

KILLER WHALES, WHALING, AND SEQUENTIAL MEGAFANAL COLLAPSE IN THE NORTH PACIFIC: A COMPARATIVE ANALYSIS OF THE DYNAMICS OF MARINE MAMMALS IN ALASKA AND BRITISH COLUMBIA FOLLOWING COMMERCIAL WHALING

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ABSTRACT

The hypothesis that commercial whaling caused a sequential megafaunal collapse in the North Pacific Ocean by forcing killer whales to eat progressively smaller species of marine mammals is not supported by what is known about the biology of large whales, the ecology of killer whales, and the patterns of ecosystem change that took place in Alaska, British Columbia, and elsewhere in the world following whaling. A comparative analysis shows that populations of seals, sea lions, and sea otters increased in British Columbia following commercial whaling, unlike the declines noted in the Gulf of Alaska and Aleutian Islands. The declines of seals and sea lions that began in western Alaska around 1977 were mirrored by increases in numbers of these species in British Columbia. A more likely explanation is that the seal and sea lion declines and other ecosystem changes in Alaska stem from a major oceanic regime shift that occurred in 1977. Killer whales are unquestionably a significant predator of seals, sea lions, and sea otters—but not because of commercial whaling.

Key words: killer whales, whaling, ecosystem change, North Pacific Ocean, ocean climate, regime shift, predation.

A compelling and eloquently simple hypothesis was proposed to explain a cascade of declines in populations of marine mammals that began in the late 1970s in the Gulf of Alaska, Aleutian Islands, and Bering Sea (Springer *et al.* 2003). The core of the argument is that killer whales were forced to switch to a diet of progressively smaller pinnipeds and other species of marine mammals after commercial whalers severely depleted the fin, sei, and sperm whales in Alaskan waters between 1949 and 1969. This, it is suggested, accounts for a sequential decline of harbor seals, northern fur seals, Steller sea lions, and sea otters that followed through the 1980s and 1990s (Pitcher 1990, Trites 1992, Trites and Larkin 1996, Estes *et al.* 1998, Doroff *et al.* 2003, Small *et al.* 2003).

Although stated as a hypothesis, many people may regard the whaling theory (Springer *et al.* 2003) as a forgone conclusion—*i.e.*, that the commercial removal of large whales (Fig. 1) actually did launch a tidal wave of ecosystem changes. Regrettably, information that would help to assess this hypothesis was not brought forward, and ways in which it might be tested were not discussed. The hypothesis, therefore, warrants comment given the potential it has to misdirect scientific effort that is focused on resolving why seals, sea lions, fur seals, and other species have declined in Alaska.

There are a number of different ways in which to test the likelihood that commercial whaling could have produced the cascade of population changes that took place in Alaska. One is to critically examine the data and assumptions that form the basis for the original hypothesis (DeMaster *et al.* 2006, Mizroch and Rice 2006, Wade *et al.*

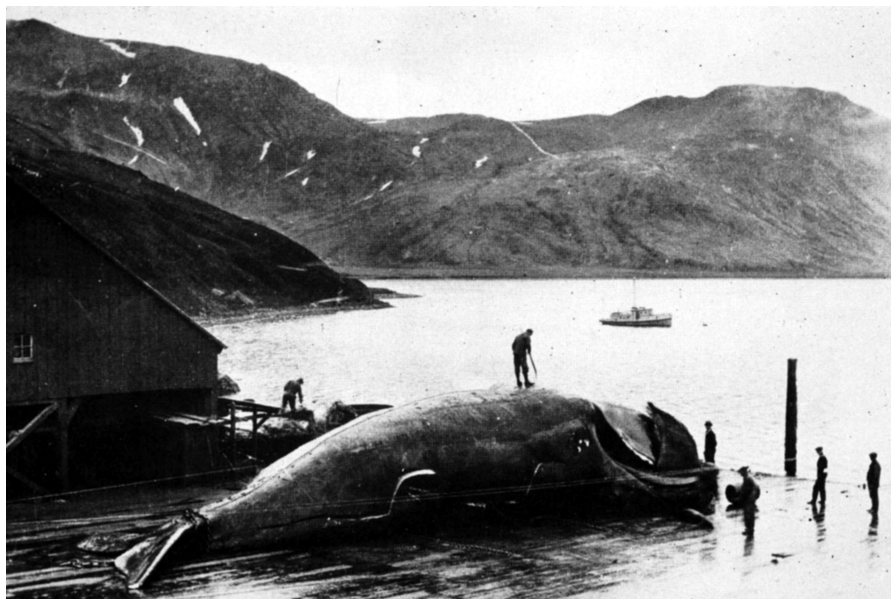


Figure 1. A right whale on the flensing platform of the former whaling station at Akutan in the Aleutian Islands, Alaska (Historical Photography Collection, University of Washington Libraries, Seattle).

2007). Another is to comparatively analyze the dynamics of other ecosystems subjected to intensive whaling, such as occurred in coastal British Columbia, Canada.

METHODS

Commercial whaling took place in British Columbia between 1905 and 1967 (Gregr *et al.* 2000, Nichol *et al.* 2002) during which time over 24,862 whales were removed by coastal whaling stations. The reported take included 7,605 fin whales (*Balaenoptera physalus*), 6,158 sperm whales (*Physeter macrocephalus*), 5,639 humpback whales (*Megaptera novaeangliae*), 4,002 sei whales (*B. borealis*), and 1,398 blue whales (*B. musculus*). Few North Pacific right whales (*Eubalaena japonica*, $n = 8$) and gray whales (*Eschrichtius robustus*, $n = 11$) were taken due to the reduced population sizes caused by earlier exploitation (*i.e.*, mid-1800s to early 1900s). Few minke whales (*B. acutorostrata*) were also taken, but only because of their small size and low commercial value. Today, blue whales, sei whales, and right whales are all listed as endangered species in Canada (COSEWIC 2005).

For the sake of comparison with the data compiled for Alaska we applied the same methodology used by Springer *et al.* (2003) to determine trends in great whale biomass, as well as sizes of marine mammal populations. First, we limited our analysis to the post World War II period of commercial whaling (*i.e.*, after 1945). We then calculated the biomass of great whales removed by the British Columbia whaling industry by multiplying the number of individuals landed (see Gregr *et al.* 2000) with the mean weight for each species. We included landings of blue, fin, sei, minke, humpback, gray, North Pacific right, and sperm whales. Mean weights for all species, except sperm whales, were estimated by taking the average of the population mean weights of males and females from Trites and Pauly (1998). For sperm whales, we only used the mean estimated weight of males, because this was the sex primarily caught in British Columbia waters (Gregr *et al.* 2000). For North Pacific right whales, we used the weight of the North Atlantic right whale (*E. glacialis*) because this information was unavailable for the Pacific species (Trites and Pauly 1998).

We drew information about the abundances of British Columbia harbor seals (*Phoca vitulina*), Steller sea lions (*Eumetopias jubatus*), and sea otters (*Enhydra lutris*) from published reports. Harbor seal counts for British Columbia coastal waters excluded the Strait of Georgia and were derived from aerial counts of known haul-outs in index areas corrected for animals not hauled out or otherwise missed during the survey (Olesiuk *et al.* 1990, Olesiuk 1999). The Strait of Georgia is not a region where commercial whaling occurred post 1945. Harbor seal abundance in the Strait of Georgia followed a similar trend compared to the rest of the province, but reached higher densities. Counts of Steller sea lions consisted of totals (pups, juveniles, and adults) present at breeding areas, which provide a good index of total abundance, though they were not corrected for animals at sea when the aerial photographs were taken (Bigg 1985, COSEWIC 2003, Olesiuk 2003). We included counts for Forrester Island, a large breeding area situated just a few kilometers north of the British Columbia–Alaska border that became established and flourished as populations in British Columbia were being depleted by predator control programs. Data on sea otter abundance were counts of animals made during dedicated aerial or boat surveys throughout the known range of this species along the British Columbia coast (northwest coast of Vancouver Island and central British Columbia coast) (Bigg and MacAskie 1977, Watson *et al.* 1997). Northern fur seals (*Callorhinus ursinus*) occur seasonally in British Columbia

waters (Bigg 1990, Trites and Bigg 1996), but were excluded from our analysis because they do not breed along this coast.

We normalized the estimated removals of whale biomass and the trends in counts of pinnipeds and otters from British Columbia to compare them with the data compiled and presented by Springer *et al.* (2003) for the Gulf of Alaska and Aleutian Islands. Thus, we expressed our data as a percentage of the maximum value for each of the data series in question for the study period. We also estimated the whale densities removed from the two study areas to ensure that the ecosystem effect of whale biomass removal was comparable between the two regions.

RESULTS

Based on the description of the study area provided by Springer *et al.* (*i.e.*, “waters within 370 km [200 nmi] of the Aleutian Islands and north coastal Gulf of Alaska”), we estimated the Alaskan study area to be 2,340,000 km² (Fig. 2). The 62,858 animals or 1.8 million tonnes of biomass removed as reported by Springer *et al.* (2003) represents an average removal of 0.0269 whales or 0.77 tonnes per km² from their study area. Defining our study area as the waters of British Columbia within 200 nmi of shore resulted in an area of 451,800 km² and a similar level of removal of 0.0214 whales or 0.77 tonnes per km² (based on catching at least 9,674 whales in British Columbia between 1948 and 1967, with a mean biomass of 35.8 tonnes). Thus the two regions are comparable in terms of the numbers and biomass of whales removed per km².

The data presented by Springer *et al.* (2003) are reproduced in Figure 3A, which shows their estimate of biomass of large whales removed from the Gulf of Alaska and Aleutian Islands from 1952 to 1975. It also shows numbers of harbor seals counted at a single site in Alaska at Tugidak Island, near Kodiak Island in the Gulf of Alaska, as well as counts of fur seal pups from St. Paul Island in the eastern Bering Sea, and counts of juvenile and adult Steller sea lions from trend sites throughout the entire range of the western population in Alaska (from Prince William Sound to the western

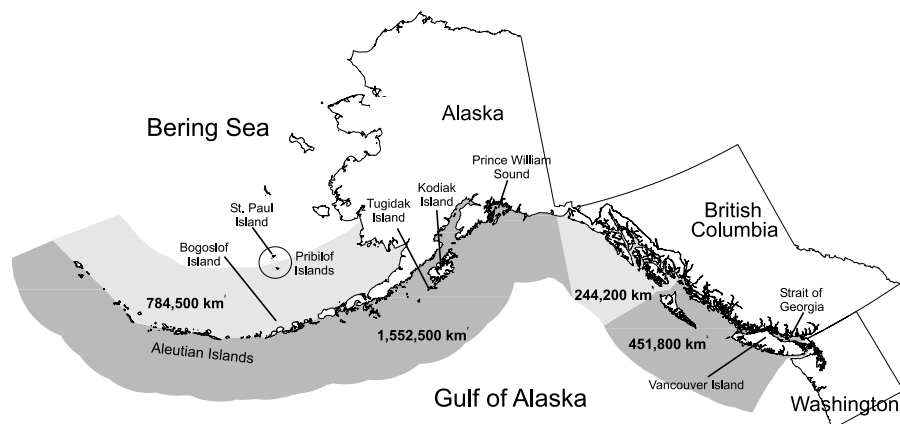


Figure 2. The calculated areas (in square kilometers) of marine regions within 370 km (200 nmi) of the Aleutian Islands (Bering Sea only), western Gulf of Alaska, southeast Alaska, and British Columbia. Places mentioned in the text are also shown.

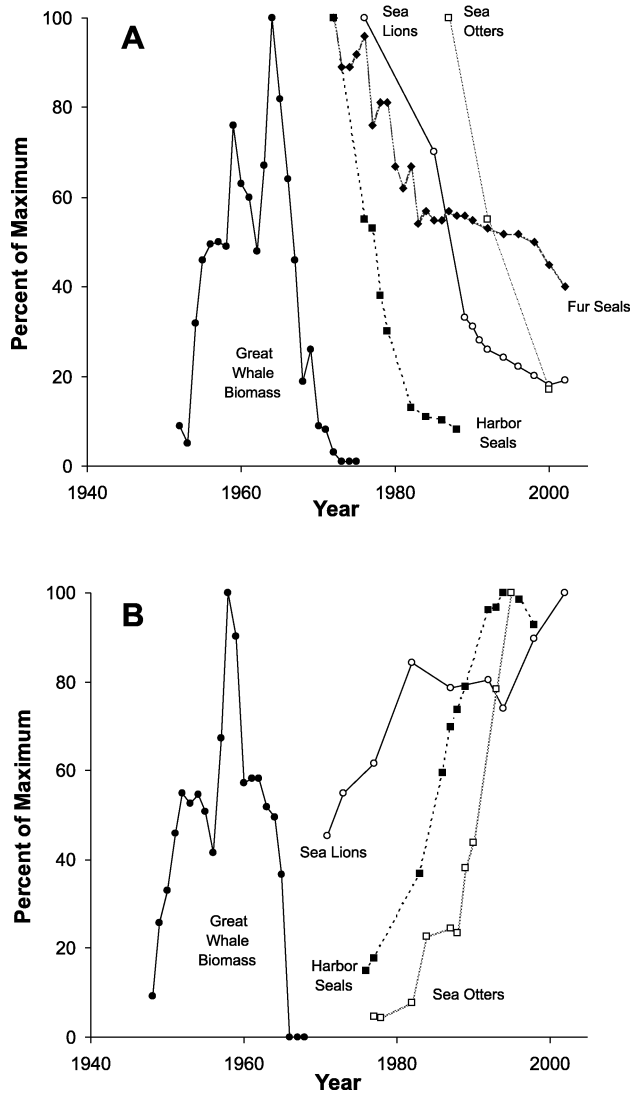


Figure 3. Biomass of large whales removed and changes in abundance of harbor seals, Steller sea lions, northern fur seals and northern sea otters in (A) the Gulf of Alaska and Aleutian Islands, and (B) British Columbia. Data are from Springer *et al.* (2003) for Alaska, and from Olesiuk *et al.* (1990) Olesiuk (1999, 2003), COSEWIC (2003) and Watson *et al.* (1997) for British Columbia. Note that “Great Whale Biomass” is the estimated biomass of whales removed from the respective ecosystems and is not an index of numbers or biomass of whales present. See text for further details.

Aleutian Islands), plus sea otter counts from some Aleutian Islands (see Springer *et al.* 2003 for complete details).

Population information for marine mammals in British Columbia is presented in Figure 3B. It shows a rise and fall in biomass of whales removed that is similar to

the pattern observed in Alaska, with the exception that whaling started and ended slightly earlier in British Columbia. However, populations of harbor seals, sea lions and sea otters increased in British Columbia following the cessation of whaling, unlike in the Gulf of Alaska and Aleutian Islands where they declined.

DISCUSSION

Whaling was widespread and synchronous in the North Pacific (Webb 1988, Mizroch and Rice 2006, Wade *et al.* 2007), and should have had similar effects on all North Pacific coastal ecosystems. Thus the scope of harvest along the British Columbia coast, which was as great as anywhere in the eastern North Pacific, should have been capable of altering the purported prey base of killer whales and expressing the effects suggested by Springer *et al.* (2003). Springer *et al.* (2003) proposed that whaling altered the feeding behavior of killer whales, and had large and measurable effects on other top predators in western Alaska. However, we can find no evidence of such a trophic cascade having occurred in British Columbia following the removal of similar densities of whales. Nor can we find any reason to think that the proposed trophic cascade hypothesis should apply only to western Alaska given that the basic tenets of the theory should have broad ecological applicability.

The population trends of seals, sea lions, and sea otters in British Columbia are not consistent with the predictions of the whaling hypothesis posed by Springer *et al.* (2003). In fact, the population trends are opposite those in Alaska (Fig. 3). In theory, the abundance of seals, sea lions and sea otters in British Columbia should have also declined, or remained at low numbers if killer whales that once depended on eating large whales were forced to switch to alternative prey following the demise of the large whales. Instead, the positive response of otters, seals and sea lions in the 1980s and 1990s shows that they were not limited by killer whale predation.

The increases of sea lions, harbor seals, and sea otters in British Columbia can be largely attributed to their protection from culling and over hunting. Sea otters, for example, were re-introduced off Vancouver Island from 1969 to 1972 (89 individuals), and numbered a minimum of 1,522 in 1995 (Watson *et al.* 1997). They increased at a rate of 18.6% per year, as they have in Washington and southeast Alaska (Watson *et al.* 1997). Harbor seals were maintained below natural levels by bounties until the 1960s, and were then severely depleted by intense commercial harvesting. After being protected in 1970, numbers increased exponentially through the 1980s and early 1990s, stabilizing at about 108,000 (including 37,300 in the Strait of Georgia) in the mid-1990s (Fig. 3B; Olesiuk *et al.* 1990, Olesiuk 1999). Harbor seals also appear to have increased in California, Oregon, Washington, and southeast Alaska (Jeffries *et al.* 2003, Small *et al.* 2003, Angliss and Lodge 2004, Carretta *et al.* 2004, Brown *et al.* 2005).

As for Steller sea lions in British Columbia, an estimated 49,100 individuals (including pups) were destroyed in predator-control programs, and another 5,700 were taken in commercial harvests between 1913 and 1969 (Pike and Maxwell 1958, Bigg 1985). About 14,000 animals are believed to have inhabited British Columbia rookeries (all ages, including pups) when the first counts were made in 1913–1916—but the population fell to about 3,390 animals (including pups) by the time the first aerial survey was conducted in 1971. Abundance of sea lions in British Columbia is difficult to separate from southern southeast Alaska because Forrester Island,

situated just a few kilometers north of the British Columbia–Alaska border, became established as a rookery and flourished while control programs were underway in British Columbia. The number of Steller sea lions breeding on British Columbia rookeries and at Forrester Island has increased steadily since the last major predator control kills were made in the mid-1960s. Steller sea lion populations have also been increasing throughout southeast Alaska since surveys were initiated in the late 1970s (Calkins *et al.* 1999). The total number of Steller sea lions inhabiting coastal waters of British Columbia during the breeding season are now (2002) estimated at about 18,400–19,700 individuals (Olesiuk 2003).

While the increases in seals, sea lions and otters in British Columbia can be seen as the recovery from culling and hunting—the depleted populations should not have recovered if predation by killer whales had increased (as predicted by the whaling hypothesis). Thus the changes noted in British Columbia, where removals of whales were comparable to Alaska, are inconsistent with the predictions of the whaling induced megafaunal collapse hypothesis proposed by Springer *et al.* (2003). There is no indication of killer whales having trapped seals and sea lions in a predator pit. The changes purported to have occurred in Alaska due to whaling are also inconsistent with the demographic trends of penguins and pinnipeds following commercial whaling in the southern hemisphere—assuming that a significant portion of mammal-eating killer whales present in the Antarctic also once specialized on large whales (Knox 1994, Pitman and Ensor 2003, Trites *et al.* 2004). The hypothesis is also not consistent with what is known about the ecology of killer whales and the patterns of ecosystem change that took place in Alaska and British Columbia.

Killer Whales and Their Prey

Twenty-five years of intensive studies along the west coast of North America have shown that the eastern North Pacific is home to three distinct forms of killer whales that differ in their morphology, diet, and behavior (Ford *et al.* 1998, Ford *et al.* 2000, Saulitis *et al.* 2000). Genetic studies have shown that these forms do not interbreed and have been reproductively isolated for many generations (Hoelzel and Dover 1991, Hoelzel *et al.* 1998, Barrett-Lennard 2000). Only one of the three—*transient* killer whales—is known to feed on marine mammals.

Transient killer whales appear to be specialist predators that use a wide range of hunting tactics to detect and subdue different species of prey. Dietary studies in the inshore water of British Columbia, southeastern Alaska, and Prince William Sound, Alaska have consistently shown that transient killer whales primarily feed on pinnipeds (mainly harbor seals and Steller sea lions) as well as small cetaceans (porpoises and dolphins) (Ford *et al.* 1998, Saulitis *et al.* 2000, Heise *et al.* 2003). Although most of the dietary studies were conducted in coastal areas during the summer months, they do point to a noted absence of attacks on large whales even in areas where they have been available (*e.g.*, humpback whales in coastal British Columbia and Alaska). Studies of killer whales in the Gulf of Alaska and Aleutian Islands have only recently been initiated, but suggest that the distinctions in ecotypes and diets match those noted in southern Alaska and British Columbia (Herman *et al.* 2005).

The only species of large whale known to be regularly attacked by North Pacific transients are gray whale calves and minke whales (Jefferson *et al.* 1991,

Ford *et al.* 1998, Saulitis *et al.* 2000, Heise *et al.* 2003, Ford *et al.* 2005, Mizroch and Rice 2006). There is no evidence that larger, faster species such as fin and sei whales have ever played anything but a marginal role in their diet. Indeed, there is only one report of a successful attack by killer whales on a fin whale—and it comes from the North Atlantic and is thought to be unreliable (Jonsgard 1968*a, b*; Jefferson *et al.* 1991; Clapham 2001). Successful attacks on sei whales have never been recorded. All documented attacks on sperm whales targeted groups with calves and occurred in tropical and subtropical waters (Jefferson *et al.* 1991, Pitman *et al.* 2001). Although observational evidence is lacking, it seems doubtful that killer whales would have succeeded in killing full-grown male sperm whales—the only component of the population found off western Alaska, and the predominant sex class in British Columbia.

Population trends of transient killer whale prey in the North Pacific are also inconsistent with the trophic cascade hypothesis. The two species of large whales that transients are known to attack either recovered to historic levels as the seals and sea lions declined in Alaska (*i.e.*, gray whales) or were never exploited (*i.e.*, minke whales) (Buckland and Breiwick 2002, Angliss and Lodge 2004, Carretta *et al.* 2004). Removing large whales from Alaskan waters between 1949 and 1969 should have also resulted in killer whales gradually shifting their diet to harbor seals to replace their presumed dependence on large whales. However, harbor seals declined a decade after whaling ceased, and the drop was precipitous (Pitcher 1990). In addition, the large populations of Dall's porpoise and other small cetaceans have not shown evidence of decline, yet are taken preferentially by transient killer whales (Ford *et al.* 1998, Saulitis *et al.* 2000).

The physical challenges posed by killing and eating a large adult whale and the risk of injury involved may mean that they are not profitable for killer whales to pursue. Even if a large whale was subdued, only a small portion may be eaten by the killer whales before the carcass sinks and becomes unavailable (Ford *et al.* 2005). It seems even less likely that killer whales would specialize on eating large migratory whales because large whales in Alaska and British Columbia are most abundant in summer and fall. Instead, it makes more sense for killer whales to target smaller species such as pinnipeds, dolphins, and porpoises that are easier to kill and are available year round. Available data (from scarring and direct observation of attacks off California and elsewhere) suggest that the majority of successful predation events on large whales occur on calves along the migratory corridor, and that except for minke whales, predation on adult baleen whales on the feeding grounds is extremely rare or non-existent. Thus the available dietary data for marine mammal-eating killer whales suggest that large whales (*i.e.*, fin, sei, and sperm whales) are unlikely to have ever contributed more than an infrequent windfall to the diet of North Pacific killer whales; and that whaling may have in fact supplemented the diets of some transient killer whales rather than depleted their prey base (Whitehead and Reeves 2005).

Pinnipeds and small cetaceans appear to represent a profitable food source for transient killer whales in British Columbia and southeastern Alaska (Ford *et al.* 1998, Saulitis *et al.* 2000). This is supported by the observations that killer whales focus on pinnipeds and small cetaceans in areas where large whales are locally abundant (Dolphin 1987), suggesting that the preferred and profitable sources of food for transients are the smaller species of marine mammals. These smaller species probably also formed the core of the transient killer whale diet in western Alaska, and are unlikely to have ever been a larder waiting for the demise of the great whale stocks

before being fully exploited. It is difficult to imagine any niche or abundant food source being left untouched or underexploited within an ecosystem.

An Alternative Hypothesis

The declines of seals and sea lions in Alaska represent the tip of an iceberg of documented changes in the Gulf of Alaska and Bering Sea ecosystems that began around 1977. These changes included declines of shrimp, crabs, and possibly small pelagic fishes (herring and sand lance)—while flatfish (halibut and arrowtooth flounder) and gadids (Pacific cod and walleye pollock) increased (Anderson and Piatt 1999, Trites *et al.* 1999).

The trends in pinniped abundance are more complicated than the data selected by Springer *et al.* (2003) imply (see Fig. 3A). Declines of harbor seals at Tugidak Island (Fig. 3A; Pitcher 1990) and declines of sea lions from this same region (see Trites and Larkin 1996, Winship and Trites 2006) were in fact simultaneous rather than sequential (DeMaster *et al.* 2006). Moreover, harbor seal populations in the Kodiak area, including Tugidak Island, have actually increased since the early 1990s (Small *et al.* 2003)—over the same period that sea otters declined. Similarly, the unexplained decline of fur seals on the Pribilof Islands that followed cessation of the female harvest also began in the late 1970s and continued through the 1980s and 1990s (Trites 1992)—while the much smaller population of fur seals on Bogoslof Island increased (Angliss and Lodge 2004). The major difference between the declines of seals and sea lions was the magnitude and rate of population declines that each experienced. A closer inspection of the data plotted by Springer *et al.* (2003) in Figure 3A reveals errors in data compilation, which—when corrected—indicate a simultaneous decline of harbor seals, Steller sea lions and northern fur seals in geographical similar areas (DeMaster *et al.* 2006).

Attempts have been made using ecosystem models to test the effects of whaling in the Bering Sea and Antarctic Ocean, but no link has yet been found between changes in species abundance and the commercial removal of whales (Trites *et al.* 1999, Trites *et al.* 2004). Shootings and entanglements are known to have been significant contributing factors in the declines of sea lions and fur seals, but do not appear to have occurred at levels sufficient to have caused the population declines (Trites 1992, Trites and Larkin 1992, Loughlin and York 2002). Competition with fisheries could also be a complicating factor, but has yet to be demonstrated.

The “ocean climate hypothesis” is an alternative explanation for the rapid changes that were observed to cross all trophic levels of the North Pacific (National Research Council 1996, Trites *et al.* in press). This bottom-up hypothesis is supported by a large and growing body of evidence (*e.g.*, Ware and Thomson 2005, Trites *et al.* in press). For the past 100 yr, 10–30-yr periods of stable physical conditions have been punctuated by rapid shifts to alternative stable physical oceanographic conditions (Ebbesmeyer *et al.* 1991, Graham 1994, Beamish *et al.* 2000, McKinnell *et al.* 2001, King 2005). These sudden and well-documented “regime shifts” significantly affect sea temperatures, currents, and ice coverage—and correspond in space and time with ecosystem changes noted in Alaska and in British Columbia (Hare and Mantua 2000, Benson and Trites 2002, King 2005).

The most significant regime shift recorded this past century occurred around 1977 and appears to have touched all trophic levels, favoring the survival of one suite of species over another (Mantua *et al.* 1997, Trites *et al.* 1999, Benson and Trites 2002). For sea lions, the regime shift appears to have altered the relative abundances of

high- and low-energy prey species they were able to obtain, which may have affected successful pregnancies, ages of sexual maturity, and susceptibility to diseases and predation by killer whales (Alverson 1992, Merrick *et al.* 1997, Calkins *et al.* 1998, Pitcher *et al.* 1998, Rosen and Trites 2000, Matkin *et al.* 2002, Burek *et al.* 2003, Trites 2003, Trites and Donnelly 2003, Winship and Trites 2003, Rosen and Trites 2004).

Data from the five large oceanic production domains between California and the western Aleutian Islands show that the 1977 regime shift affected the biology of northern and southern areas of the North Pacific in different ways (Benson and Trites 2002). Steller sea lions (and other pinnipeds) were likely closer to natural (*i.e.*, unexploited) levels in the western part of their range during the early 1970s, and would have declined rapidly if the regime shift had reduced their carrying capacities. The decline of pinnipeds in western Alaska was in sharp contrast to the increases that occurred from California to southeast Alaska following the 1977 regime shift.

It is debatable whether any single simple explanation can be found for the declines of four species of marine mammals. However, it seems more than coincidental that all three pinniped species declined at about the same time as so many other changes (both positive and negative) were noted for a wide range of species occurring across all trophic levels in the North Pacific. The ocean climate hypothesis may be an oversimplified picture of a complex ecological issue, just as the commercial whaling hypothesis can also be considered to be an oversimplification. However, the ocean climate hypothesis is consistent with the wide range of reported changes and is supported by a growing body of research. Furthermore, unlike the proposed trophic cascade hypothesis, it does not discount the other leading hypotheses that have been proposed to explain the decline of Steller sea lions and other pinnipeds, such as nutritional stress, fishing, disease, and killer whale predation (see DeMaster and Atkinson 2002, Burek *et al.* 2003, National Research Council 2003, Trites and Donnelly 2003). Instead, the ocean climate hypothesis provides a holistic framework within which each of the alternative hypotheses can be aligned, and the changes that occurred to the ecosystem as a whole can be associated (Trites *et al.* in press).

Research Needs

Research conducted during the past decade on North Pacific marine mammals has focused primarily on the decline of Steller sea lions. Relatively little research has been done on the decline of Alaskan harbor seals, fur seals and sea otters. Thus, while the timing of the 1977 regime shift parallels some changes of species abundances in the North Pacific, the mechanisms linking ocean climate with top predators have yet to be fully explored.

Predation is undoubtedly a significant source of mortality for seals, sea lions, and sea otters. Direct observations of killer whales preying on sea otters in the Aleutian Islands have demonstrated the impact that predators can have on their prey populations (Estes *et al.* 1998, Doroff *et al.* 2003). Similarly, mathematical models of killer whale predation on sea lions and sea otters have shown how just a few individual killer whales with highly specialized diets can theoretically depress their prey populations to critically low numbers (Barrett-Lennard *et al.* 1995, Williams *et al.* 2004). However, there is no evidence that commercial whaling led to a change in killer whale predatory behavior, leading to a sequential collapse of the megafauna of the North Pacific.

Investigations are needed into the subtleties of killer whales prey selection. One approach is to examine living and stranded whales for tooth rakes in order to estimate

rates of attack for different species (Mehta and Clapham 2003). Another means for gaining insight into dietary preferences is to determine fatty acid profiles from blubber, and nitrogen isotope ratios in the teeth, skin, and bones of killer whales (*e.g.*, Herman *et al.* 2005).

Conclusions

The great whales of the North Pacific are large in size and often larger in our minds and imaginations. But ecologically speaking, large whales may simply be small fish in a big pond—part of a trophic web that is far more complex than it has been made out to be. The coincidental timing of the end of whaling with the declines of seals and sea lions does not prove the whaling hypothesis—and the accumulated knowledge about the biology of large whales, the feeding ecology of killer whales, and the patterns of ecosystem changes in the North Pacific is not consistent with it. In the end, it is important to recognize that killer whales are one of a number of contributing factors in the disappearances of seals, sea lions, and sea otters in Alaska, but that whaling was not the key that unleashed a cascade of population declines.

ACKNOWLEDGMENTS

The debate about what has happened to the North Pacific has provoked considerable discussion among marine mammal researchers and others concerned with the health of our marine ecosystems. We have benefited from these discussions and would particularly like to acknowledge the insightful comments of Justin Cooke, Doug DeMaster, Lance Barrett-Lennard, Craig Matkin, Daniel Pauly, Ward Testa, Paul Wade, and the journal reviewers. We also thank Ryan Coatta for GIS assistance and express our gratitude for the financial support provided by the North Pacific Marine Science Foundation to the North Pacific Universities Marine Mammal Research Consortium.

LITERATURE CITED

- ALVERSON, D. 1992. A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): The conflict arena. *Reviews in Aquatic Sciences* 6:203–256.
- ANDERSON, P. J., AND J. F. PIATT. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189:117–123.
- ANGLISS, R. P., AND K. L. LODGE. 2004. Alaska marine mammal stock assessments, 2003. NOAA Technical Memorandum No. NMFS-AFSC-124. 237 pp.
- BARRETT-LENNARD, L. G. 2000. Population structure and mating patterns of killer whales (*Orcinus orca*) as revealed by DNA analysis. Ph.D. thesis, University of British Columbia, Vancouver, BC, Canada. 97 pp.
- BARRETT-LENNARD, L. G., K. HEISE, E. SAULITIS, G. ELLIS AND C. MATKIN. 1995. The impact of killer whale predation on Steller sea lion populations in British Columbia and Alaska. University of British Columbia, Fisheries Centre, 2202 Main Mall, Vancouver, B.C. V6T 1Z4, Canada, Unpublished Report. 77 pp.
- BEAMISH, R. J., G. A. MCFARLANE AND J. R. KING. 2000. Fisheries climatology: Understanding decadal scale processes that naturally regulate British Columbia fish populations. Pages 94–145 in T. R. Parsons and P. J. Harrison, eds. *Fisheries oceanography: A science for the new millennium*. Blackwell Science, Oxford, U.K.
- BENSON, A. J., AND A. W. TRITES. 2002. Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. *Fish and Fisheries* 3:95–113.
- BIGG, M. A. 1985. Status of the Steller sea lion (*Eumetopias jubatus*) and California sea lion (*Zalophus californianus*) in British Columbia. Canadian Special Publication of Fisheries and Aquatic Sciences 77:1–20.

- BIGG, M. A. 1990. Migration of northern fur seals (*Callorhinus ursinus*) off western North America. Pacific Biological Station, 1764:1–64 pp.
- BIGG, M. A., AND I. B. MACASKIE. 1977. Sea otters re-established in British Columbia. *Journal of Mammalogy* 59:874–876.
- BROWN, R. F., B. E. WRIGHT, S. D. RIEMER AND J. LAAKE. 2005. Trends in abundance of harbor seals in Oregon: 1977–2003. *Marine Mammal Science* 21:657–670.
- BUCKLAND, S. T., AND J. M. BREIWICK. 2002. Estimated trends in abundance of eastern Pacific gray whales from shore counts (1967/68 to 1995/96). *Journal of Cetacean Research and Management* 4:41–48.
- BUREK, K. A., F. M. D. GULLAND, G. SHEFFIELD, E. KEYES, T. R. SPRAKER, A. W. SMITH, D. E. SKILLING, J. EVERMANN, J. L. STOTT AND A. W. TRITES. 2003. Disease agents in Steller sea lions in Alaska: A review and analysis of serology data from 1975–2000. *Fisheries Centre Research Reports* 11:1–26.
- CALKINS, D. G., E. F. BECKER AND K. W. PITCHER. 1998. Reduced body size of female Steller sea lions from a declining population in the Gulf of Alaska. *Marine Mammal Science* 14:232–244.
- CALKINS, D. G., D. C. MCALLISTER, K. W. PITCHER AND G. W. PENDLETON. 1999. Steller sea lion status and trend in Southeast Alaska: 1979–1997. *Marine Mammal Science* 15:462–477.
- CARRETTA, J. V., K. A. FORNEY, M. M. MUTO, J. BARLOW, J. BAKER AND M. LOWRY. 2004. U.S. Pacific marine mammal stock assessments: 2003. NOAA Technical Memorandum No. NMFS-AFSC-124, 295 pp.
- CLAPHAM, P. J. 2001. Why do baleen whales migrate? A response to Corkeron and Connor. *Marine Mammal Science* 17:432–436.
- COSEWIC. 2003. COSEWIC assessment and update status report on the Steller sea lion *Eumetopias jubatus* in Canada. Available from <http://www.sararegistry.gc.ca>. vii + 47 pp.
- COSEWIC. 2005. Canadian species at risk, May 2005. Committee on the status of endangered wildlife in Canada. Available from <http://www.cosewic.gc.ca>. 49 pp.
- DEMASTER, D., AND S. ATKINSON, eds. 2002. Steller sea lion decline: Is it food II? University of Alaska Sea Grant, AK-SG-02–02.
- DEMASTER, D. P., A. W. TRITES, P. CLAPHAM, S. MIZROCH, P. WADE, R. J. SMALL AND J. V. HOEF. 2006. The sequential megafaunal collapse hypothesis: Testing with existing data. *Progress in Oceanography* 68:329–342.
- DOLPHIN, W. F. 1987. Observations of humpback whale, *Megaptera novaeangliae*—killer whale, *Orcinus orca*, interactions in Alaska: Comparison with terrestrial predator-prey relationships. *Canadian Field-Naturalist* 101:70–75.
- DOROFF, A. M., J. A. ESTES, M. T. TINKER, D. M. BURN AND T. J. EVANS. 2003. Sea otter population declines in the Aleutian archipelago. *Journal of Mammalogy* 84:55–64.
- EBBESMEYER, C. C., D. R. CAYAN, D. R. McLAIN, F. H. NICHOLS, D. H. PETERSON AND K. T. REDMOND. 1991. 1976 step in the Pacific climate: Forty environmental changes between 1968–1975 and 1977–1984. Proceedings of the Seventh Annual Pacific Climate (PACLIM) Workshop, Asilomar, California, April, 1990. California Department of Water Resources. Interagency Ecological Study Program Report. 26: 115–126.
- ESTES, J. A., M. T. TINKER, T. M. WILLIAMS AND D. F. DOAK. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–476.
- FORD, J. K. B., G. M. ELLIS, L. G. BARRETT-LENNARD, A. B. MORTON, R. S. PALM AND K. C. BALCOMB III. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology* 76:1456–1471.
- FORD, J. K. B., G. M. ELLIS AND K. C. BALCOMB. 2000. Killer whales: The natural history and genealogy of *Orcinus orca* in British Columbia and Washington. 2nd edition. University of British Columbia Press, Vancouver, BC, Canada.

- FORD, J. K. B., G. M. ELLIS, D. R. MATKIN, K. C. BALCOMB, D. BRIGGS AND A. B. MORTON. 2005. Killer whale attacks on minke whales: Prey capture and antipredator tactics. *Marine Mammal Science* 21:603–618.
- GRAHAM, N. E. 1994. Decadal variability in the 1970s and 1980s: Observations and model results. *Climate Dynamics* 10:60–70.
- GREGG, E. J., L. NICHOL, J. K. B. FORD, G. ELLIS AND A. W. TRITES. 2000. Migration and population structure of northeast Pacific whales off the coast of British Columbia: Analysis of commercial whaling records from 1908–1967. *Marine Mammal Science* 16:699–727.
- HARE, S. R., AND N. J. MANTUA. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47:103–145.
- HEISE, K., L. G. BARRETT-LENNARD, E. SAULITIS, C. G. MATKIN AND D. BAIN. 2003. Examining the evidence for killer whale predation on Steller sea lions in British Columbia and Alaska. *Aquatic Mammals* 29:325–334.
- HERMAN, D. P., D. G. BURROWS, P. R. WADE, J. W. DURBAN, C. O. MATKIN, R. G. LEDUC, L. G. BARRETT-LENNARD AND M. M. KRAHN. 2005. Feeding ecology of eastern North Pacific killer whales from fatty acid, stable isotope, and organochlorine analyses of blubber biopsies. *Marine Ecology Progress Series* 302:275–291.
- HOELZEL, A. R., AND G. A. DOVER. 1991. Genetic differentiation between sympatric killer whale populations. *Heredity* 66:191–195.
- HOELZEL, A. R., M. DAHLHEIM AND S. J. STERN. 1998. Low genetic variation among killer whales (*Orcinus orca*) in the eastern North Pacific and genetic differentiation between foraging specialists. *Journal of Heredity* 89:121–128.
- JEFFERSON, T. A., P. J. STACEY AND R. W. BAIRD. 1991. A review of killer whale interactions with other marine mammals: Predation to co-existence. *Mammal Review* 21:151–180.
- JEFFRIES, S. J., H. HUBER, J. CALAMBOKIDIS AND J. LAAKE. 2003. Trends and status of harbor seals in Washington state: 1978–1999. *Journal of Wildlife Management* 67:208–219.
- JONSGARD, A. 1968a. Another note on the attacking behaviour of the killer whale (*Orcinus orca*). *Norsk Hvalfangst-Tidende* 57:175–176.
- JONSGARD, A. 1968b. A note on the attacking behaviour of the killer whale (*Orcinus orca*). *Norsk Hvalfangst-Tidende* 57:84–85.
- KING, J. R., ed. 2005. Report of the study group on fisheries and ecosystem responses to recent regime shifts. Volume 28. PICES Scientific Report.
- KNOX, G. A. 1994. The biology of the Southern Ocean. Cambridge University Press, Cambridge, U.K.
- LOUGHLIN, T. R., AND A. E. YORK. 2002. An accounting of the sources of Steller sea lion mortality. Pages 9–13 in D. DeMaster and S. Atkinson, eds. Steller sea lion decline: Is it food II. University of Alaska Sea Grant, AK-SG-02–02, Fairbanks, AK.
- MANTUA, N. J., S. R. HARE, Y. ZHANG, J. M. WALLACE AND R. C. FRANCIS. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:1069–1079.
- MATKIN, C. G., L. BARRETT-LENNARD AND G. ELLIS. 2002. Killer whales and predation on Steller sea lions. Pages 61–66 in D. DeMaster and S. Atkinson, eds. Steller sea lion decline: Is it food II? University of Alaska Sea Grant, AK-SG-02–02, Fairbanks, AK.
- MCKINNELL, S. M., R. D. BRODEUR, K. HANAWA, A. B. HOLLOWED, J. J. POLOVINA AND C. I. ZHANG. 2001. An introduction to the Beyond El Nino conference: Climate variability and marine ecosystem impacts from the tropics to the Arctic. *Progress in Oceanography* 49:1–6.
- MEHTA, A. V., AND P. J. CLAPHAM. 2003. How important are large whales as prey for killer whales (*Orcinus orca*) in high latitudes? A proposal. *International Whaling Commission SC/55/019:1–4*.
- MERRICK, R. L., M. K. CHUMBLEY AND G. V. BYRD. 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: A potential relationship. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1342–1348.

- MIZROCH, S. A., AND D. W. RICE. 2006. Have North Pacific killer whales switched prey species in response to depletion of the great whale populations? *Marine Ecology Progress Series* 310:235–246.
- NATIONAL RESEARCH COUNCIL. 1996. The Bering Sea ecosystem. National Academy Press, Washington, DC.
- NATIONAL RESEARCH COUNCIL. 2003. The decline of the Steller sea lion in Alaskan waters: Untangling food webs and fishing nets. National Research Council, Washington, DC.
- NICHOL, L. M., E. J. GREGR, R. FLINN, J. K. B. FORD, R. GURNEY, L. MICHALUK AND A. PEACOCK. 2002. British Columbia commercial whaling catch data 1908 to 1967: A detailed description of the B.C. historical whaling database. Canadian Technical Report of Fisheries and Aquatic Sciences No. 2396. viii +76 pp.
- OLESIUKE, P. F. 1999. An assessment of the status of harbour seals (*Phoca vitulina*) in British Columbia. Department of Fisheries and Oceans Canada, Canadian Stock Assessment Secretariat Research Document No. 99/33. 71 pp.
- OLESIUKE, P. F. 2003. Recent trends in the abundance of Steller sea lions (*Eumetopias jubatus*) in British Columbia. NMMRC Working Paper No. 2001–2010.
- OLESIUKE, P. F., M. A. BIGG AND G. M. ELLIS. 1990. Recent trends in the abundance of harbour seals, *Phoca vitulina*, in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 47:992–1003.
- PIKE, G. C., AND B. E. MAXWELL. 1958. The abundance and distribution of the northern sea lion (*Eumetopias jubata*) on the coast of British Columbia. *Journal of the Fisheries Research Board of Canada* 15:5–17.
- PITCHER, K. W. 1990. Major decline in number of harbor seals, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. *Marine Mammal Science* 6:121–134.
- PITCHER, K. W., D. G. CALKINS AND G. W. PENDLETON. 1998. Reproductive performance of female Steller sea lions: An energetics based reproductive strategy? *Canadian Journal of Zoology* 76:2075–2083.
- PITMAN, R. L., AND P. ENSOR. 2003. Three forms of killer whales (*Orcinus orca*) in Antarctic waters. *Journal of Cetacean Research and Management* 5:131–139.
- PITMAN, R. L., L. T. BALLANCE, S. I. MESNICK AND S. J. CHIVERS. 2001. Killer whale predation on sperm whales: Observations and implications. *Marine Mammal Science* 17:494–507.
- ROSEN, D. A. S., AND A. W. TRITES. 2000. Pollock and the decline of Steller sea lions: Testing the junk-food hypothesis. *Canadian Journal of Zoology* 78:1243–1258.
- ROSEN, D. A. S., AND A. W. TRITES. 2004. Satiation and compensation for short-term changes in food quality and availability in young Steller sea lions (*Eumetopias jubatus*). *Canadian Journal of Zoology* 82:1061–1069.
- SAULITIS, E. L., C. O. MATKIN, K. HEISE, L. BARRETT-LENNARD AND G. M. ELLIS. 2000. Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. *Marine Mammal Science* 16:94–109.
- SMALL, R. J., G. W. PENDLETON AND K. W. PITCHER. 2003. Trends in abundance of Alaska harbor seals, 1983–2001. *Marine Mammal Science* 19:344–362.
- SPRINGER, A. M., J. A. ESTES, G. B. VAN VLIET, T. M. WILLIAMS, D. F. DOAK, E. M. DANNER, K. A. FORNEY AND B. PFISTER. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences of the United States of America* 100:12223–12228.
- TRITES, A. W. 1992. Northern fur seals: Why have they declined? *Aquatic Mammals* 18: 3–18.
- TRITES, A. W. 2003. Food webs in the ocean: Who eats whom and how much? Pages 125–143 in M. Sinclair and G. Valdimarsson, eds. *Responsible fisheries in the marine ecosystem*. FAO Rome and CABI Publishing, Wallingford, U.K.
- TRITES, A. W., AND M. A. BIGG. 1996. Physical growth of northern fur seals (*Callorhinus ursinus*): Seasonal fluctuations and migratory influences. *Journal of Zoology, London* 238:459–482.

- TRITES, A. W., AND C. P. DONNELLY. 2003. The decline of Steller sea lions in Alaska: A review of the nutritional stress hypothesis. *Mammal Review* 33:3–28.
- TRITES, A. W., AND P. A. LARKIN. 1992. The status of Steller sea lion populations and the development of fisheries in the Gulf of Alaska and Aleutian Islands. A report of the Pacific States Marine Fisheries Commission pursuant to National Oceanic and Atmospheric award no. NA17FD0177. Available from the Fisheries Centre, University of British Columbia, Vancouver, BC, Canada. 134 pp.
- TRITES, A. W., AND P. A. LARKIN. 1996. Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: How many were there? *Aquatic Mammals* 22:153–166.
- TRITES, A. W., AND D. PAULY. 1998. Estimating mean body masses of marine mammals from maximum body lengths. *Canadian Journal of Zoology* 76:886–896.
- TRITES, A. W., P. A. LIVINGSTON, S. MACKINSON, M. C. VASCONCELLOS, A. M. SPRINGER AND D. PAULY. 1999. Ecosystem change and the decline of marine mammals in the eastern Bering Sea: Testing the ecosystem shift and commercial whaling hypotheses. Fisheries Centre Research Reports 7. 106 pp.
- TRITES, A. W., E. L. BREDESEN AND A. P. COOMBS. 2004. Whales, whaling and ecosystem change in the Antarctic and eastern Bering Sea: Insights from ecosystem models. Pages 85–92 in *Investigating the roles of cetaceans in marine ecosystems*. CIESM Workshop Monographs no. 25, Monaco.
- TRITES, A. W., A. J. MILLER, H. D. G. MASCHNER, M. A. ALEXANDER, S. J. BOGRAD, J. A. CALDER, A. CAPOTONDI, K. O. COYLE, E. D. LORENZO, B. P. FINNEY, E. J. GREGG, C. E. GROSCH, S. R. HARE, G. L. HUNT, J. JAHNCKE, N. B. KACHEL, H.-J. KIM, C. LADD, N. J. MANTUA, C. MARZBAN, W. MASLOWSKI, R. MENDELSSOHN, D. J. NEILSON, S. R. OKKONEN, J. E. OVERLAND, K. L. REEDY-MASCHNER, T. C. ROYER, F. B. SCHWING, J. X. L. WANG AND A. J. WINSHIP. In press. Bottom-up forcing and the decline of Steller sea lions in Alaska: Assessing the ocean climate hypothesis. *Fisheries Oceanography*
- WADE, P., L. BARRETT-LENNARD, N. BLACK, R. BROWNELL, V. BURKANOV, A. BURDIN, J. CALAMBOKIDIS, S. CERCHIO, M. DAHLHEIM, J. FORD, N. FRIDAY, L. FRITZ, J. JACOBSEN, T. LOUGHLIN, M. LOWRY, C. MATKIN, D. MATKIN, S. MCCLUSKEY, A. MEHTA, S. MIZROCH, M. MUTO, D. RICE, D. SINIFF, R. SMALL, G. STEIGER, J. STRALEY, G. VAN BLARICOM AND P. CLAPHAM. 2007. Marine mammal abundance, biomass, and trends in the North Pacific—a re-examination of evidence for sequential megafauna collapse. *Marine Mammal Science* 23:000–000.
- WARE, D. M., AND R. E. THOMSON. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *Science* 308:1280–1284.
- WATSON, J. C., G. M. ELLIS, T. G. SMITH AND J. K. B. FORD. 1997. Updated status of the sea otter, *Enhydra lutris*, in Canada. *Canadian Field-Naturalist* 111:277–286.
- WEBB, R. L. 1988. On the Northwest: Commercial whaling in the Pacific Northwest, 1790–1967. University of British Columbia Press, Vancouver, BC, Canada.
- WHITEHEAD, H., AND R. REEVES. 2005. Killer whales and whaling: The scavenging hypothesis. *Biology Letters* doi:10.1098/rsbl.2005.0348.
- WILLIAMS, T. M., J. A. ESTES, D. F. DOAK AND A. M. SPRINGER. 2004. Killer appetites: Assessing the role of predators in ecological communities. *Ecology* 85:3373–3384.
- WINSHIP, A. J., AND A. W. TRITES. 2003. Prey consumption of Steller sea lions (*Eumetopias jubatus*) off Alaska: How much prey do they require? *Fishery Bulletin* 101:147–167.
- WINSHIP, A. J., AND A. W. TRITES. 2006. Risk of extirpation of Steller sea lions in the Gulf of Alaska and Aleutian Islands: A population viability analysis based on alternative hypotheses for why sea lions declined in western Alaska. *Marine Mammal Science* 22:124–155.

Received: 3 December 2004

Accepted: 1 February 2006