KILLER WHALES AND MARINE MAMMAL TRENDS IN THE NORTH PACIFIC—A RE-EXAMINATION OF EVIDENCE FOR SEQUENTIAL MEGAFAUNA COLLAPSE AND THE PREY-SWITCHING HYPOTHESIS

PAUL R. WADE
VLADIMIR N. BURKANOV
MARILYN E. DAHLHEIM
NANCY A. FRIDAY
LOWELL W. FRITZ
THOMAS R. LOUGHLIN
SALLY A. MIZROCH
MARCIA M. MUTO
DALE W. RICE

National Marine Mammal Laboratory,
NOAA Fisheries, 7600 Sand Point Way NE,
Seattle, Washington 98115, U.S.A.
E-mail: paul.wade@noaa.gov

LANCE G. BARRETT-LENNARD

Vancouver Aquarium Marine Science Center,
Vancouver, British Columbia V6B 3X8, Canada

NANCY A. BLACK

Monterey Bay Cetacean Project, P.O. Box 52001,
Pacific Grove, California 93950, U.S.A.

ALEXANDER M. BURDIN

Alaska Sealife Center, 301 Railway Avenue,
P.O. Box 1329, Seward, Alaska 99664, U.S.A.

JOHN CALAMBOKIDIS

Cascadia Research Collective,
218 1/2 W Fourth Avenue,
Olympia, Washington 98501, U.S.A.

SAL CERCHIO

Molecular Systematics Lab,
American Museum of Natural History,
Central Park West at 79th Street,
New York, New York 10024, U.S.A.

JOHN K. B. FORD

Pacific Biological Station,
Fisheries and Oceans Canada,
3190 Hammond Bay Road,
Nanaimo, British Columbia V9T 6N7, Canada

JEFF K. JACOBSEN

Department of Biological Sciences,
Humboldt State University,
Arcata, California 95521, U.S.A.

CRAIG O. MATKIN

North Gulf Oceanic Society,
3430 Main Street, Suite B1,
Homer, Alaska 99603, U.S.A.

DENA R. MATKIN

North Gulf Oceanic Society,
Gustavus, Alaska 99826, U.S.A.

AMEE V. MEHTA

Boston University Marine Program,
Woods Hole, Massachusetts 02543, U.S.A.

ROBERT J. SMALL

Alaska Department of Fish and Game,
1255 West 8th Street, P.O. Box 25526,
Juneau, Alaska 99802, U.S.A.

JANICE M. STRALEY

University of Alaska Southeast,
Sitka, Alaska 99835, U.S.A.

SHANNON M. MCCLUSKEY

Washington Cooperative Fish and Wildlife Research Unit,
School of Aquatic and Fishery Sciences,
University of Washington,
Seattle, Washington 98195, U.S.A.

GLENN R. VANBLARICOM

Washington Cooperative Fish and Wildlife Research Unit,
School of Aquatic and Fishery Sciences,
University of Washington,
Seattle, Washington 98195, U.S.A.
and
Biological Discipline, U.S. Geological Survey,
Seattle, Washington 98195, U.S.A.

PHILLIP J. CLAPHAM

National Marine Mammal Laboratory
NOAA Fisheries, 7600 Sand Point Way NE,
Seattle, Washington 98115, U.S.A.

Abstract

Springer *et al.* (2003) contend that sequential declines occurred in North Pacific populations of harbor and fur seals, Steller sea lions, and sea otters. They hypothesize that these were due to increased predation by killer whales, when industrial whaling's removal of large whales as a supposed primary food source precipitated a prey switch. Using a regional approach, we reexamined whale catch data, killer whale predation observations, and the current biomass and trends of potential prey, and found little support for the prey-switching hypothesis. Large whale biomass in the Bering Sea did not decline as much as suggested by Springer *et al.*, and much of the reduction occurred 50–100 yr ago, well before the declines of pinnipeds and sea otters began; thus, the need to switch prey starting in the 1970s is doubtful. With the sole exception that the sea otter decline followed the decline of pinnipeds, the reported declines were not in fact sequential. Given this, it is unlikely that a sequential megafaunal collapse from whales to sea otters occurred. The spatial and temporal patterns of pinniped and sea otter population trends are more complex than Springer *et al.* suggest, and are often inconsistent with their hypothesis. Populations remained stable or increased in many areas, despite extensive historical whaling and high killer whale abundance. Furthermore, observed killer whale predation has largely involved pinnipeds and small cetaceans; there is little evidence that large whales were ever a major prey item in high latitudes. Small cetaceans (ignored by Springer *et al.*) were likely abundant throughout the period. Overall, we suggest that the Springer *et al.* hypothesis represents a misleading and simplistic view of events and trophic relationships within this complex marine ecosystem.

Key words: North Pacific, killer whale, Steller sea lion, sea otter, harbor seal, fur seal, ecosystem, predation, whaling, population dynamics.

Springer *et al.* (2003) have contended that North Pacific populations of pinnipeds and sea otters (*Enhydra lutris*) in the Bering Sea, Aleutian Islands, and Gulf of Alaska declined in a marked sequence, and hypothesize that the declines were due to increased predation by so-called "transient-type" (mammal-eating) killer whales (*Orcinus orca*). In brief, the hypothesis posits that the primary prey of killer whales originally constituted the large whales, that is, baleen whales and sperm whales (*Physeter macrocephalus*), but that the depletion of this prey source by whaling in the Aleutian Islands and Gulf of Alaska by ~1970 reduced whale biomass to the point where killer whales were forced to switch to other marine mammal prey. The hypothesis posits that the biomass of this alternative prey was lower than preexploitation whale populations, and the killer whale predation thus caused the sequential decline of harbor seals (*Phoca vitulina richardii*), Steller sea lions (*Eumetopias jubatus*), northern fur seals (*Callorhinus ursinus*), and sea otters.

The "prey-switching" hypothesis regarding declines of pinnipeds and sea otters in the North Pacific is superficially attractive. As presented by Springer *et al.*, the picture of whale catch statistics and pinniped and sea otter trend data would indeed suggest that these events happened sequentially: As they describe the sequence of events, whale catches declined in the late 1960s, harbor seals and fur seals declined in the 1970s, Steller sea lions declined in the 1980s, and sea otters declined in the 1990s.
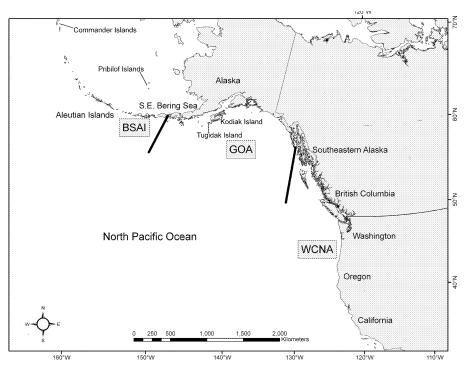
As we demonstrate below, however, this assertion of sequential decline throughout the North Pacific is based upon a selective and simplistic analysis of trend data. A more detailed examination of these data, and consideration of information from other

North Pacific populations of these same species, results in a picture that is not nearly as simple or as elegant as that suggested by the Springer *et al.* hypothesis.

In this critique, we systematically review the data and assumptions underlying the Springer *et al.* paper and suggest that the large whale depletion hypothesis is an unlikely explanation for the observed declines. In brief, the primary assumption regarding the importance of large whales as prey items for killer whales prior to commercial whaling is poorly supported, and the assertion that populations of pinnipeds and sea otters declined in sequence throughout the North Pacific is not born out by the evidence. Alternative analyses presented here reveal—contrary to the suggestion of the prey-switching hypothesis—that, in some regions of the North Pacific, pinniped populations have grown substantially since 1970, despite a history of commercial whaling in those regions and the presence there of killer whales that prey upon pinnipeds.

There are essentially four different components to the Springer *et al.* hypothesis, which we evaluate separately: (1) Was there a large population of mammal-eating killer whales that preyed primarily on large whales? (2) If so, did the removal of large whales by commercial whaling leave this population with insufficient prey biomass, such that the killer whales needed to find an alternative food source? (3) Did pinnipeds and sea otters decline in a sequential manner following commercial whaling? (4) Could killer whale predation be responsible, partly or wholly, for any of the observed declines in pinnipeds and sea otters, independent of the whale depletion hypothesis?

In this review, we focused primarily on the eastern North Pacific (waters east of 180°W), in waters north of 30°N. We reexamined whale catch data, trends in abundance and biomass of potential marine mammal prey of killer whales, and observations of killer whale prey in three regions of the North Pacific: the Bering Sea and Aleutian Islands, the Gulf of Alaska, and the Western Coast of North America (from Southeast Alaska to California) (Fig. 1). Each of these regions is large and contains many independent populations of the killer whale prey species in question. A regional approach allows a more detailed review of the trend and abundance data. Springer *et al.* combined trend data from the Bering Sea and Aleutian Islands region with the Gulf of Alaska region. We examine those regions separately and also examine a third region not considered by Springer *et al.*, the Western Coast of North America. Marine mammal trend data are available for a large number of species in these areas (by contrast, less information is available for the western North Pacific). We also examine pinniped and sea otter trend data from the Commander (Commadorski) Islands in Russian waters of the northwestern Pacific. The Commander Islands are of particular interest because trend data are available for all four species considered by Springer *et al.* The islands are adjacent to the area in the Aleutians where sea otter and Steller sea lion declines have occurred, and are essentially part of the region on which Springer *et al.* based their hypothesis. In particular, we carefully examined data from the four species that are the focus of the Springer *et al.* paper: harbor seals, northern fur seals, Steller sea lions, and sea otters. These four species all have distributions that range across the North Pacific at higher latitudes. Some of the information summarized and synthesized here is either unpublished or from sources not widely available, such as government documents. Therefore, much of this information may not have been available to Springer *et al.*, or the wider scientific community, and so we have attempted to provide sufficient detail for the reader to examine the hypothesis in light of the available data.

A comparative regional approach is used to examine whether substantial takes of large whales occurred in all three areas and, if so, whether prey switching and declines

Figure 1. Map of North Pacific with labels of place names mentioned in the text. BSAI is the Bering Sea and Aleutian Islands, GOA is the Gulf of Alaska, and WCNA is the Western Coast of North America. The vertical thick lines mark the boundaries between these areas as defined for this study.

of pinnipeds and sea otters occurred there, as would be predicted by the Springer *et al.* hypothesis. A regional approach also allows us to examine in more detail whether declines in potential killer whale prey occurred and whether or not those declines were sequential.

METHODS

REGIONAL APPROACH

As noted above, our approach focuses on three main regions: the Bering Sea and Aleutian Islands, the Gulf of Alaska, and the Western Coast of North America (from Southeast Alaska to California).

Three types of killer whales have been identified in the northeast Pacific, labeled as "resident," "transient," and "offshore" ecotypes (Bigg *et al.* 1990, Ford *et al.* 2000) based on aspects of morphology, ecology, genetics, and behavior (Ford and Fisher 1982; Baird and Stacey 1988; Baird *et al.* 1992; Hoelzel *et al.* 1998, 2002; Barrett-Lennard 2000). Only one type, transients, is known to prey on marine mammals (Ford *et al.* 1998; Saulitis *et al.* 2000). Until recently in Alaska, transient killer whales had been studied intensively only in Southeast Alaska and in the Gulf of Alaska (from Prince William Sound, through the Kenai Fjords). In the Gulf of Alaska, Matkin *et al.* (1999) described two communities of transients. Neither of the

two Gulf of Alaska communities commonly associate with transient killer whales that range from California to Southeast Alaska (the "West Coast community"), although there is at least one case of Gulf of Alaska transient whales associating with West Coast transients in Southeast Alaska (D. Matkin *et al*., in press). The West Coast transient community ranges from Southeast Alaska to California (Goley and Straley 1994). All three communities have significant differences in mtDNA and nuclear (microsatellite) DNA (Barrett-Lennard 2000) and are considered discrete populations. Over 300 whales have been identified in the West Coast population (Black *et al*. 1997; Dahlheim *et al*. 1997; Ford and Ellis 1999). A substantial number (>75) of transient killer whales have been identified in the two Gulf of Alaska populations (Dahlheim 1997; Matkin *et al*. 1999). Recent studies in western Alaska have confirmed that at least several hundred transient killer whales are also found along the Alaska Peninsula and Aleutian Islands.[1, 2] In summary, there are substantial populations of mammal-eating killer whales in all three regions that we consider here.[3]

We summarize information on commercial whale catches as well as on abundance, trend, and biomass (both historically removed and presently available) for all relevant species of marine mammals in the three regions. Although complete data are not available for many species, considerable information exists. We also examine what is known about predation by mammal-eating killer whales in the North Pacific.

Most available data on abundance of marine mammal species are from coastal or nearshore areas. Conveniently, the distribution of harbor seals, Steller sea lions, northern fur seals, and sea otters is largely confined to this part of the ocean. The exception is that, for some age classes, fur seals have a broad pelagic distribution during some periods of the year. Most of the abundance data come from surveys conducted during the period April to October, as do the majority of the whale catch data. The majority of northern fur seals are on or near rookeries in summer and are therefore within the area we examine, the one main exception being that some (perhaps most) juveniles remain at sea for several years. Similarly, we have also restricted the whale catch data to broad regions adjacent to land and excluded catches from pelagic regions far from land.

Fortuitously, then, most marine mammal abundance data are from the areas where Steller sea lions, harbor seals, northern fur seals, and sea otters also represent potential killer whale prey. In these areas, it would be conceivable for killer whales to turn to pinniped and/or sea otter prey if other species became unavailable. In contrast, it seems less likely that killer whales from pelagic habitats in the North Pacific, if deprived of a preferred prey source in such areas, would relocate to coastal waters to prey on pinnipeds and sea otters. However, given the known long-range movements of some killer whales, this latter idea cannot be entirely ruled out.

Western Coast of North America (Southeast Alaska to California, WCNA)

Each of the four killer whale prey species of interest has a breeding population in the WCNA region. Harbor seals are widely distributed from California to Southeast

[1] Unpublished data provided by National Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA Fisheries, 7600 Sand Point Way NE, Seattle, WA 98115, May 2006.

[2] Unpublished data provided by North Gulf Oceanic Society, 3430 Main Street, Suite B1, Homer, AK 99603, May 2006.

[3] In this review, the term "killer whale" refers to the mammal-eating transient ecotype, unless otherwise noted.

Alaska. Steller sea lions also occur over this range; however, rookeries south of British Columbia are few and relatively small. Northern fur seals have a small breeding population on San Miguel Island in southern California, and sea otters occur as discrete populations in California, Washington, British Columbia, and Southeast Alaska. Other pinniped species, including California sea lions and elephant seals, are also common in portions of this region.

Gulf of Alaska (GOA)

Only three of the four species of interest have breeding populations in the Gulf of Alaska: Steller sea lions, harbor seals, and sea otters. Northern fur seals in the GOA occur primarily in offshore pelagic waters in lower densities than in the Bering Sea and Aleutian Islands, and they do not haul out in appreciable numbers.

Bering Sea and Aleutian Islands (BSAI)

In the eastern North Pacific, none of the four species of interest are found in large numbers north of the southeastern Bering Sea. Large concentrations of harbor seals are found in southern Bristol Bay, and several large Steller sea lion rookeries are found in the eastern Aleutian Islands. The main northern fur seal rookeries in the eastern North Pacific are found on the Pribilof Islands. Sea otters are found throughout the Alaska Peninsula and in southern Bristol Bay. None of these species are found in appreciable numbers north of St. Matthew Island and the Yukon Delta. Therefore, the focus here was on species found in the southeastern Bering Sea from April to October. For example, data from bowhead whales (*Balaena mysticetus*) were not used because bowheads spend the summer in the Beaufort Sea and cannot be considered a likely alternative prey source in summer for killer whales that prey on Steller sea lions. Additional pinniped species in the southeastern Bering Sea include Pacific walrus (*Odobenus rosmarus divergens*) and spotted seals (*Phoca largha).*

All of the species of interest are also found in the Aleutian Islands. Northern fur seals are found at sea in this area in summer and have established a small but growing rookery on Bogoslov Island in the eastern Bering Sea.

Commander Islands

The Commander Islands consist of two main islands, Bering and Medney. Substantial colonies of northern fur seals exist on both islands, together with harbor seals, Steller sea lions, and sea otters. Though separated from the Near Islands (the "nearest" of the Aleutian Islands to Russia) by approximately 200 nm, the Commander Islands can be considered part of the same archipelago and are similar in that they are surrounded by a narrow shelf, with a habitat that is primarily oceanic.

WHALE CATCH DATA

Whaling History in the Eastern North Pacific

The first commercial whaling in the North Pacific occurred in the early 1800s with the pursuit of sperm whales (Webb 1988). Most of this occurred in lower latitudes,

near the equator, in Panama Bay, and off Baja California (Mexico). During this early period, the whalers operating furthest north were American vessels that killed sperm whales on the Japan Grounds in the 1820s. Commercial whaling in high latitudes in the North Pacific did not begin until a few whaling ships pushed north in 1835 and discovered right whales[4] in a region from approximately the Queen Charlotte Islands in the east to Kodiak Island and beyond to the west. Shortly after the discovery of these "Northwest" or "Kodiak" whaling grounds, a major right whale fishery developed, and right whales were depleted in this region (and elsewhere in the North Pacific) between 1840 and 1865. Whaling ships subsequently pushed even farther north and began taking bowhead whales in large numbers in 1849. Commercial whaling of gray whales (*Eschrichtius robustus*) began in about 1845, and by 1874 the gray whale fishery had ended because so few whales were left. It was not until the advent of major technological developments in the late 19th and early 20th centuries (faster steam-powered ships, exploding harpoons, and the use of compressors to prevent dead whales from sinking) that systematic whaling began on the faster rorquals, notably fin (*Balaenoptera physalus*) and blue whales (*B. musculus*).

Humpback whales (*Megaptera novaeangliae*) were initially depleted in the North Pacific in areas such as Washington and British Columbia, from about 1905 to 1915 (Webb 1988). Catches in California declined substantially in the 1920s, indicating depletion of the population (Clapham *et al*. 1997), and humpbacks were depleted along the entire western coast of North America by 1930 (Tønnessen and Johnson 1982). Similarly, catches of blue whales from coastal whaling stations along the west coast of North America declined rapidly in the 1910s, and catches in the 1920s were sustained only at a single whaling station (Akutan) in the Aleutian Islands (Tønnessen and Johnson 1982). In British Columbia, catches of humpback and blue whales also declined dramatically in the early period of modern whaling (1905–1943) (Gregr *et al*. 2000). In the mid-1930s, both Russian and Japanese factory ships entered the Bering Sea and worked along the eastern North Pacific rim, catching mainly fin, humpback, and sperm whales. However, the majority of catches of these species occurred after World War II.

After World War II, Japanese and Soviet whaling ships resumed widespread operations in the North Pacific, including in the Aleutian Islands, Bering Sea, Gulf of Alaska, and along the edge of the continental shelf of Canada and the United States. This period included substantial illegal whaling and falsification of data by the USSR, which depleted populations of several species, notably North Pacific right whales (Doroshenko 2000*a*). As noted above, humpback and blue whales were thought to be initially depleted in the early 1900s, and the resumption of whaling on these species after World War II was believed to have severely depleted them in the North Pacific by the 1960s (Webb 1988). Consequently, the International Whaling Commission (IWC) banned the taking of blue and humpback whales in 1966. Fin whale catches off British Columbia had also declined during the early 1900s but rebounded during the second whaling era (1948–1967) and then, with sei whale (*Balaenoptera borealis*) catches, declined again in the mid 1960s (Tønnessen and Johnson 1982; Gregr *et al*. 2000). Catches of sperm whales in this region during the post-war period showed no trend (Gregr *et al*. 2000).

Fin whales continued to be hunted legally in the North Pacific until 1976, and catches of sei and sperm whales were still allowed until 1981, although this was not binding on some countries that filed an objection to a worldwide moratorium. A

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[4] Referred to as *Balaena glacialis* by Rice (1998) and as *Eubalaena japonica* by Rosenbaum *et al*. (2000).

moratorium on catches of minke whales (*Balaenoptera acutorostrata*) came into effect in 1986.

Whaling Catch Summary

Whaling catch data were obtained from the IWC's catch database and summarized within each of the three regions defined above. Summaries for the BSAI and GOA regions were restricted to catches north of 50°N latitude. Although catches occurred south of this latitude, we selected this boundary to restrict the catches to regions in the vicinity of the pinniped and sea otter species of interest, as explained above. The BSAI region for catches was defined as the area from 180°W to 163°W longitude. The border between the BSAI and GOA regions was set at 163°W longitude because this has been selected as a breakpoint for Steller sea lion trend data between the Gulf of Alaska and the Aleutian Islands and Bering Sea, and it provides a reasonable division between the "Kodiak" ("Northwest") whaling ground and catches that occurred south of the Aleutian Islands. The border between the GOA region and the WCNA region was set at 130°W longitude, as this corresponds well to the population division between Southeast Alaska and the Gulf of Alaska that occurs in many marine mammal species, and it also appropriately includes catches that occurred on the "Vancouver" whaling ground from catcher boats associated with British Columbia shore-stations into the WCNA region. The southern boundary of the WCNA region was set at 20°N latitude. Catch data were converted to biomass by multiplying the number of takes by an average biomass per individual (see below).

As noted above, it is known that substantial falsification of whaling data occurred in the North Pacific, primarily by the Soviet Union in the 1960s and 1970s. In particular, where true records are available for comparison, catches of sperm whales by the Soviet Union in the North Pacific from 1948 to 1973 were 1.8 times greater than reported to the IWC (Brownell *et al*. 2000). Catches of humpback whales by the Soviet Union in the North Pacific from 1961 to 1971 were 1.6 times greater than reported (Doroshenko 2000*b*). Catches of fin whales by the Soviet Union in the North Pacific during this time period were somewhat overreported, presumably to cover up illegal takes of protected species. Although an ongoing revision of the North Pacific catch history to correct this falsification remains incomplete, these "correction factors" will be considered when interpreting the results of the official (incorrect) IWC catch database used here.

KILLER WHALE PREDATION OBSERVATIONS

Killer whale predation observations were reviewed using published literature and unpublished field data. For all three regions, the number of observations of marine mammal prey taken by killer whales was tallied by species and taxonomic groups. Numbers tallied included all observations of prey seen killed by killer whales, observations of a carcass being eaten by killer whales, or prey remains identified in the stomach contents of killer whales. Prey observations were summarized by regional areas in the North Pacific and were restricted to observations since 1950. Observations that could be classified only as an attack, with no confirmation of a kill, were not included. Each confirmed predation event was counted as a single event, regardless of how many individuals were killed during the event. Predation events reported as occurring on separate days were counted as separate events. Stomach contents were tallied as the minimum number of individuals consumed. Primary reviews consulted

included Rice (1968); Lowry *et al*. (1987); Jefferson *et al*. (1991); Matkin and Saulitis (1994); Barrrett-Lennard *et al*. (1995); Ford *et al*. (1998); Hatfield *et al*. (1998); Saulitis *et al*. (2000); Heise *et al*. (2003); and Ford *et al*. (2005). Substantial unpublished data were used from Southeast Alaska (J. Straley and D. Matkin, unpublished data), California (N. Black, unpublished data), and Alaska.[1] Details of the sources of the prey data are given in Appendix A.

The great majority of the records are from observations, not from stomach contents. There are potential biases in such data, primarily regarding the probability that a given type of predation event will be observed. For example, more killer whale observations occur in protected, inland waters than in open exposed seas, and this may influence the probability of reporting for predation on certain species. Therefore, these data should not be viewed as representing exact percentages of prey preferences for mammal-eating killer whales in the North Pacific, but rather they provide a qualitative sense of what kind of prey are known to be taken. Similarly, stomach content analyses are subject to bias, notably that the hard parts of baleen whales (bones and baleen) are not consumed and therefore are unlikely to persist in stomachs; this is not the case for teeth or bones of odontocete prey.

MARINE MAMMAL ABUNDANCE AND TREND DATA

Although the primary focus of our analysis was the four species discussed by Springer *et al*. (2003), we also examined abundance and trend data for other taxa that are available as potential prey for killer whales in the North Pacific. Abundance estimates for each species were compiled and converted to biomass for each region, including all large whale species and all other species of marine mammals that have been observed to be killer whale prey in that region. If more than one stock (population) occurred in a region, the abundance for the species was summed across all stocks within the region. If a population occurred in more than one region, the abundance of the population was split between the regions. Trend data for pinnipeds and sea otters were compiled for the Commander Islands. Compiled tables and details of the sources of the abundance and trend data for each species are given in Appendix B.

BIOMASS CALCULATIONS

Whale catch data and marine mammal abundance data were converted to biomass by multiplying catch or abundance by an average biomass of individuals of that species (Mizroch and Rice 2006). Calculations of average biomass for large whales were based upon actual length data in the Bureau of International Whaling Statistics/IWC catch database. Weight was estimated for each whale caught based upon a method developed by Mizroch (1983) using length/weight curves developed for the various species concerned, using parameters estimated by Lockyer (1976) for most of the large whales. For Baird's beaked whales, Mizroch and Rice (2006) estimated parameters directly from length/weight tables published in Balcomb (1989). For each species, the method involved using a single value for body mass at a specific length (*e.g.*, any 20-m fin whale was assigned a value of 48 tons as derived from the length/body mass curves). Although the true body mass of individual whales would undoubtedly have varied from these averaged values, depending on body condition and reproductive state, we consider the figures sufficiently precise for the purposes of this review. Biomass calculations for other marine mammal species were derived from various sources in the literature. The mean body mass of each species used in the biomass calculations is listed in Table 1 of Appendix C.

In order to calculate current available biomass and trends in biomass, the total estimated abundance for each species in each region was multiplied by the average biomass per individual. This provided, for each species, an estimate of the biomass (in million kg) available as prey for killer whales in each of the three geographic areas (see Tables 2–4 in Appendix C). The percentage of the total available biomass represented in various taxonomic groups was also calculated for each of the three geographic areas. Finally, trends in biomass for some species were similarly calculated where abundance estimates through time were multiplied by the average biomass per individual.

RESULTS

WHALE CATCHES

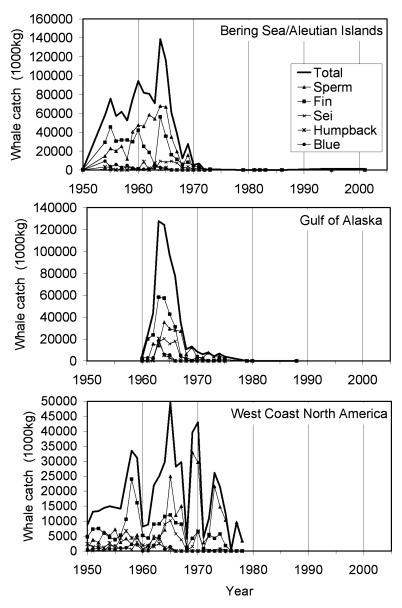### Western Coast of North America

In the WCNA region, total whale biomass (summed across all species) taken in commercial catches increased during the 1950s, peaked in the 1960s, and declined during the 1970s, with the last substantial catches occurring in 1978 (Fig. 2). Total biomass taken remained relatively high through 1974. From 1950 to 1978, the greatest biomass taken was that of sperm whales (44%), followed by fin whales (34%), sei whales (11%), humpback whales (7%), and blue whales (4%). Biomass reported taken was dominated by fin whales in the late 1950s and early 1960s. From 1965 to 1978, the biomass of the reported catch was dominated by sperm whales. However, given the under reporting of sperm whale catches and over reporting of fin whale catches by the Soviet Union, the biomass of sperm whales removed in the 1950s and early 1960s might have been on the same order as that of fin whales. Sei whale catches peaked from 1962 to 1970. Humpback and blue whales were caught mainly from the late 1940s to the mid-1960s.

Gulf of Alaska

Catches in the GOA region after World War II did not resume until 1960. Total whale biomass taken in commercial catches increased rapidly to a peak in 1965–1966 and then declined to a relatively low level by 1968 (Fig. 2). Takes continued at low levels in the early 1970s and had essentially ceased by 1975. From 1960 to 1975 the greatest biomass reported taken was that of fin whales (42%), followed by sperm whales (33%), sei whales (14%), blue whales (6%), and humpback whales (5%). Most of the fin whale biomass was taken between 1961 and 1966; after 1966, the greatest biomass reported taken was that of sperm whales. However, given the under reporting of sperm whale catches and over reporting of fin whale catches by the Soviet Union, it may be that the greatest biomass removed over this entire time period in this region was that of sperm whales. Takes of sei, blue, and humpback whales mainly occurred from 1960 to 1966.

Bering Sea and Aleutian Islands

Substantial commercial whale catches in the BSAI region began in 1954, remained at relatively high levels until 1966, and had essentially ceased by 1973 (Fig. 2). The peak of biomass removal occurred in 1964–1965. From 1954 to 1973, the greatest

Figure 2.   Biomass of whale catches from the International Whaling Commission Catch database in the three regions of interest from 1950 to 2002. The five species with the highest catches are plotted individually. Total also includes catches of additional species (*e.g.*, gray whales). See text for details on conversion of catches to biomass.

biomass taken was that of sperm whales (50%), followed by fin whales (39%), sei whales (5%), blue whales (4%), and humpback whales (2%). The greatest biomass taken in the 1950s was that of fin whales, and by 1959 the greatest biomass taken was that of sperm whales, which continued to be the case until 1968. However, given

the under reporting of sperm whale catches and over reporting of fin whale catches that occurred by the Soviet Union, it may be that the greatest biomass removed over this entire time period in this region was that of sperm whales. Humpback and blue whales were caught primarily from the mid-1950s to the mid-1960s. Sei whales were mainly taken in the mid-1960s.

Killer Whale Prey Observations

Western Coast of North America

In the WCNA region 73% of all observed predation events ($n = 466$) were of pinnipeds, including (in order of occurrence) harbor seals, California sea lions (*Zalophus californianus*), Steller sea lions, and northern elephant seals (*Mirounga angustirostris*) (Table 1, Appendix B). The next largest category was small odontocetes, with 17% of the observations, including harbor porpoise (*Phocoena phocoena*), Dall's porpoise (*Phocoenoides dalli*), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), and long-beaked common dolphins (*Delphinus capensis*). Large baleen whales represented 8% of the observations, with all of these observations of predation on gray whales. Minke whales represented 1% of the total. Little predation (<1%) has been reported on sperm whales and sea otters.

Gulf of Alaska

In the GOA region, 57% of the total predation event observations ($n = 74$) involved pinnipeds (Table 1), including harbor seal and Steller sea lion predation events. The

Table 1. Summary of observations of marine mammal prey killed or eaten by killer whales in the three regions considered in the eastern North Pacific since 1950. Most records are visual observations of live killer whales, but recent data from stomach contents of killer whales are also included. Attacks which were not confirmed as kills were not included.

Species	WCNA	GOA	BSAI
Sea otter	1	2	1
Pacific walrus	0	0	2
Harbor seal	240	25	2
Northern elephant seal	21	0	0
California sea lion	48	0	0
Steller sea lion	22	16	1
Unidentified sea lion	7	1	0
Northern fur seal	0	0	2
Harbor porpoise	38	4	0
Dall's porpoise	33	16	0
Longbeaked common dolphin	3	0	0
Pacific white-sided dolphin	7	0	0
Beluga	0	3	4
Minke whale	6	6	2
Gray whale	39	0	3
Fin whale	0	1	0
Sperm whale	1	0	0
Total	466	74	17

next largest category was small odontocetes (31%)—consisting of observations of Dall's porpoise, harbor porpoise, and beluga (*Delphinapterus leucas*) predation events—followed by minke whales (8%) and sea otters (3%). Only one predation event on a large baleen whale (a fin whale) has been reported for this region, and none were reported on sperm whales (it should be noted that most reports are from shelf waters which do not include the habitat of sperm whales, but substantial numbers of fin and humpback whales are on the shelf).

Bering Sea and Aleutian Islands

There have been relatively few reports of killer whale predation in the BSAI region ($n = 17$). This is likely primarily due to the lack of killer whale studies in this region until recently. In the BSAI region, 41% of the observations of predation involved pinnipeds, including northern fur seals, walrus, harbor seals, and Steller sea lions (Table 1). The next largest category was small odontocetes (belugas), with 24% of the observations. Large baleen whales represented 18% of the observations, and all of these reports involved predation on gray whales. Minke whale predation events represented 12% of the observations, and a confirmed kill of a sea otter has been reported once (the three other attacks reported in Hatfield *et al*. [1998] were not reported as confirmed kills). No predation events on sperm whales have been reported. It should be noted that several observations of killer whales killing and eating northern fur seals in the Bering Sea have been reported in the literature before 1950 (Hanna 1922, Zenkovich 1938, Tomilin 1957) and were not included in these totals.
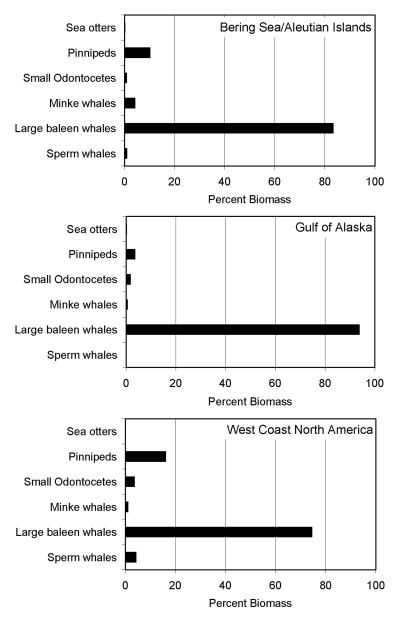
CURRENT BIOMASS

Abundance estimates used for calculating current marine mammal biomass of potential prey of killer whales are listed in Appendix C, Table 2 (WCNA), Table 3 (GOA), and Table 4 (BSAI). In all three regions, the majority of the biomass is represented by large baleen whales and sperm whales (Fig. 3), ranging from 5 to 24 times the biomass of pinnipeds. The biomass of minke whales and small odontocetes was roughly similar to the biomass of pinnipeds across the three regions. In terms of being prey for killer whales, the total biomass of large whales and sperm whales is probably not very comparable to that of the smaller species because killer whales probably only consume a small fraction of a large whale carcass. However, in terms of giving a general picture, even if killer whales only consumed about one-tenth as much of a large whale carcass as they do of the carcasses of smaller prey, there would still be roughly the same order of biomass "available" in large whales as there is in pinnipeds. A detailed examination of available biomass of prey would involve estimates of the percent biomass consumed and assimilated by prey type, which is beyond the scope of this paper. The main point to make is that current large whale biomass is not trivial, in contrast to the impression given by Springer *et al*.
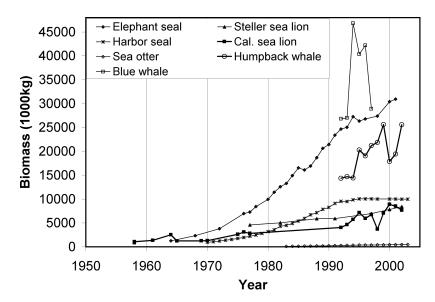
TRENDS IN BIOMASS

Western Coast of North America

At least three species of large whales have increased within the WCNA region in recent decades: humpback, gray, and blue whales have likely been increasing since commercial catches ceased, although conclusions are limited by an inadequate time

Figure 3. Percent biomass currently represented by potential marine mammal prey of killer whales in the three regions. See text for details on conversion of abundance to biomass. Biomass was summed across all species in the categories in each region, then converted to a percent for the region.

series. Biomass of blue whales is the highest of any species; estimates of abundance of blue whales have been relatively stable since 1992, but this species is strongly believed to have increased from previous decades. Mark-recapture abundance estimates indicate that humpback whales have increased since 1992 (Fig. 4). Gray whales,

Figure 4. Trends in biomass of marine mammals from the Western Coast of North America region from 1950 to 2003. As complete a time series as possible was plotted for all species. Data for Steller sea lions, harbor seals, and sea otters were summed from California to Southeast Alaska. See Appendix B for details. Trend data are not available for many cetacean species.

which seasonally pass through this region, have increased since at least 1967 (but are not plotted here—see BSAI region). Fin whales and sperm whales have also likely increased since the cessation of commercial catches, but trend data are not available. Minke whales were never heavily exploited in the eastern North Pacific, and may not have experienced significant changes in abundance.

Pinniped species and sea otters have all increased overall since the 1960s (Fig. 4). Some of these species were hunted for fur (sea otters and northern fur seals) or were subject to bounty hunting in parts of their range (*e.g.*, harbor seals and sea lions) because they were perceived as competitors with humans for fish. With the cessation of bounties in the 1960s, pinniped populations have increased. Elephant seals represent by far the largest biomass of the pinnipeds in this region (three times the biomass of harbor seals, the species with the second greatest biomass). Elephant seal biomass has increased by ~25 times since the 1960s, and they have increased the range of their haul-outs in California. Harbor seal biomass has increased by a factor of ten since 1970 and has been relatively stable since the mid-1990s. This overall trend is reflected in most areas within the region, with harbor seal populations having increased and then leveled off in British Columbia (Olesiuk *et al.* 1990), Washington (Jeffries *et al.* 2003), and Oregon (Brown *et al.* 2005); they may also be leveling off in California. Available count data indicate that harbor seals have increased or remained stable in two regions of Southeast Alaska since the mid-1980s (Small *et al.* 2003) yet declined substantially in Glacier Bay during the 1990s (Mathews and Pendleton 2006). In the WCNA region, the next greatest current biomass is that of California sea lions, which have increased by a factor of eight since the late 1950s. Steller sea lion biomass has approximately doubled since the mid-1970s; most of this biomass is in Southeast Alaska, followed by British Columbia, with relatively little biomass in
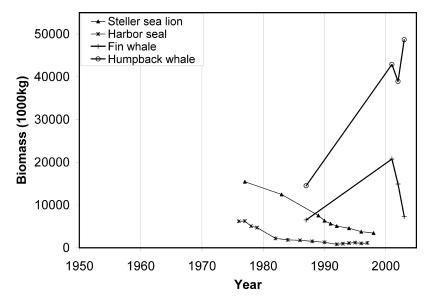
California and Oregon. Sea otters have also shown an overall increasing trend during this time period but currently represent less than 2% of the biomass of elephant seals and less than 10% of the biomass of Steller sea lions.

Several species of dolphin that are preyed on by killer whales are found in this region, including longbeaked common dolphins and Pacific white-sided dolphins. Dall's porpoise and harbor porpoise also exist in relatively high abundances. Little trend data are available for these species, but there is no specific information to suggest that they have changed in abundance through time in this area. Harbor porpoise are thought to have declined during the 1980s because of fisheries bycatch in gillnets but have been relatively stable since 1990 (Forney 1995, 1999).

Gulf of Alaska

In the GOA region, humpback whales represent the greatest biomass and have increased since at least the late 1980s (Fig. 5). Humpbacks have likely been increasing since the 1970s following the cessation of whaling in the 1960s. Estimates of fin whale abundance have increased since the late 1980s, but the increase is not significant. Humpback and fin whale biomass was similar to that of Steller sea lions in the mid-1980s but is much greater now.

Steller sea lions represent the largest pinniped biomass but have declined since monitoring started in the mid-1970s (Fig. 5). Harbor seals have been monitored in the eastern Kodiak Archipelago and in Prince William Sound, with declines in Kodiak from the late 1970s through the early 1980s, followed by increasing numbers
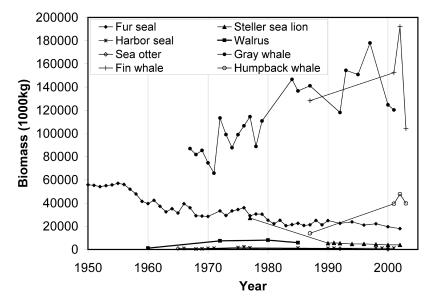

Figure 5. Trends in biomass of marine mammals from the Gulf of Alaska region. As complete a time series as possible was plotted for all species. See Appendix B for details. Trend data are not available for many cetacean species. Quantitative trend data are not available for sea otters, but declines in sea otter abundance have been reported for part of this region in recent years (see text for details).

since the early 1990s (Pitcher 1990, Small *et al*. 2003) when the Steller sea lion decline continued. Seal numbers in Prince William Sound have declined since the mid-1980s.

Quantitative trend data have not been reported for sea otters in this region, but unpublished descriptions of trends are available. The sea otter population is reported to have declined throughout a large portion of the range of the Southwest Alaska stock in the GOA, particularly along the southern side of the Alaska Peninsula and in the Kodiak Archipelago (U.S. Fish and Wildlife Service [USFWS] Stock Assessment Report: Appendix 8 in Angliss and Lodge 2004). However, sea otters have slightly increased in the Shelikof Strait area, although this does not offset the declines seen in other portions of the stock's range. The south-central Alaska stock of sea otters includes Prince William Sound, Cook Inlet, and Kenai Fjords. Although sea otters were killed during the *Exxon Valdez* oil spill in 1989, the current trend of this stock is thought to be stable or slightly increasing.

Bering Sea and Aleutian Islands

There is significant biomass of gray, fin, and humpback whales in the BSAI region. The gray whale population has substantially increased since the late 1960s and has been roughly stable in size since the mid-1980s (Fig. 6). Note that the gray whale biomass is plotted as 50% of the total population biomass—this was an arbitrary determination to reflect that the great majority of the gray whale population is

Figure 6. Trends in biomass of marine mammals from the Bering Sea and Aleutian Islands region from 1950 to 2003. As complete a time series as possible was plotted for all species. See Appendix B for details. Trend data are not available for many cetacean species. Gray whale biomass is shown as 50% of the population's biomass to reflect that gray whales are only available in this region for roughly half of the May–October time period. Walrus biomass is shown as 20% of the population's biomass, the portion estimated to be in the southeastern Bering Sea (see text for details).

farther north in the Bering Sea for about half of the summer and is thus unavailable to killer whales in the eastern Bering Sea and Aleutian Islands. Fin whale biomass is approximately equal to this gray whale biomass and was estimated to be about three times greater than humpback whale biomass. Humpbacks have been documented to have increased in the eastern Aleutians Islands; fin whales appear to have increased but the increase is not significant. Both species are thought to have increased since the 1970s following the cessation of commercial whaling.
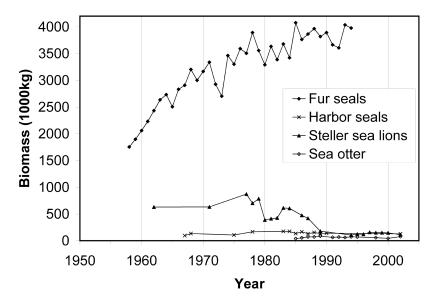
The species with the next greatest biomass is the northern fur seal, reflecting the very large breeding population on the Pribilof Islands. Overall, fur seals declined from 1950 until recent years. There is a rich history of information and data, extending back hundreds of years, associated with the population of northern fur seals that breeds on the Pribilof Islands (Gentry 1998). There were at least three periods of population decline between the mid-1800s and 1984, the last of which (mid-1950s to 1984) is discussed by Springer *et al*. (2003). Based on pup production estimates, the Pribilof Island northern fur seal population declined from 1956 to 1970, increased slightly from 1970 to 1976, then declined again through 1984 for a total decline of approximately 57%. Between 1984 and the late 1990s, the fur seal population on the Pribilof Islands was relatively stable but has declined at approximately 6% per year since 1998 (Towell *et al*., 2006).

A conservative estimate of minke whale abundance (uncorrected for whales missed on the trackline) leads to an estimate of biomass similar to that of the current biomass of fur seals. No trend information is available for minke whales; the lack of substantial commercial takes suggests that minke whale abundance may have been relatively stable over the last several decades.

In the mid 1970s, the biomass of Steller sea lions was similar to the biomass of fur seals, but Steller sea lions declined substantially during the 1980s and by the 1990s were only about one-fourth the biomass of fur seals. Observations reported in the literature suggest that Steller sea lions started declining prior to the 1980s, perhaps as early as the late 1960s. Northern fur seals and Steller sea lions appear to have declined simultaneously during the early 1980s, but the fur seal population leveled off while the Steller sea lion population continued to decline. Both populations declined during the 1990s, but during this time period fur seals declined at a greater rate than Steller sea lions.

Walrus were estimated to have increased substantially during the 1960s and were roughly stable in the 1970s and early 1980s. Walrus biomass in the southeast Bering Sea (note that this is only ~20% of the total population biomass) was approximately the same as the biomass of Steller sea lions in the 1990s. The largest concentrations of harbor seals are in southern Bristol Bay, and numbers in the late 1980s and early 1990s appear similar to the late 1960s and early 1970s, with an apparent increase in the mid-1970s. A preliminary comparison of counts in the Aleutian Islands, west of Samalga Pass, indicates that numbers decreased substantially from the late 1970s through 1999.[5] Harbor seal biomass was never great in the Aleutian Islands and therefore regional biomass is dominated by the harbor seals in Bristol Bay. Sea otter biomass in the 1960s was similar to harbor seal biomass but declined substantially in the 1990s (Estes *et al*. 1998).

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[5] Unpublished data provided by U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, AK 99503, May 2006; Peter Boveng, National Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA Fisheries, 7600 Sand Point Way NE, Seattle, WA 98115, May 2006; Bob Small, Alaska Department of Fish and Game, 1255 West 8th Street, Juneau, AK 99802, May 2006.

Figure 7. Trends in biomass of marine mammals from the Commander Islands in the western Bering Sea from 1950 to 2003. As complete a time series as possible was plotted for all species. See Appendix B for details. Trend data are not available for cetacean species.

Sperm whales occur in deeper water areas of the BSAI, including the continental slopes, but no surveys have been conducted to reliably estimate their abundance.

Commander Islands

The largest pinniped biomass in the Commander Islands has been that of northern fur seals. Overall, fur seals have increased throughout the entire time period they have been monitored, (1958–1994) (Fig. 7). In the 1970s, fur seal biomass was approximately five times greater than Steller sea lion biomass, and twenty-five times greater than harbor seal biomass. Steller sea lions declined from the late 1970s through the 1980s and approximately leveled off in the 1990s at a similar biomass to that of harbor seals. Harbor seals were roughly stable throughout the period they were monitored. Sea otters increased in the 1980s, declined in the 1990s, increased again in the early 2000s, and overall were roughly stable. In the 1990s, sea otter biomass was roughly half the biomass of both harbor seals and Steller sea lions.

DISCUSSION

The Springer *et al.* hypothesis has generated considerable controversy (*e.g.*, DeMaster *et al.* 2006, Mizroch and Rice 2006, Trites *et al.*, in press), and has significant ramifications scientifically, as well as in the realms of management and politics. However, is it plausible and supported by existing data? Our analyses of a broad range of information lead us to conclude that the hypothesis—that killer whale predation induced declines in populations of pinnipeds and sea otters—is based upon a simplistic and highly selective analysis of trend data. We also conclude that the

prey-switching hypothesis rests upon a poorly supported assumption regarding the importance of large whales as prey items for killer whales, notably in the high-latitude areas of the North Pacific (the focus of Springer *et al.*) where most commercial whaling occurred. Below, we discuss in detail the available data in each region in the context of the Springer *et al.* hypothesis.

WESTERN COAST OF NORTH AMERICA

The available data from the WCNA region show an opposite result to that of the northern North Pacific. Despite extensive removals of large whales and the presence of a substantial transient killer whale population, this region has seen increases in four populations of harbor seals, one population of elephant seals, one population of Steller sea lions, one population of California sea lions, and three or more populations of sea otters. In most cases, the increase has been quite dramatic. Whale catches remained high until the mid-1970s (Fig. 1), but no population of marine mammal was seen to decline in response (Fig. 4). In fact, by 1980 it appears that all four main species of pinniped were increasing (although fur seals represent only a minor component of the marine mammal fauna in both the WCNA and GOA regions in summer). Several species of large whales in this region have been increasing over the last few decades. Transient killer whale predation has been extensively studied in some areas within this region. They have been observed to prey primarily on harbor seals, Dall's and harbor porpoise, and Steller sea lions (*e.g.*, Ford *et al.* 1998), while at the same time foregoing predation upon the substantial populations of large whales found in some of these areas. The only killer whale predation on large whales (excluding minke whales) that is known in this region is upon young gray whale calves on their migration north in the spring in locations such as central California. Accordingly, the Springer *et al.* hypothesis does not explain trends in pinniped and sea otter populations in the WCNA region. Trites *et al.* (in press) examine trends in British Columbia in detail within this region and come to the same conclusion.

GULF OF ALASKA

A substantial number of whales were removed from the GOA region, and catches of whales had essentially collapsed by ∼1968. Harbor seals and Steller sea lions were declining by the late 1970s, and although spatial variability exists in the timing of sea lion declines, overall the declines of those two species were *not* sequential as reported by Springer *et al.* (2003). When the pinniped declines were reanalyzed, a statistical test concluded that these declines (along with northern fur seals and sea otters from the BSAI region) were not sequential (DeMaster *et al.* 2006), as can be seen in Figures 5 and 6. However, declines have also been verbally reported for the 1990s for sea otters in the GOA, and a substantial population of transient killer whales occurs there. Do these declines provide support for the Springer *et al.* hypothesis?

The cause of the decline of Steller sea lions has been the subject of prolonged debate, but several plausible explanations exist that have nothing to do with killer whale predation (see below). The decline of harbor seals in this region has not received as much scientific scrutiny, but plausible explanations also exist that do not involve killer whales. The cause of the recent decline of sea otters in part of this region does not yet have a satisfactory explanation. Substantial observations of transient killer whales in Prince William Sound show that predation occurs on harbor seals, Dall's

and harbor porpoise, and Steller sea lions, with no predation observed on the abundant humpback whales found there (Saulitis *et al*. 2000). Humpback and fin whales are both thought to have been increasing since at least 1987 and were likely increasing earlier. These species are currently abundant enough in many areas that, if they were preferred prey, much more predation on these species would be seen. The possibility that killer whales contributed to the declines of harbor seals and sea otters in this region cannot be excluded, but the declines were not sequential and therefore cannot be explained by the sequential prey-switching hypothesis.

BERING SEA AND ALEUTIAN ISLANDS

The removal of large whale biomass in the BSAI region took place over a longer time period but collapsed at approximately the same time (∼1968) as it did in the Gulf of Alaska. Northern fur seals were declining at the same time, during the late 1950s and 1960s. Immediately following the collapse of whale removals, the fur seal population actually stabilized during the 1970s before declining again in the late 1970s and early 1980s, while Steller sea lions were likely declining. The decline of fur seals and Steller sea lions was initially simultaneous, but Steller sea lions declined severely while the fur seal population stabilized for most of the 1980s and early 1990s. Other populations were stable or increasing in the 1970s and 1980s, such as gray whales, walrus, and Bristol Bay harbor seals. Humpback and fin whales appear to have increased since the late 1980s. As in the other regions, substantial large whale biomass was available throughout the 1980s and 1990s. Thus, the declines of the species considered by Springer *et al*. were not sequential in this region, with the exception of the decline of sea otters in the 1990s.

Most telling is that fur seal biomass at its lowest value was still two orders of magnitude larger than sea otter biomass at its highest value in this region (Fig. 5). Therefore, although the killer whales in this region may well have caused or contributed to the decline of sea otters (Estes *et al*. 1998), it cannot be argued that they did this because of a lack of fur seal biomass. Although there is little disagreement that fur seals have declined in the Bering Sea, they cannot be said to exist in low numbers: indeed, the most recent estimate of abundance puts the population at 888,120 animals (Angliss and Lodge 2004). Thus, the available biomass of fur seals remains so high in this region that it is inconceivable that killer whales would have needed to switch to sea otters as their primary prey. This appears to strongly refute the hypothesis that prey switching would have occurred by killer whales for the reasons proposed by Springer *et al*. (*i.e.*, that killer whales were "fishing-down" the marine food web, sequentially switching to less desirable prey as more desirable prey became unavailable).

COMMANDER ISLANDS

The history of catches in the Commander Islands is similar to that of the BSAI region, and it is thought that large whales were depleted from this area in the same way as in the eastern North Pacific, though slightly earlier (Mizroch and Rice 2006). The only population known to have declined in this area is Steller sea lions, and this decline did not begin until 1980 (Fig. 7). The fur seal population increased substantially during the post-World War II whaling boom, and harbor seal and sea otter populations were stable after the collapse of whale catches in the late 1960s. This is just one island group rather than a large region, and the amount of marine

mammal biomass available here is small relative to the amount available in the other regions discussed here. However, given the lack of declines seen in other species, and the timing of the Steller sea lion decline, there is no evidence for a link to industrial whaling and no evidence of any prey switching. Thus, there is no evidence supporting the idea that the Springer *et al*. hypothesis is the explanation for the decline of Steller sea lions in the Commander Islands. Given that the Commander Islands are essentially an extension of the Aleutian Islands (on which a major portion of the prey-switching case is made), this further weakens the plausibility of the Springer *et al*. hypothesis.

REGIONAL SUMMARY

Overall, the major point here is that all three of the regions as well as the Commander Islands include areas, ignored by Springer *et al*., in which industrial whaling depleted populations of large whales, and where transient-type killer whales are known to occur but where populations of pinnipeds and/or sea otters are stable or increasing rather than in decline. That this is so despite a history of whaling and killer whale presence in these areas argues strongly against the validity of prey switching as a general pattern. Although this does not exclude the possibility that killer whale predation was partly responsible for some of the declines noted by Springer *et al*., it greatly weakens the case that those declines were the result of a prey-switching event initiated by industrial whaling.

It is worth reiterating the key point that Springer *et al*. support their hypothesis using trend data from only four populations at five sites: Tugidak Island (harbor seals), St. George and St. Paul Islands in the Pribilofs (northern fur seals), western Alaska (Steller sea lions), and the Aleutian Islands (sea otters). As we have documented here, selection of these sites ignores other populations of the same species that are either stable or increasing, or which remain large despite a recent decline. For example, the northern fur seal and sea otter data that Springer *et al*. used are from the BSAI region, but the harbor seal data are from near Kodiak Island in the GOA. Springer *et al*. have also inappropriately extrapolated trends from these sites to the entire stock, or even to the entire ocean basin. Additionally, the use of relative abundance as the scale in Figure 2 of Springer *et al*. does not show the dramatically large differences in biomass between some species (*e.g.*, see Fig. 6).

The Western U.S. stock of Steller sea lions certainly declined substantially in the central and western Gulf of Alaska and in the Bering Sea and Aleutian Islands (NMFS 1992). However, Springer *et al*. oversimplify the temporal and geographic pattern of the population decline as well as its possible causes, and they ignore substantial literature that gives alternative explanations for the decline of Steller sea lions. The decline was first observed in the eastern Aleutian Islands and may have begun as early as the late 1960s or early 1970s (Braham *et al*. 1980). The decline spread west through the Aleutian Islands and east throughout the central and western Gulf of Alaska, reaching its maximum rate of decline between 1985 and 1989 at approximately 15% per year (Loughlin *et al*. 1992; York 1994). Through the 1990s, the decline slowed across the range of the Western stock to approximately 5% per year (Sease and Gudmundson 2002), and may have nearly abated since 2000 (Fritz and Stinchcomb 2005).

During the 30 yr of population decline, both top-down and bottom-up forces likely affected the Steller sea lion population. Over 20,000 Steller sea lions were killed between the 1960s and 1980s as a result of being accidentally caught during

groundfish fishing operations (Loughlin and Nelson 1986; Perez and Loughlin 1991); but, in the 1990s, incidental catches totaled less than 300 (Perez 2003). In addition, approximately 45,000 pups were killed in the eastern Aleutian Islands and Gulf of Alaska between 1963 and 1972 (Pascual and Adkison 1994). Numbers of Steller sea lions shot illegally may also have been high in the 1980s (Trites and Larkin 1992). However, direct mortality sources alone were not responsible for the decline experienced by the Steller sea lion population in the 1970s and 1980s (Pascual and Adkison 1994), suggesting that other factors were also implicated.

The primary bottom-up hypotheses for the Steller sea lion decline both involve a reduction in prey biomass and quality caused by either environmental variability (Trites and Donnelly 2003, Trites *et al.*, in press) or commercial fisheries (Braham *et al.* 1980, NMFS 2000). In apparent response to reduced prey availability, lower growth and pregnancy rates were observed in the Western Steller sea lion population in the 1980s than in the 1970s (Calkins and Goodwin 1988; Pitcher *et al.* 1998). Thus, during and following a period when direct sources of Steller sea lion mortality were at high levels, the carrying capacity was likely declining as well. This apparently continued through the 1990s as evidenced by the persistent decline in Steller sea lion counts (Sease and Gudmundson 2002) as well as a possible decline in fecundity (Holmes and York 2003), even as the rates of human-related direct mortality were greatly reduced. These shifts in life history parameters during the declines argue against killer whale predation as a main cause of the decline, as, for example, there is no direct reason why increased killer whale predation would lead to a decline in fecundity.

For northern fur seals, York and Hartley (1981) estimated that known direct kills of females alone explained approximately 70% of the decline in the Pribilof northern fur seal population from 1956 to 1980. From 1956 to 1968, approximately 315,000 female fur seals were killed on land at the Pribilof Islands in an attempt to increase the productivity of the stock (York and Hartley 1981, Gentry 1998). In addition, approximately 40,000 northern fur seals (roughly three-fourths females) were killed as part of U.S., Canadian, and Japanese scientific pelagic collections in the North Pacific Ocean from 1958 to 1974.[6] Interestingly, instead of increasing the productivity of the stock, pregnancy rates declined and the mean age at first reproduction increased (Trites and York 1993). The remaining 30% of the decline is unexplained, but York and Hartley (1981), Fowler (1987), and Gentry (1998) attributed it largely to one or all of a variety of factors: (1) methodological problems associated with pup production estimation, (2) changes in oceanic conditions, (3) entanglement in marine debris such as packing bands or discarded trawl netting, or (4) competition with groundfish fisheries whose catches in the eastern Bering Sea increased considerably in the early 1970s and have remained at approximately 2 million mt per year (NPFMC 2004). Furthermore, an unknown number of female northern fur seals and pups were killed by Russia during both on-land and pelagic collections. With the major portion of the population decline from 1956 to 1980 due to direct kills of females by humans, and the population being relatively stable thereafter until 1998, it is unlikely that killer whale predation contributed significantly to the population dynamics of Pribilof northern fur seals during this period.

Not all northern fur seal breeding colonies in the North Pacific had similar population dynamics through the late 20th century. Interestingly, with respect to the

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[6] Personal communication with Rolf Ream, National Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA Fisheries, 7600 Sand Point Way NE, Seattle, WA 98115, May 2006.

Springer *et al*. (2003) hypothesis, pup production increased at the Commander and Kuril Island fur seal rookeries from the mid-1960s through the mid-1980s while the Robben and Pribilof Island populations were declining by over 50% (Gentry 1998). Furthermore, rookeries became reestablished on San Miguel Island, California (in the mid-1970s), and on Bogoslof Island, Alaska (in the late 1980s) (Gentry 1998, Ream *et al*. 1999).

In the harbor seal example, counts from a single haulout on Tugidak Island are taken by Springer *et al*. to be representative of harbor seals throughout the GOA and BSAI; they also noted declines in counts at Otter Island (Pribilof Islands) from 1974 to 1978, and from 1978 to 1995. However, the largest concentration of harbor seals in the BSAI region (southern Bristol Bay) appears to have remained relatively stable during the time period concerned (Hoover-Miller 1994). Counts are not available to estimate population trend for the greater Gulf of Alaska region; specifically, for the south side of the Alaska Peninsula, Cook Inlet, the western Kodiak Archipelago, or the Kenai Peninsula. Counts from the eastern Kodiak Archipelago, primarily Tugidak Island, indicate that a substantial decline, which began in 1976 or earlier, continued through the late 1980s prior to an increase that began in the early 1990s. The trend in counts from south-central Prince William Sound has decreased since the mid-1980s. Of interest are the increasing trend in the Kodiak region and the continued decreasing trend in Prince William Sound, which suggests disparate population dynamics within separate stocks, a view of population structure that is supported by genetic and movement data (O'Corry-Crowe *et al*. 2003).

The amount of research on harbor seals has been substantially less than for Steller sea lions or for northern fur seals. Unfortunately, the information that would be required to fully assess the possible causes of harbor seal declines in the 1970s and 1980s was not obtained during the period of decline. In particular, unlike that of Steller sea lions, there are no data to investigate whether reduced growth or pregnancy rates occurred for harbor seals and, thus, evidence for reduced survival or reproduction due to reductions in prey biomass or quality does not exist. There is some indirect evidence, based on the timing of pupping and haul-out behavior, that harbor seals may have been nutritionally limited in the late 1970s in the Kodiak area (Jemison and Kelly 2001); however, this evidence is not definitive. Thus, although predation could have been a factor in the decline of harbor seals, numerous other factors could also have been the cause, including contaminants, disease, parasites, subsistence hunts, disturbance, illegal shooting, incidental take, and reduction in prey biomass and quality.

Availability of Large Whales and Other Potential Prey

If large whales represented an important prey item for killer whales, there are at least two lines of evidence that argue against any need to prey switch to pinnipeds and sea otters because of an insufficient supply of such fare. First, the decline of large whale biomass was not as dramatic as suggested by Springer *et al*. and most of it occurred in the 1800s and first half of the 1900s, well before the start of the decline of pinniped populations. Instead of showing the trend in available biomass of large whales alongside the biomass trend curves for pinnipeds and sea otters, Figure 2 of Springer *et al*. uses the decreasing numbers of whales *caught* by whalers to make the case for a decline. This provides a neat set of sequentially declining curves. However, if one adopts instead the former metric (available biomass) for whales, a very

different and far less elegant picture emerges. There probably remained a significant standing biomass of large whale prey, even for some species that were subject to intensive whaling. Although Figure 3 in Springer *et al*. suggests there has been a dramatic decline in cetacean biomass in the Bering Sea and Aleutian Islands region, this figure is based on a major error of calculation. The reduction in sperm whale biomass was calculated by comparing an estimate of current abundance of adult males for the Bering Sea and Aleutian Islands (15,000) to an estimate of historic abundance of adult males for the *entire* North Pacific (195,000) (see Pfister 2004: p. 5). This obviously greatly overestimates the decline in sperm whale abundance. Instead, a current estimate of 172,000 should be compared to the historic estimate of 195,000 for the entire Pacific; this equates to comparing a current estimate of 15,000 to a historic estimate of 17,006 in the Bering Sea and Aleutian Islands. Using those latter numbers for sperm whales combined with the estimates in Pfister (2004) for other large whales leads to a recalculated drop in whale biomass from historic to current levels of only 45%, not the 82% reported in Figure 3 of Springer *et al*.

Additionally, the sperm whale abundance estimates are considered unreliable because they were based on methods that have been discredited (Perry *et al*. 1999, Whitehead 2002, Pfister 2004); therefore, we do not recommend giving those numbers any credence. The overall reduction of cetacean biomass excluding sperm whales was calculated to be 54%, and most of this decline was noted to have occurred 50–100 yr ago (Pfister 2004), well before the declines of pinnipeds began in the northern North Pacific.

It is also important to note that the two large whale species (gray and humpback), which killer whales are regularly (gray) or occasionally (humpback) reported to attack, at least as calves, did not have a major drop in biomass in the 1950s and 1960s. Relatively few humpbacks were caught because they were already depleted from pre-World War II takes, and gray whales were increasing during that time period.

Furthermore, other cetacean prey was available for killer whales. Minke whales—known to be taken as adults by killer whales—were never subject to whaling in Alaska, nor in many other areas of the North Pacific. Accordingly, they have likely been an abundant potential prey item for killer whales throughout the entire period. In addition, although available data suggest that other cetaceans (*e.g.*, various small odontocetes, notably Dall's porpoise) have represented an alternative food source of substantial abundance and biomass during the period concerned, and are some of the most frequently observed prey of killer whales in most areas, this information was not considered by Springer *et al*. It is noteworthy that in some areas of Southeast Alaska, killer whales are known to prey on Dall's and harbor porpoise despite the local abundance of large whales, notably humpbacks.

In short, even if large whales are or were a significant prey item for killer whales, the evidence indicates that there has been no lack of this and other potential prey in higher latitudes. Thus, a switch by killer whales to pinnipeds and sea otters as primary prey because of a lack of cetacean prey seems unlikely. Indeed, if cetaceans (large or small) were once the primary prey for killer whales, the increasing biomass of this taxon in the areas concerned would suggest that they should by now have switched back to this food source. If they have, two predictions from the Springer *et al*. hypothesis would be that (1) observed attacks on large whales should increase over the next decade, and (2) depleted populations of pinnipeds should increase in response to the reduction in predation pressure.

PREY SELECTION BY KILLER WHALES: DOES THIS COMMONLY
INVOLVE LARGE WHALES?

Springer *et al.* suggested that depletion of large whales by industrial whaling forced killer whales to switch to other prey species. The key question here is therefore whether killer whales regularly attack large whales in the high-latitude areas that are the focus of the prey-switching hypothesis. In all three regions, the majority of observations of predation by mammal-eating killer whales involve pinnipeds and small odontocetes. The prey observations are remarkably consistent from region to region, with pinnipeds and small odontocetes (in that order) taken most frequently in all areas (although it should be remembered that the majority of these observations take place in summer and in coastal waters). Killer whales have been observed scavenging carcasses of large whales killed by whalers (Scammon 1874, Mitchell and Reeves 1988, Whitehead and Reeves 2005), events in which the killer whales have usually attempted to consume the tongue (Heptner *et al.* 1996). However, there are relatively few reports of predation on living large whales, particularly in the northern North Pacific (Mizroch and Rice 2006). It is also noteworthy that logbooks and journals from hundreds of North Pacific whaling voyages in the 1800s (notably to the Gulf of Alaska) almost never reported killer whales attacking large whales.

Although there are not many observations of killer whales preying on marine mammals in the North Pacific prior to 1950, those that were reported included harbor seals (Moran 1924, Scheffer and Slipp 1948), northern fur seals (Hanna 1922, Zenkovich 1938, Tomilin 1957), Steller sea lions (Scammon 1874, Zenkovich 1938), and Pacific walrus (Bailey and Hendee 1926, Zenkovich 1938, Tomilin 1957). These records suggest that pinnipeds have always been a primary prey of mammal-eating killer whales, including before the depletion of many large whale species in the 1950s and 1960s.

Observations of attacks on large whales are not common, and for those species seen attacked most frequently, the attacks are often on calves (Weller 2002). There are very few observations of lethal attacks on large whales in the high-latitude areas that were the site of industrial whaling, and still fewer of fin and sperm whales (the two species hunted most intensively). An isolated exception may be the Aleutian Islands, where in spring a population of transients has been observed feeding primarily on carcasses of gray whales (C. Matkin and L. Barrett-Lennard, unpublished data). If the carcasses result from predatory attacks, this may represent a strategy in which the killer whales intercept northbound migrants. However, even in this case it remains unclear whether age classes other than calves are commonly targeted. Killer whale attacks on young gray whales have also been reported from areas farther north than we considered, including the Russian Chukotka Peninsula[7] and the Bering Strait (Lowry *et al.* 1987). Reported killer whale attacks from the BSAI region in summer include Steller sea lions, Dall's porpoise, fur seals, minke whales, and (in Bristol Bay) harbor seals and beluga. These observations are consistent with predation described from well-studied areas such as Southeast Alaska and British Columbia, with some modifications that reflect regional differences (*e.g.*, fur seals are abundantly available in the Bering Sea but not in British Columbia). This could be interpreted as suggesting that killer whales preferentially pursue smaller prey that can be captured with a minimum of energy expenditure and risk.

In epistemological terms, one can never conclusively rebut the argument that lethal attacks on large whales are common but not observed: in the absence of perfect observational data, one can never prove that an event does *not* occur. However, it is very hard to accept the plausibility of this argument given that some populations of large whales have been under study for years or decades in areas where they co-exist with killer whales, yet where serious attacks are rarely, if ever, seen. This is all the more surprising given the obvious and dramatic nature of a killer whale attack on a large whale, which stands in contrast to the much more cryptic acts of predation on species far less conspicuous to observers, such as harbor seals (Ford *et al.* 2000).

Two prominent examples in this regard are Southeast Alaska and Prince William Sound. These are both well-studied areas where large whales (notably humpbacks) and killer whales are abundant, yet where a lethal attack has yet to be witnessed (Dolphin 1987; D. Matkin *et al.*, in press; M. Dahlheim, unpublished data). In contrast, in both of these areas numerous killer whale attacks *have* been documented on smaller cetaceans and pinnipeds, including Dall's and harbor porpoise, harbor seals, Steller sea lions, Pacific white-sided dolphins, and (less commonly) minke whales. It makes little sense to hold that killer whale attacks on large whales occur regularly, but are somehow never witnessed, while at the same time other species are commonly observed being taken, often in exactly the same areas. In some species, such as humpback whales, there are many individuals with killer whale tooth-mark scars on the tails and bodies (Weller 2002). However, further analysis of tooth-mark scars supports the view that attacks on adult large whales in high latitudes are uncommon (Mehta 2004, Mehta *et al.*, in review, Steiger *et al.*, submitted). The timing of acquisition of scars originating from killer whales is key here: the majority of scarred whales tracked by long-term individual identification studies have such scars on their first sighting, rather than acquiring them from year to year. This strongly argues that most attacks occur during an animal's natal year, and in lower latitudes (rather than in the areas subject to the Springer *et al.* hypothesis). This conclusion is consistent with observations in the Archipiélago Revillagigedo in Mexico between 1996 and 2001 where researchers reported several humpback whale calves with fresh rake marks on their flukes and/or bodies, including chewed fluke tips that were still bleeding (J. Jacobsen and S. Cerchio, unpublished data), whereas fresh rake marks on humpback whales are not reported from high latitudes. Furthermore, killer whale scars are quite rare on some of the species reduced by commercial whaling, notably fin and sei whales. This argues that these species—which are a focus of the Springer *et al.* hypothesis—are of little importance as potential killer whale prey in the regions concerned.

It is certainly possible that killer whales made a significant living on whale calves. However, the evidence (from scar acquisition and direct observations) that calf attacks occur primarily in lower latitudes presents a serious problem for the Springer *et al.* hypothesis. For the hypothesis to remain tenable, killer whales would have had to be distributed primarily in offshore or tropical/subtropical waters during the period before whaling depleted whale populations, then have shifted their distribution substantially to high-latitude areas to exploit populations of pinnipeds and sea otters (all the while ignoring increasing populations of some large whale species in the latter regions). In fact, killer whales from Mexico and California are genetically distinct from killer whales in the northern North Pacific and are not part of the same population.

Summary and Conclusions

In summary, the evidence outlined here leads us to doubt that the mechanisms proposed by the sequential prey-switching hypothesis were the cause of the declines of pinnipeds and sea otters that have occurred in the northern North Pacific. As we noted at the beginning of this review, the hypothesis can be broken down into four component questions, the answers to which are summarized below.

Was There a Large Population of Mammal-Eating Killer Whales That Preyed Primarily Upon Large Whales?

With the sole exception of killer whales apparently preying seasonally upon migrating gray whales (in the Aleutians), there is no empirical evidence that large whales have ever been a significant, regular prey item for this predator in the high-latitude areas that are the focus of the prey-switching hypothesis. The lack of observed attacks in long-term studies of large whales, and the strong indication in both scarring data and field observations that most attacks occur on calves in low latitudes, all combine to discount killer whales as regular predators of large whale species (either currently or historically) in high latitudes. Killer whales that are predators on calves at low latitudes off California and Mexico are not part of the same population of killer whales found in Alaska that prey on pinnipeds and sea otters. The absence of evidence of regular high-latitude attacks is particularly relevant to fin and sperm whales, which were the most intensively exploited species by recent whaling and thus should represent a lynchpin of the Springer *et al.* argument.

Did the Removal of Large Whales by Commercial Whaling Leave This Population With Insufficient Biomass, Such That the Killer Whales Needed to Find an Alternative Food Source?

In light of the above, we consider the answer to this question to be moot. However, even if killer whales did regularly consume large whales, large whale biomass did not decline as severely as suggested by Springer *et al.* The decline from historic to current biomass was recalculated here to be 45%–54% (excluding or including sperm whales, respectively), with much of that reduction occurring in earlier time periods, well before declines of pinnipeds started. The focus in Springer *et al.* on the post-World War II commercial whaling time period and the use of whale catch data (in their Fig. 2) instead of whale biomass data inappropriately focused attention on the sharp decline in what was predominantly fin and sperm whale catches in the late 1960s. This ignored information on whale biomass, such as the fact that the gray whale population was already above 10,000 individuals by 1970 and continued increasing through the 1980s, and we show that other large whale populations have increased since that time. In summary, it is not clear that there was any dramatic and sudden drop in large whale biomass in the 1960s and early 1970s. Furthermore, minke whales and small cetaceans have likely always been available in the regions concerned. All that being said, it is possible that large whales presented a more dangerous prey source that was worth pursuing only when densities were high enough that killer whales could readily find weak or debilitated individuals, or that killer whales scavenged carcasses from whaling, as suggested by Whitehead and Reeves (2005). However, the prey-switching hypothesis remains untenable in view of the timing of events (see below) and the failure of the hypothesis in other areas.

Published data and theoretical considerations for socially foraging mammals (both marine and terrestrial) clearly indicate that unidirectional prey switches of extended duration are rare and maladaptive (O'Donoghue *et al*. 1998, van Baalen *et al*. 2001). For such species of predator, all switching events reported in the literature are known to have reversed once the originally favored prey increased in abundance following relaxed predatory mortality (van Baalen *et al*. 2001). Failure of the originally favored prey to recover following a switching event indicates that predation may not have been regulating population numbers in the first place.

Did Pinnipeds and Sea Otters Decline in a Sequential Manner Consistent with Killer Whales Switching to Progressively Less Desirable Prey Following Commercial Whaling?

First, an examination of the available data shows that the declines cited by Springer *et al*. were in fact not sequential, as has been shown by DeMaster *et al*. (2006). Fur seals and Steller sea lions declined simultaneously in the BSAI region, followed by sea otters. Similarly, in the GOA, Steller sea lions and harbor seals declined simultaneously, followed by sea otters. In addition, the Steller sea lion decline may have begun much earlier than Springer *et al*. suggest. Thus, the pattern of decline relative to industrial whaling is not nearly as elegant nor as simple as the prey-switching hypothesis would suggest. Therefore, the data indicate that there has not been a sequential megafaunal collapse in the North Pacific Ocean, as hypothesized by Springer *et al*. At the least, the hypothesis needs revision to be consistent with the available data. Additionally, the remaining biomass of northern fur seals in the Bering Sea appears by itself to refute the prey-switching hypothesis: The sea otter population started to decline while northern fur seals were still more than two orders of magnitude greater in biomass, making it implausible that killer whales would have needed to "fish-down" the marine food web from fur seals to sea otters because of a lack of available biomass of fur seals.

Second, the WCNA and Commander Islands are areas that have both killer whales and a history of large whale depletions, yet they are currently host to populations of pinnipeds and sea otters that are stable or increasing. Other contradictions exist in the BSAI region, where walrus and harbor seals in Bristol Bay (the dominant area of harbor seal biomass in the region) apparently did not decline. This indicates that, even if some declines could have been due to killer whale predation, the existence of a general pattern as implied by the prey-switching hypothesis is not supported.

Could Killer Whale Predation be Responsible, Partly or Wholly, for any of the Observed Declines in Pinnipeds and Sea Otters, Independent of the Whale Depletion Hypothesis?

First, we reiterate that there have been no population declines in many areas with a history of whaling and with the presence of mammal-eating killer whales. However, even if killer whales were not forced to switch to other prey because of depleted whale populations, one cannot automatically rule out that killer whale predation was partly responsible for the four population declines cited by Springer *et al*. On the face of it, estimates of killer whale energetic requirements relative to biomass in the four declining populations concerned (Springer *et al*. 2003, Williams *et al*. 2004) present a plausible argument that killer whales could have caused population declines, particularly for sea otters (Estes *et al*. 1998).

Killer whale predation certainly occurs on all four species and is a source of mortality. However, it is a large leap from this fact to the belief that such predation caused the population declines in question. As we detailed here, demographic responses (*e.g.*, declines in fecundity and body condition) argue against killer whale predation as the cause of population decline for Steller sea lions, and a variety of alternative explanations are supported by substantial published literature. Barrett-Lennard *et al*. (1995) and the NMFS Steller Sea Lion Recovery Team (NMFS 1992) have concluded that killer whale predation was unlikely to be a significant factor in the 1970–1980's Steller sea lion decline but suggested that such predation could be an impediment to recovery (see also NRC 2003). Alternative explanations exist for the decline of fur seals, and there is no evidence for or against killer whales as the cause of the harbor seal decline at Tugidak Island. Trites *et al*. (this volume) suggest that bottom-up forcing is a more plausible explanation for the decline of pinniped populations than the prey-switching hypothesis, and DeMaster *et al*. (2006) suggest a combination of bottom-up forcing and several top-down factors, including fisheries bycatch and direct takes, can better explain the declines. Overall, the fact that we do not have a complete understanding of the causes of these population declines is not an argument for accepting the Springer *et al*. hypothesis. Indeed, we suggest that there are little data to support this hypothesis and much to contradict it. Marine ecosystems represent complex webs of innumerable and often subtly interacting variables. Consequently, hypotheses that tender neat explanations for apparent changes in trophic relationships are often wrong; in this regard, it is all too easy to confuse parsimony with oversimplification.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:
Supplementary Appendix A.
Supplementary Appendix B.
Supplementary Appendix C.

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