alaskan pinniped populations. Journal of Wildlife Diseases 33 (1), 64–71.

Literature cited

Bain, L.J., Engelhardt, M., 1987. Introduction to probability and mathematical statistics. Duxbury Press, Boston, 565pp.

Broyden, G., 1970. The convergence of a class of double-rank minimization algorithms, parts I and II. Journal of the Institute of Mathematics and Its Applications 6, 76–90, 222–231.

Fletcher, R., 1970. A new approach to variable metric algorithms. Computer Journal 13, 317–322.

Goldfarb, D., 1970. A Family of Variable Metric Methods Derived by Variations Means. Mathematics of Computation 24, 23–26.

Shanno, D.F., 1970. Conditioning of quasi-newton methods for function minimization. Mathematics of Computation 24, 647–656.