Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling?

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

The abrupt decline of the western stock of Steller sea lions (*Eumetopias jubatus*)[h] across most of the northern North Pacific Ocean and southern Bering Sea is one of the world's most well known yet poorly understood marine conservation problems. For years, scientists attributed this decline to nutritional limitation, the presumed consequence of a climate regime shift and/or competition with regional fisheries (1). Although fisheries and regime shifts undoubtedly influenced both the fishes and their associated food webs (2–5), several recent reviews of the available information on sea lions and their environment, including an assessment by the National Research Council, cast doubt on the nutritional limitation hypothesis (6, 7), notwithstanding evidence from field and laboratory studies that diet quality is a factor in sea lion energetics (8). The doubt stems from three main findings. First, most measures of behavior, physiology, and morphology from surviving adult sea lions and pups in the western Gulf of Alaska and Aleutian Islands are inconsistent with nutritional limitation. These animals have better body condition, reduced foraging effort, and reduced field metabolic rates relative to similar measures from the increasing sea lion population in southeast Alaska (7). Second, sea lion prey is abundant in most areas of the decline (9). Known changes in prey availability and other features of the oceanic ecosystem are particularly incongruous with the most precipitous phase of the decline, which occurred during the mid- to late 1980s, and can be accounted for only by greatly increased adult mortality (6). Third, populations of piscivorous sea birds, many of which feed on earlier life stages of the same fish species consumed by sea lions, have remained stable or increased in the same area and over the same period that the sea lions have declined (10). Top-down forcing now appears to have been an important contributor to declines of Steller sea lions and other marine mammal populations in the region (6). Likely top-down forcing factors include purposeful shooting, incidental mortality in fishing gear, and predation. We will suggest that increased predation was paramount among these factors, and that altered food web dynamics brought about by human overharvesting initiated the change.

A Megafaunal Collapse

Steller sea lions are only one of several marine mammal species in the far North Pacific region whose numbers have crashed in recent decades. Northern fur seal (*Callorhinus ursinus*), harbor seal (*Phoca vitulina*), and sea otter (*Enhydra lutris*) populations have also fallen precipitously. Causes of the pinniped declines are poorly known, except that incidental mortality from commercial fishing activities and intentional harvesting in the 1960s and early 1970s appear to explain substantial portions of the initial declines. The failure of these factors to explain the continued rapid collapses, the failure of the nutritional limitation hypothesis to explain the decline of the western stock of Steller sea lions, the recent demonstration that harbor seals thrive on prey with a wide range of nutritional quality (11), and the discovery that killer whales (*Orcinus orca*) were likely responsible for the sea otter decline (12), led us to suspect that the pinniped declines also were caused by increased killer whale predation.[i]

If this explanation is indeed true, why did the collapse occur? We propose that decimation of the great whales during the modern era of industrial whaling ultimately caused the declines by forcing the great whales' foremost natural predators, killer whales, to turn elsewhere for food.

Killer Whales Prey on Great Whales

Our hypothesis rests on the supposition that the great whales were an important prey resource for killer whales before industrial whaling severely reduced their numbers. Although there is debate over the nature and importance of killer whale predation on great whales (13, 14), this supposition is supported by several lines of evidence. Killer whales are known to attack and consume all species of great whales (15, 16). Such attacks have been observed regularly in modern times, despite the reduced abundance of most great whale stocks. Early whalers apparently recognized the importance of killer whale–great whale interactions: historical accounts from that era referred to these animals as "whale killers," a term that later was transposed to killer whales (17). Scars and rake marks from the teeth of killer whales on living great whales support the idea that killer whale attacks are fairly common (18), although the rate of scarring appears to

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[h]Steller sea lions range across the North Pacific Ocean from California to Japan. The western stock of this species, which ranges westward from Cape Suckling (longitude 144° W), was listed as Endangered under the U.S. Endangered Species Act in 1997.

[i]The absence of beach-stranded carcasses is one of the most intriguing and perplexing features of these declines. Sea otter mortality from nutritional limitation, disease, and pollution typically results in large numbers of stranded carcasses. Pinnipeds often sink when killed at sea, although many such individuals float to the surface and wash ashore later. Malnourished or diseased pinnipeds commonly haul out to die. The near absence of stranded carcasses and a lack of reports of distressed animals on beaches or of emaciated animals taken by subsistence hunters thus are most consistent with losses to predators.

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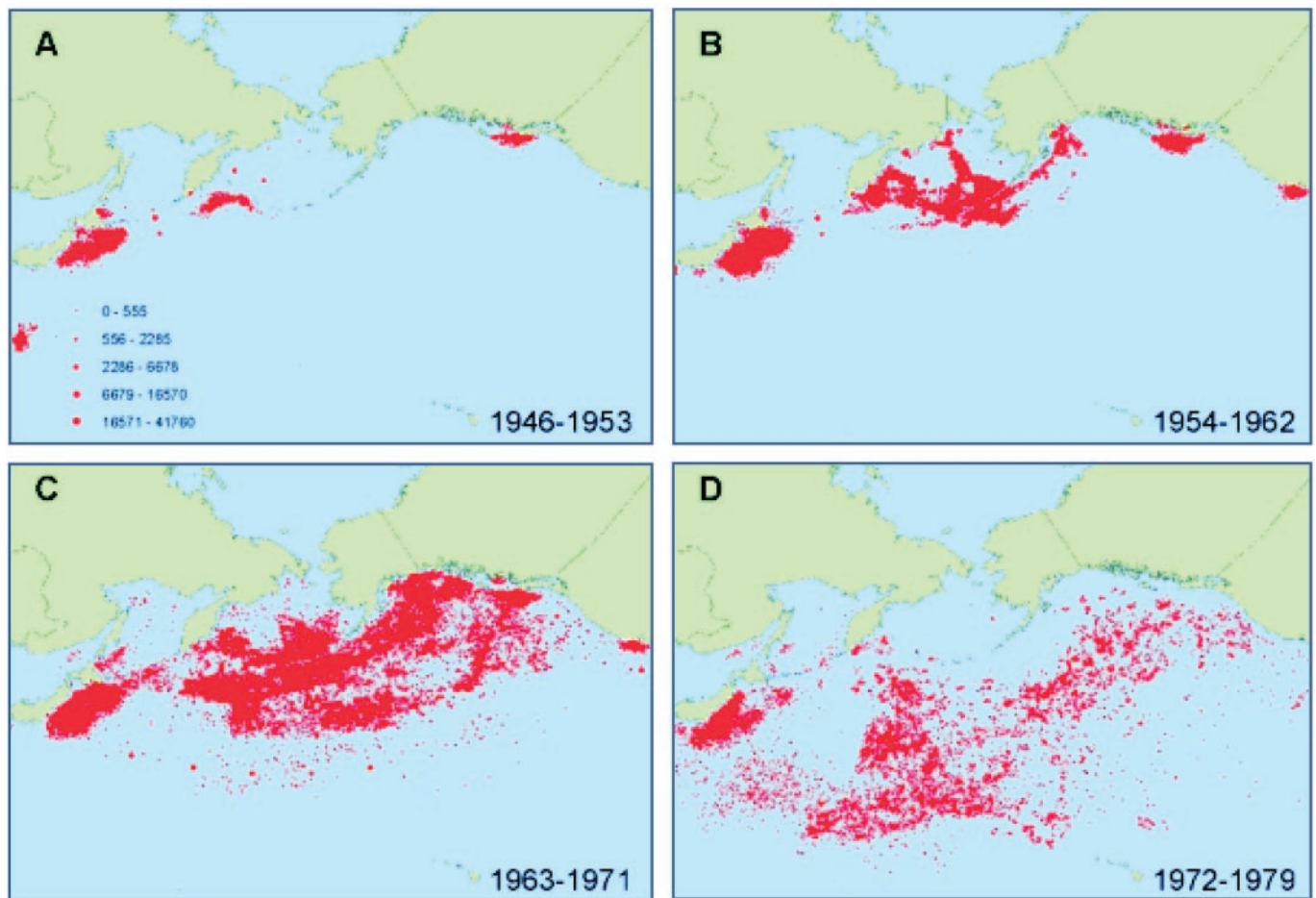
Fig. 1. Geography of reported whale harvests (all species) in the North Pacific Ocean and Bering Sea from 1946 through 1976. Data (latitude/longitude and number of individuals) are from International Whaling Commission records and are binned by sequential 7- to 8-year intervals to show temporal trends.

vary by region and species. Measured scarring on 20–40% of the individuals in some large whale species is not unusual; the highest known scarring rate is >60% reported for sperm whales in the southern ocean (19).

Several features of great whale life history and behavior may also function to reduce the likelihood of killer whale predation. For instance, sperm whales, long thought to be immune to killer whales, are now known to be preyed on by them and to assume stereotypical formations to ward off the attacks (20, 21). Many large whale species migrate from high-latitude feeding grounds to low-latitude calving grounds. Because of their very large size, this behavior does not confer a thermal benefit or energy saving, even to calves (13). The lack of thermal benefit raises the question of why large whales undertake such long migrations to nutritionally impoverished tropical oceans. Corkeron and Connor (13) contend this behavior may substantially reduce losses from killer whale predation by placing the most vulnerable newborns in environments where killer whales are comparatively rare. Likewise, the northward migration of bowhead whales (*Balaena mysticetus*) from wintering and feeding areas in the extremely productive northwestern Bering Sea to summering areas in the comparatively impoverished Beaufort Sea may reduce their exposure to killer whale predation (22). It has been further suggested that the failure of bowheads in the eastern Canadian Arctic to recover from commercial whaling is due in part to predation by killer whales (23, 24).

Industrial Whaling in the North Pacific Ocean

Modern industrial whaling in the North Pacific Ocean began in the late 1940s as Japan and the Soviet Union turned a maritime technology that developed during World War II toward postwar economic growth. Several species, including North Pacific right whales (*Eubalena japonica*), bowhead whales, humpback whales (*Megaptera novaeangliae*), blue whales (*Balaenoptera musculus*), and gray whales (*Eschrichtius robustus*), were depleted some 50–100 years earlier (25–27), but the more abundant fin whales (*Balaenoptera physalus*), sei whales (*Balaenoptera borealis*), and sperm whales (*Physeter macrocephalus*) were not exploited in large numbers until after the war. Our analysis of the depletions is based on International Whaling Commission records, which include geographical coordinates and species of all legally killed whales reported by whaling nations. These "official" records minimize the true magnitude of the catch in the North Pacific because of underreporting by the Russian fleet, by as much as 60% in the case of sperm whales taken between 1949 and 1971 (28), and because some unknown proportion of all kills were animals that were struck and lost. Nonetheless, the data provide a reasonable indication of the timing and spatial pattern of the whale declines.

Early postwar whale landings were mostly from the far western North Pacific Ocean (Fig. 1*A*), presumably because at the time, Japan was the region's only significant whaling nation, and great whales were still abundant throughout the North Pacific; thus, the Japanese whalers did not have to venture far from their home ports. Other nations, mainly the Soviet Union, subsequently entered the whale fishery. As stocks close to the home ports were progressively reduced, the fishery spread eastward and intensified (Fig. 1 *B* and *C*). By the early 1970s, the whaling industry had

abandoned this region because of severely depleted stocks and catch restrictions imposed by the International Whaling Commission and moved south into the central North Pacific (Fig. 1D) to exploit smaller Bryde's whales (*Balaenoptera brydei*) and female sperm whales.

The vast majority of whales were removed from rich summer feeding grounds in a small portion of the northern North Pacific Ocean and Bering Sea. In waters within 370 km (200 nautical miles) of the Aleutian Islands and north coastal Gulf of Alaska alone, a minimum of 62,858 whales and an estimated 1.8 million tonnes of whale biomass were taken between 1949 and 1969. As a measure of the magnitude of change in whale abundance in this region over this time, only 156 whales were harvested there after 1969. Altogether, at least a half million great whales were removed from the North Pacific Ocean and southern Bering Sea during this period. By the mid-1970s, all great whale stocks in the North Pacific Ocean were severely diminished. Although some species have exhibited remarkable recoveries (e.g., gray whale and humpback whale), the combined current biomass (1990s and early 2000s) is estimated to be only ≈14% of preexploitation levels (B.P., unpublished data).

The extreme, rapid, concentrated reduction of whale biomass from the northern North Pacific Ocean must have profoundly influenced the workings of the ecosystem by altering population level interaction strengths of two general kinds: those extending downward in the food web from the great whales to their prey and those extending upward in the food web from the great whales to their predators. Our focus is on the potential consequences of altered interaction strengths between the great whales and their predators.

Response of Killer Whales to Whaling

Before commercial whaling, the great whales likely provided an important food resource for killer whales in the North Pacific Ocean, just as gray whales do today along their eastern Pacific migratory route (29–31). Killer whales are organized around cultural matrilines with foraging preferences that define distinct ecotypes (32). Three killer whale ecotypes are recognized in the eastern North Pacific Ocean: transients, which feed largely on other marine mammals; residents, which feed largely on fish; and offshores, whose diet is less known (33, 34). Shifts in diet within specific ecotypes are known or suspected. For example, in the Southern Ocean, one particular ecotype (or species) feeds mostly on large cetaceans at high latitude during the austral summer and pinnipeds, fish, and squid at lower latitude during the austral winter (35). Because mammal-eating killer whales in the North Pacific feed on a wide variety of marine mammals, and because killer whales alter their diets in response to changing prey availability, the decline of great whales could have led to increased consumption of other marine mammal species by at least some of the whale-eating killer whales.

The sequential declines of pinnipeds and sea otters after human depletion of the great whales (Fig. 2) are consistent with this expectation. Pinniped populations in the Aleutian Islands, Bering Sea, and Gulf of Alaska began to fall during the 1960s and 1970s, shortly after the whale fishery collapsed and after the cessation of human harvest, but in advance of the late 1970s regime shift.[j] Harbor seals declined first (36),[k] followed by fur seals and then sea lions. Killer whales may have preferred harbor seals and fur seals to sea lions for nutritional or behavioral reasons, such as the higher energy density of harbor seals and the ease of capturing and handling both species because of their smaller size and less aggressive nature.

We surmise that as the last of the pinnipeds became comparatively rare, some of the killer whales that preyed on them further expanded their diet to include the even smaller and calorically least profitable sea otters. Sea otter populations in the Aleutian Islands began to collapse in ≈1990, after the pinniped declines, and by the late 1990s their numbers had decreased by an order of magnitude in many areas, converging on a common low density throughout the archipelago (39) and causing sea urchins to overgraze the kelp forest ecosystem (12).[l] Our subsequent analyses of the likely reason for these changes are limited to the Aleutian archipelago, because this is where our
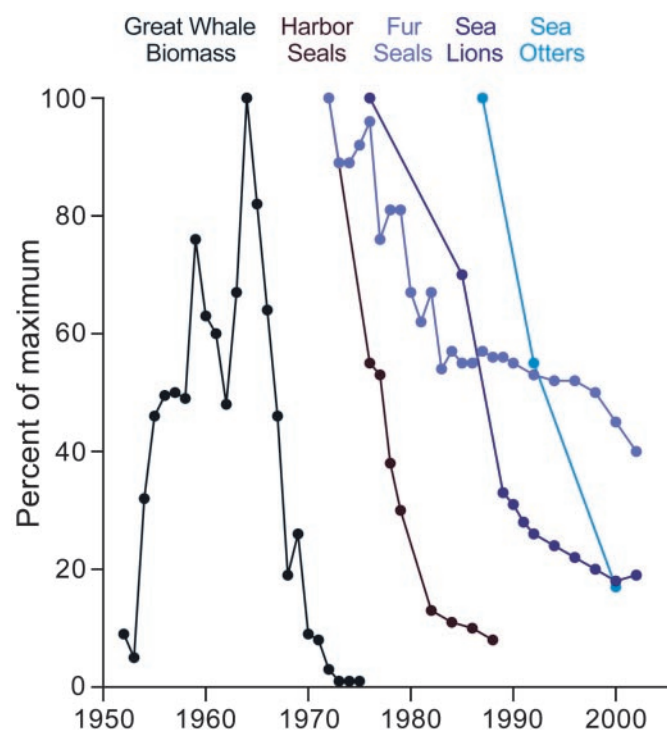
Fig. 2. The sequential collapse of marine mammals in the North Pacific Ocean and southern Bering Sea, all shown as proportions of annual maxima. Great whales: International Whaling Commission reported landings (in biomass) within 370 km of the Aleutian archipelago and coast of the western Gulf of Alaska. Harbor seals: counts and modeled estimate (1972) of Tugidak Island (36). Fur seals: average pup production on St. Paul and St. George islands, Pribilof Islands (from ref. 37 and A. E. York, personal communication). Steller sea lions: estimated abundance of the Alaska western stock (from ref. 38). Sea otters: counts of Aleutian Islands (from ref. 39). For fur seals and harbor seals, 100% represents population sizes at the time effects of excessive harvesting ended and "unexplained" declines began.

[j]Initial declines of fur seals on the Pribilof Islands (in the Bering Sea) and harbor seals on Tugidak Island (in the Kodiak archipelago, depicted in Fig. 2) prior to the 1970s were caused in substantial part by excessive human killing, of fur seals during an experimental harvest in 1956–1968 and of harbor seals by a commercial harvest in 1964–1972. After cessation of these harvests, numbers of both species continued to decline because of elevated mortality of juveniles and adults. It is particularly noteworthy that these "unexplained" declines began well in advance of the climate regime shift of 1977, which has been blamed for altering many facets of marine ecosystems of the North Pacific (3–5).

[k]Although these data are from a single location, Tugidak Island, they are representative of the timing and magnitude of harbor seal declines that occurred elsewhere. For instance, the harbor seal population at Otter Island (in the Pribilof Islands), which numbered ≈1,200 when first counted in 1974, declined 40% from 1974 to 1978 and an additional 70% from 1978 to 1995 (L. Jemison, personal communication). Similar harbor seal declines, although not quantified, have occurred throughout the Aleutian archipelago (J.A.E., unpublished observations).

[l]A corollary is that the increase in abundance of killer whales in the late 1980s on the continental shelf of the eastern Bering Sea, in the region of the Pribilof Islands and in Bristol Bay (40, 41), also resulted from the collapse of pinnipeds in the Aleutian Islands. The increase of killer whales on the shelf was accompanied by the resumption of the overall decline of fur seals at the Pribilofs after a brief interval of stability at St. Paul Island (Fig. 2) and by numerous observations of attacks on a variety of marine mammal species in Bristol Bay.

field studies were done, and it is the region from which we have the best information on key players.

Killer Whale Abundance

Killer whales were long thought to be too rare to account for the pinniped declines,[m] but current information indicates this is not the case. By using standard line transect techniques (42), killer whale density in waters up to 370 km south of the eastern and central Aleutian archipelago was conservatively estimated at 3.6 individuals per 1,000 km^2, based on 2,897 km of shipboard search effort during a 1994 survey (K.A.F., unpublished data). [This estimate is comparable to densities of 2.5 per 1,000 km^2 for the southeast Bering Sea (43) and 2.3–7.6 per 1,000 km^2 for Antarctic waters (44).] If the density were similar in the western Aleutian Islands, the estimate of 3.6 individuals per 1,000 km^2 would translate into an abundance of 3,888 killer whales (95% confidence interval, 1,707–8,857) in waters within 370 km (1,080,000 km^2) of the entire archipelago. This estimate presumably includes killer whales of all three ecotypes.

Demographic Influences of Killer Whale Predation

Although changes in fish stocks due to fishing or climate regime shifts may have contributed to the losses (45), as did directed killing by people (6), both the sea otter and sea lion declines could be accounted for by remarkably small changes in killer whale foraging behavior. We computed these changes by combining estimates of the abundance and nutritional requirements of killer whales, the nutritional value of sea lions and sea otters, and the number of additional deaths required to explain the observed sea lion and sea otter declines in the Aleutian archipelago. We were unable to conduct similar analyses for harbor seals, because the predecline population size there is unknown.

Population matrix models were used to estimate the number of additional deaths required to drive the sea otter and sea lion declines. These models were parameterized by using published life table data for Steller sea lions (46), age-specific fertility and mortality rates for sea otters (12), and predecline abundance estimates for both species (39, 46). We then fit the added mortality required to generate the observed speed and magnitude of population declines for each species. For sea otters, we assumed age independence and a constant number of animals lost per year (12). The resulting loss estimate was 9,982 deaths per year from 1991 through 1997. For Steller sea lions, we used maximum likelihood methods (47) to fit the demographic model with an added time-varying logit function for predation risk. The age-specific probability of elevated mortality is unknown for Steller sea lions, and thus a series of models was fitted, ranging from age constancy to 5-fold higher predation risk for pups and younger animals. These models predict from as many as 15,006 additional animals lost to predation in the Aleutian Islands in 1979 to as few as 170 in 2000.

Caloric values for sea otters were determined by bomb calorimetry of homogenized whole carcasses and measurements of adult body mass (12). Resulting estimates range from 41,630 to 61,540 kcal per individual. Caloric values for Steller sea lions, determined similarly for skeletal muscle and blubber, ranged from 1.5 to 6.7 kcal·g^{-1} wet weight. These latter data were combined with published estimates of body mass and composition for pups, adult females, and adult males to provide estimates of caloric value for individual sea lions (T.M.W., unpublished data).

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[m]Dahlheim, M. E. (1994) *Abundance and Distribution of Killer Whales in Alaska* (Unpublished Report, National Oceanic and Atmospheric Agency, National Marine Mammal Laboratory, 7600 Sand Point Way N.E., Seattle).
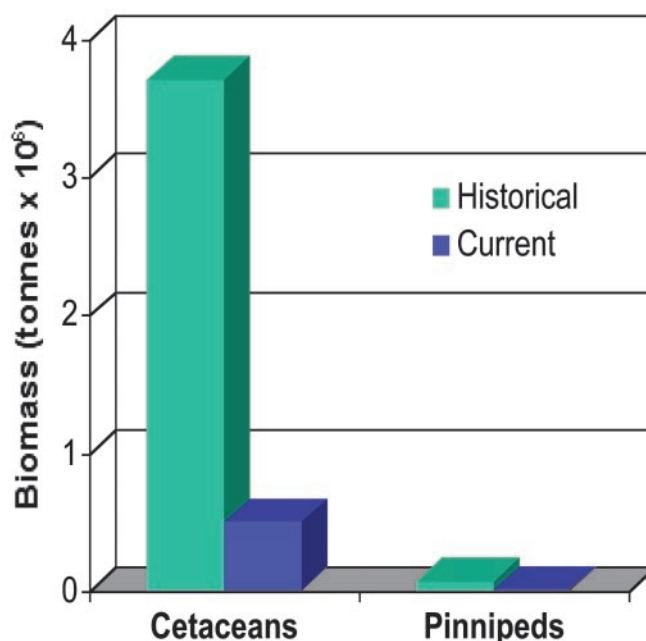
Fig. 3. Biomass estimates for great whales and pinnipeds before and after recent declines in the Aleutian Islands and Bering Sea region. These estimates were derived from current and historical estimates of abundance and per capita biomass, in some cases adjusted for estimates of sex and size composition (from B.P., unpublished work). Historic and current abundance estimates are species-specific. ''Historical'' is defined as the period before large-scale commercial exploitation, ranging from the mid-1800s to the mid-1900s. ''Current'' is defined as the most recent available estimate of abundance, reflecting population levels during the mid-1990s to early 2000s.

The nutritional requirements of killer whales were estimated from field metabolic rates and assimilation efficiency. Field metabolic rate estimates ranged from 163,738 to 243,501 kcal·day^{-1}, depending on sex and age [Barrett-Lennard *et al.* (48) estimated similar metabolic rates for free-ranging killer whales]. Assimilation efficiency was taken as 82% (49).

These data can be translated into potential killer whale dietary change in various ways. If we assume the change was spread evenly across all of the region's 3,888 killer whales, then a dietary shift of <1% in total caloric intake (0.99% for sea lions; 0.17% for sea otters) is sufficient to drive the respective population declines. In view of the killer whale's complex social structure and associated dietary variation, a larger dietary change by some smaller number of individuals is more likely. If we assume that ≈7% of the killer whale population are transient mammal eaters (P. Wade, personal communication), the resulting 272 killer whales is >10-fold larger than the minimum number needed to drive the Steller sea lion decline and >45-fold larger than the minimum number needed to drive the sea otter decline if they derived 100% of their total caloric intake from either species. These various estimates show that our conclusions are robust to anything but massive errors in the input parameters, something we believe is unlikely.

The inability of sea otters and pinnipeds to sustain increased mortality from redirected killer whale predation ultimately derives from their much smaller aggregate biomass compared with that of the great whales (Fig. 3). When all of these marine mammals were maximally abundant, the estimated biomass of great whales was ≈60-fold larger than the combined total for pinnipeds and sea otters. These gross inequalities suggest that the great whales were capable of sustaining vastly more killer

whales than were the pinnipeds and sea otters, despite the fact that in some cases only portions, e.g., tongues, of great whales are consumed. From these estimates and analyses, it is easy to see how industrial whaling could have caused killer whales to "fish down" (50) other components of the marine mammal food web.

Discussion

Our proposed explanation for the collapse of sea otters and pinnipeds in the northern North Pacific Ocean and southern Bering Sea, although speculative, is based on a logical interpretation of known patterns and feasibility analyses of the hypothesized causal process. Although killer whales likely drove the sea otter declines and are known to prey on harbor seals, northern fur seals, and sea lions, there is presently no direct evidence that killer whale predation drove the pinniped declines. In contrast with the sea otters, detailed field studies of killer whales and pinnipeds are lacking from the most critical time periods. Studies of the modern-day predator–prey system in the western Gulf of Alaska and Aleutian Islands are unlikely to resolve this matter, because pinnipeds and sea otters are now relatively rare and their populations comparatively stable, and numbers of mammal-eating killer whales in the region also may be much reduced. Thus, few losses from predation would be expected, and the demographic significance of those that might be seen would be difficult to interpret. However, it is worth mentioning that recent localized declines of harbor seals (www.sfgate.com/cgi-bin/article. cgi?file=/news/archive/2003/02/24/state1900EST7458.DTL) and Steller sea lions[n] elsewhere have been attributed to killer whale predation. A further complication is that some recovering whale populations, particularly gray, humpback, and bowhead whales, are increasingly providing alternate prey resources for killer whales in this region.

The most promising source of information on the cause of the pinniped declines is the retrospective analysis of materials from individual pinnipeds or killer whales that were alive during various stages of the megafaunal collapse. Recently published nitrogen isotope analyses of pinniped bones obtained during this period provide no indication of dietary change (51), a finding that appears to be inconsistent with nutritional limitation. Isotopic studies of killer whale bones and teeth could provide a more definitive test of our hypothesis by establishing whether these large predators altered their diets after the great whale reductions. It is worth noting that if the North Pacific killer whale population has remained numerically stable with a stationary age distribution over this period, ≈28–39% of the individuals alive in 1965 during the final binge of commercial whaling would still be alive in 2002. For the longer-lived females alone, 39–57% survival from 1965 is expected.[o]

There is growing evidence that large animals play important roles in ecosystem dynamics (53–57). Furthermore, retrospective analyses of numerous coastal marine systems demonstrate or suggest a pervasive influence from the historical removal of these large animals (58). Many ecosystems function in vastly different ways today than they did when large animals were common, and there is no reason to believe the open sea is an exception. If our hypothesis is correct, either wholly or in significant part, commercial whaling in the North Pacific Ocean set off one of the longest and most complex ecological chain reactions ever described, beginning in the open ocean >50 years ago and leading to altered interactions between sea urchins and kelp on shallow coastal reefs.

Whaling was a global endeavor (59), and thus ecosystem-level effects of commercial whaling undoubtedly occurred elsewhere in the world oceans. The depletion of baleen whales in the Southern Ocean is thought by some to have substantially altered krill abundance and therefore the dynamics of interactions between krill and krill consumers (60, 61). Moreover, the Southern Ocean is a region where the great whales were exploited in even larger numbers than they were in the North Pacific, pinnipeds and killer whales were abundant, and various southern elephant seal (*Mirounga leonina*) populations have declined (62–64). Barrat and Mougin (62) hypothesized that these declines were caused by whaling and increased killer whale predation, an identical explanation to the one we are proposing for the North Pacific. It is surprising to us that these proposals for community-level influences of whales and whaling have had so little effect on subsequent research. Both are supported by logic and a variety of indirect evidence, and neither has been reasonably discounted, so far as we know.

Although substantial uncertainty remains concerning the degree to which whales and whaling influenced the structure and dynamics of ocean ecosystems in top-down ways, these influences must have been sizeable. A greater appreciation of this fact is needed to properly understand the function of the oceans, now and in the past.

[n]Maldini, D., Maniscalco, J. & Burdin, A. (2002) *Fourth International Orca Symposium and Workshop* (Centre National de la Recherche Scientifique, Villiers en Bois, France), pp. 92–94 (www.cebc.cnrs.fr/Fr_collo/ORCA.pdf).

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