



Letters

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Mammal-eating killer whales, industrial whaling, and the sequential megafaunal collapse in the North Pacific Ocean: A reply to critics of Springer *et al.* 2003

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... most carnivores do not confine themselves rigidly to one kind of prey; so that when their food of the moment becomes scarcer than a certain amount, the enemy no longer finds it worth while to pursue this particular one and turns its attention to some other species instead.

C. S. Elton 1927

We (Springer *et al.* 2003) advanced an hypothesis to explain the precipitous declines of pinniped and sea otter populations in the North Pacific Ocean that centers around the ecological consequences of massive industrial whaling that began in this region at the end of World War II. We proposed that the great whales once provided large

and important nutritional resources to mammal-eating (transient) killer whales; that industrial whaling perturbed this consumer prey interaction by vastly reducing the biomass of normal prey of killer whales; and that this perturbation caused killer whales to alter their diets to include a greater proportion of other species of marine mammals. We further proposed that the resulting elevated mortality rates of pinnipeds and sea otters, which killer whales turned to, were unsustainable, thus driving those populations rapidly and sequentially downward as one species after another was depleted.

Our hypothesis was motivated, and has been sustained in our minds, by the following observations and intellectual developments. Accumulating evidence for the importance of top-down forcing processes (Pace *et al.* 1999, Shurin *et al.* 2002, Borer *et al.* 2005), especially those driven by large vertebrate consumers (Boveng *et al.* 1998, Estes *et al.* 2001, Donlan *et al.* 2006), convinced us that events such as this, while appearing remarkable, happen broadly in nature (Lucas and Stobo 2000). The discovery that the sea otter declines were likely driven by killer whale predation (Estes *et al.* 1998, 2004; Williams *et al.* 2004) solidified that view and led us to wonder if the largely sympatric pinniped declines might not have resulted from the same cause.

This latter suspicion was bolstered by broad similarities between sea otters and pinnipeds in both the pattern and geographic range of their declines and, we believe, by the lack of compelling evidence and mechanistic explanations for the popular alternative hypotheses that involve bottom-up forcing processes. The view that killer whales might alter their diets in response to declines in the abundance of important prey has been reinforced by observations of prey switching by other carnivores (*e.g.*, Patterson *et al.* 1998, Post *et al.* 2000, Kjellander and Nordström 2003, and many others), including various marine mammals (*e.g.*, Ostfeld 1982, Thompson *et al.* 1997, Iverson *et al.* 2006).

We were drawn closer still to the predation hypothesis by results of simple demographic/energetic models that demonstrated just how vulnerable pinniped populations would be to relatively small changes in the diet of transient killer whales (Williams *et al.* 2004). The most intriguing aspect of our hypothesis—that the multispecies collapse ultimately resulted from the reduction of great whales by post WWII industrial whaling—was based on four independent facts or observations: (1) that killer whales commonly attack, kill, and eat great whales; (2) that great whale biomass was far and away the major component of marine mammal biomass in the North Pacific Ocean and southern Bering Sea prior to industrial whaling; (3) that great whale biomass was not only immense, but was also highly concentrated from spring through fall in relatively small geographic areas that were and are predation hot spots for killer whales and that correspond to the region of the multispecies collapse; and (4) that the collapse followed the depletion of the great whales and began shortly after the cessation of industrial whaling in the late 1960s and early 1970s. A final factor leading us to suggest the whaling/predation hypothesis was that, in contrast with all other explanations for the decline, it did not appear to suffer from fatal flaws in the form of conflicting data or logic. As we noted when first advancing it, we do not regard this hypothesis as well-tested, but believe it is well reasoned and well supported, and hoped that in publishing it to prompt its consideration,

particularly relative to other explanations for the marine mammal declines in the North Pacific Ocean.¹

The whaling/predation hypothesis has been criticized by various authors, notably DeMaster *et al.* (2006), Mizroch and Rice (2006), Trites *et al.* (2007a), and Wade *et al.* (2007). Although these papers emphasize somewhat different points, collectively they revolve around five main arguments that the authors maintain are either inconsistent with or refute the underpinnings of Springer *et al.*: (1) that killer whales only rarely attack or eat great whales, (2) that the multispecies collapse we described was not sequential, (3) that there is reasonably convincing evidence that the declines were caused by nutritional limitation, (4) that the timing of the collapses is inconsistent with the timing of whale depletions, and (5) that the broader geographical patterns of the key species and purported processes are inconsistent with the spatial extent of the multispecies collapse. We disagree with these challenges and in the following reply explain why.

POINT 1: KILLER WHALES RARELY ATTACK OR EAT GREAT WHALES

This view seems to be based largely on three claims or observations: first, that attacks on what would arguably have been the most important prey species—fin, sperm, and humpback whales—are seldom seen, and thus presumably are rare and relatively unimportant; second, that these whales are simply too large for killer whales to subdue; and third, that large whale remains are rarely found in killer whale stomachs. In our view, these claims are unfounded. Killer whales, historically and recently, have been seen attacking and killing all of the common great whale species, including bowheads, blues, fins, sperms, and humpbacks (Andrews 1916, Tarpay 1979, Jefferson *et al.* 1991, Pitman *et al.* 2001, Reeves *et al.* 2006). Whalers of the 19th century in the Arctic knew well that killer whales attacked bowhead whales, and they continue to do so in modern times (Andrews 1916, George *et al.* 1994a). In the past, two-thirds of fin whales landed at shore stations had the tips of their flukes and flippers bitten off (Andrews 1916). High proportions of living whales have scars and rake marks from killer whale attacks, *e.g.*, blues in the Sea of Cortez, 8% of bowheads in the Beaufort Sea, 15% of humpbacks in the Gulf of Alaska, 17% of humpbacks in Australia (nearly half of which were considered “major”), “many” humpbacks and blues in Monterey Bay, and 54% of the fin whales and up to 65% of sperm whales in the Southern Ocean (Sears 1990, Jefferson *et al.* 1991, George *et al.* 1994a, Spalding 1999, Ternullo and Black 2002, Naessig and Lanyon 2004, Branch and Williams 2006). These are the survivors. If those that were killed could be accounted for, the proportion of attacked individuals would be even higher. Smaller predators are often injured or killed by larger prey (*e.g.*, Loveridge *et al.* 2006, Berger 2008) and large whales defend themselves against killer whale attacks (*e.g.*, Pitman *et al.* 2001). It is difficult for us to understand why killer whales would risk attacks on such large and potentially dangerous prey unless that risk was countered by a considerable benefit.

¹The declines of pinnipeds and sea otters in the North Pacific Ocean were centered in the western Gulf of Alaska, the Aleutian Islands, and the southern Bering Sea, hereafter referred to as southwest Alaska.

Why Attacks are Seldom Seen

Admittedly, published observations of fatal attacks on most species of great whales are few. But does the rarity with which such attacks have been observed mean that they are uncommon and unimportant? Not necessarily. Many common events in nature are seldom seen. For example, our sea otter research group has never observed a wild birth, despite the fact that many thousands of these events occur annually throughout the species' range and trained observers have spent tens of thousands of hours in the field watching sea otters. Connor and Corkeron (2001) make the same point for humpback whale births. Any number of similar examples could easily be provided. Whether unseen or rarely observed events are truly rare and unimportant can only be determined when considered along side the expected number of observations given that they are common and important. This process—the contrasting of observation with expectation under a working hypothesis—is fundamental to rigorous inferential reasoning.

Consider, for example, the observed number of killer whale attacks on sea otters during the height of the sea otter population decline (1991 through 1997) in the central and western Aleutian Islands (Doroff *et al.* 2003). Based on pre-decline estimates of sea otter abundance, life-history patterns, and the observed rate of decline, we estimated that >40,000 additional deaths would have been necessary to drive the decline in the area of our field studies (Estes *et al.* 1998). The fact that we observed only six attacks in >21,000 person-hours of field observation initially led us to believe that predation was an unlikely cause of the decline. However, that belief changed after realizing that we were able to observe (*i.e.*, sample) just over one-hundredth of 1% of the area by time sample space (>3,000 km of shoreline over 6 yr) in which these >40,000 deaths occurred. Assuming that all of the deaths were caused by killer whale predation, we would expect to have seen just 5.05 attacks, which is about the number actually witnessed.

What would one expect to have been seen over the years if trophic interactions between killer whales and large whales were important, especially considering that in the past 40 yr great whale abundance in the North Pacific has been severely depressed? Doak *et al.* (2006) used a similar approach to that of the sea otter example presented above to address this question and concluded that the probability of modern researchers observing even a single attack by killer whales on large whales in the North Pacific during an intensive research cruise was less than 0.02 for the most common great whale species, even when assuming greater than realistic observation times and very high predation rates. This of course does not mean that attacks by killer whales on great whales are or were common and ecologically important, only that sightings would be rare even if attacks were common.

The numbers of observed attacks by killer whales on any prey species are probably strongly influenced by where researchers have looked and by heavily perturbed prey populations in today's oceans. For example, many attacks on gray and minke whales have been observed, and our critics acknowledge this but claim that other large whale species are infrequently eaten. We see no logical reason why that should be the case. Gray and minke whales are common in what is essentially a one-dimensional coastal environment where observers have spent most of their time and where predation

events are comparatively easy to see. Attacks by killer whales on gray whales are commonly observed at specific locations within these coastal environments, places like Monterey Bay, California (Goley and Straley 1994; N. Black²) and False Pass, Alaska (Matkin *et al.* 2007), where the whales concentrate at certain times of the year. Killer whales probably have been ambushing and killing gray whales at these locations for many years. Moreover, these species were hardly exploited (minkes) or have substantially recovered from whaling (grays), and so in the modern world they may indeed be disproportionately targeted by transient killer whales. In contrast, offshore regions are very much larger and more difficult places to search for the much reduced great whales. As pointed out above, the likelihood of observing attacks in this immense and remote area, even if they commonly occur, is extremely low. In addition, the likelihood of witnessing killer whale attacks in all regions is further reduced because some, possibly much, predation occurs at night (Pitman *et al.* 2001, V. Deeke,³ Newman and Springer 2007).

Interestingly, it appears that the incidence of killer whale attacks on certain species of great whales has changed with their changing abundance. For example, all of the attacks on fin whales in the northeastern North Pacific reported by Matkin and Saulitis (1994) were prior to the 1970s, when fin whales were abundant, whereas all reported attacks on minke whales, which are commonly preyed upon nowadays, were after 1970 and the demise of the great whale stocks. Furthermore, four of five of the reported attacks on fin whales, but only one of seven attacks on minke whales, were in southwest Alaska, suggesting a possible geographical pattern in predation. In conjunction with this, the incidence of scarring on bowhead whales from killer whale attacks apparently rose from 1.2% to 2.5% in the mid to late 1970s, to 6%–8% in the 1980s and early 1990s (from data in table 1 of George *et al.* 1994a), a period in which the bowhead population increased considerably (George *et al.* 1994b), potentially making a more appealing target for predators that may again be altering their diets. And in this century there are already credible reports of five attacks on humpbacks in Alaska, at least three of which were fatal.^{4,5,6} One wonders if this is related to the notable increase in abundance of humpbacks in Alaskan waters in recent years, as discussed below under Point 5, and the attention that is now being given to such events.

Great Whales are too Large to be Attacked by Killer Whales

Another reason cited by critics of our hypothesis as to why great whales were not preyed upon is because they are simply too large to be killed. This point is made

²Unpublished observations by N. Black, Pacific Cetacean Group, P. O. Box 378, Moss Landing, CA 95039.

³Unpublished data from V. Deeke, Fisheries Centre, 2202 Main Mall, University of British Columbia, Vancouver, BC V6T 1Z4.

⁴Personal communication from G.H. Kruse, Juneau Center for Fisheries and Ocean Sciences, University of Alaska Fairbanks, 11120 Glacier Highway, Juneau, AK 99801, 2005.

⁵Personal communication from T. Walters, Maritime Helicopters, P. O. Box 923, Kodiak, AK 99615, 2006.

⁶Personal communication from K. Wynne, Fishery Industrial Technology Center, University of Alaska Fairbanks, 118 Trident Way, Kodiak, AK 99615, 2007.

in particular reference to sperm whales, since most sperm whales in the northern North Pacific in summer are males. But the argument presupposes that all of those individuals were full-grown males (Trites *et al.* 2007a). In reality, the average length of males taken by the whale fishery in this region was just 2 m longer than that of females (Springer *et al.* 2006), which killer whales are known to attack and kill. Moreover, as the sperm whale stock in the Bering Sea was being depleted by the late 1950s, there was a pronounced decline in the size of animals taken by the fleets (Berzin 1964). Together, these observations show that there were many comparatively small sperm whales available as potential prey in the Aleutian Islands and Bering Sea. If a 20-m blue whale is not too large to be fed upon by killer whales (Tarpay 1979), it seems unreasonable to presume that the much smaller sperm whales would be ignored as potential prey.

Although adults of many large whale species are attacked, calves apparently are preferentially hunted and killed, as noted by Trites *et al.* (2007a, and references therein). This observation in no way refutes our central hypothesis, and given the former size of large whale populations, predation on young alone could have supported a prodigious number of killer whales (Doak *et al.* 2006).

Why Large Whale Remains are Rare in Killer Whale Stomachs

Mizroch and Rice (2006) reported that the stomach contents of harvested killer whales rarely contained the remains of large whales and concluded from this that killer whales only rarely consumed these prey. Notably, just one of the 442 samples in the data they summarized came from southwest Alaska and the region of the megafaunal collapse—a fish-eating (resident) killer whale that had recently eaten halibut (Rice 1968). Of the rest, 409 came from coastal waters around Japan, 21 came from the Kurile Islands, 9 came from the region from San Francisco to San Miguel Island in central-southern California, and 2 came from the northwestern Bering Sea. The relevance of geography and diet is discussed below.

Another example of information on killer whale diets in the North Pacific that could shed light on regional and group-specific diets is the IWC database. However, this data set, which contains information on the stomach contents of 401 generic killer whales collected between 1935 and 1986, must also be interpreted cautiously. Of these stomach contents, 262 (65%) were reported as being unidentifiable, lost, or destroyed. Of the remaining 139 stomachs with identifiable prey remains, 113 contained cephalopod beaks, 23 contained fish, 2 contained pinnipeds, and none reportedly contained the remains of other cetaceans. In light of the known predation rates on pinnipeds and small cetaceans by transient killer whales, which are not in question by any author, marine mammals in general appear to be grossly underrepresented in these samples.

It is well known that diet estimates based on material in the gastrointestinal tract are biased toward prey with hard parts and greatly under represent, or miss altogether, prey where only soft tissue is consumed (*e.g.*, Jobling 1987, Hobson *et al.* 1994, Sheffield *et al.* 2001). Because the great whales are so large, soft tissue is ripped from bones, as is known from the numerous observations of killer whales eating just the tongues and lips of large whales, and flaying strips of blubber from their victims (*e.g.*,

Tarpy 1979, Hancock 1965, George and Suydam 1998). The chances of identifying this soft tissue in stomachs would be unlikely unless it was freshly consumed.

Finally, there is a significant body of behavioral evidence that large whales avoid killer whales, and that they have learned, cooperative behaviors to help thwart predation attempts by killer whales (Corkeron and Connor 1999, Pitman *et al.* 2001). Likewise, killer whales display skilled, cooperative behaviors when they attack great whales (Jonsgard 1968, Tarpy 1979, Jefferson *et al.* 1991, Pitman *et al.* 2001). Such behaviors by both predator and prey seem unlikely to have developed if killer whales did not regularly attack great whales.

In sum, the diet of transient killer whales remains poorly known, particularly in the region of pinniped and sea otter declines. It is possible that large whales are and always have been relatively unimportant prey of transient killer whales, but as demonstrated above, there is considerable evidence to the contrary.

POINT 2: THE MULTISPECIES COLLAPSE WAS NOT SEQUENTIAL

Springer *et al.* argued that the various species of pinnipeds and sea otters declined sequentially, whereas our critics dispute this claim (DeMaster *et al.* 2006). This is a significant point of contention because the purported sequential nature of the declines is a logical consequence of prey depletion and predator switching under the Springer *et al.* hypothesis, whereas an asynchronous decline is more difficult to reconcile with bottom-up processes that began with the climate regime shift in the mid-1970s (Mantua *et al.* 1997, Trites *et al.* 2007b).

Three species of coastal marine mammals underwent population collapses in southwest Alaska in the last three decades of the 20th century—harbor seals, Steller sea lions, and sea otters. A fourth pelagic species, northern fur seals, declined significantly, but did not collapse, over this same period. While few would dispute that these changes occurred, the data documenting their onset, rate, and geographic variation vary greatly in quality among the different species. The data are quite good for fur seals and sea otters, but poorer for Steller sea lions and harbor seals because of fewer monitoring programs in some regions until the declines were either well along or nearly complete.

DeMaster *et al.* base their claim that these declines were not sequential on an improper definition and on a weak and inappropriate statistical test. First, they verbally equated “sequential” with “regularly spaced in time.” In doing so, they turned our observation that these four species did not decline *simultaneously*, but instead one after another (sequentially), into a claim that the declines were *regularly spaced* in time. This is not what we observed nor is it a logical extension of our argument. Furthermore, it is not a biologically plausible result for a predator that is switching between prey populations of different sizes and nutritional values (Williams *et al.* 2004).

DeMaster *et al.* bolstered their verbal argument with a statistical test for regularity in the times between the midpoints of population collapses. As they pointed out, this is an exceptionally weak test with only four intervals, and as we noted above, it is also overly restrictive to the argument that declines were sequential. Furthermore, DeMaster *et al.* inappropriately treated their estimated decline midpoints as fixed points, rather than estimated values that cannot be used in the simple test for

regularity they performed. Despite these problems with their assessment, both in the altered sense of the meaning of sequential and in the statistical test they used, it was nevertheless invoked by Trites *et al.* (2007b), who concluded that the declines were simultaneous, which the test used by DeMaster *et al.* clearly demonstrated was not the case, and by Wade *et al.* (2007), who accepted the altered definition of sequential in rejecting our hypothesis.

To more properly address the issue of whether these population declines were sequential, we fit the data for different populations of each species, using the same approach as DeMaster *et al.*, but also calculated 95% confidence limits around the estimated midpoint of each decline (Fig. 1). DeMaster *et al.* maintained that only subsets of the available data that are from extremely close geographic areas are suitable for comparison, and further based their claim of no evidence for a sequential decline on their inability to show a statistically significant difference between just two data time series—those for harbor seals at Tugidak Island and Steller sea lions at nearby Chowiet Island. We do not agree that it is necessary to compare data sets from such closely adjoining areas, and in the case of sea lions, the established movement between rookeries and haul-outs (York *et al.* 1996, Raum-Suryan *et al.* 2002) makes the use of a single sampling area biologically unjustified in an effort to characterize population trends. However, to the extent that we could, we have fitted data for population declines in different regions in order to best document the timing of the declines.

Our results consistently indicate that the declines of harbor seals, sea lions, and sea otters were sequential, *i.e.*, they occurred one after another (Fig. 1). The only exception to this pattern is in the western Gulf of Alaska, where sea lions appear to have declined well before populations in the central and eastern Gulf, and thus overlap with the decline midpoints of harbor seals and fur seals. Fur seals declined more gradually than the other species, and the 95% confidence limits of their decline midpoints overlap with those of the harbor seal and of the western Gulf of Alaska sea lions, although they still suggest a sequential, not simultaneous, collapse (see also Battaile and Trites 2007). In light of the claims by DeMaster *et al.*, it is important to note that the central Gulf sea lion decline midpoint is distinct from that of the Tugidak I. harbor seal population, showing that even in this narrow region, the two species did not decline simultaneously.

Given these results, we stand by our initial conclusion. The declines of harbor seals, fur seals, Steller sea lions, and sea otters in southwest Alaska appear to have occurred in a sequential, though not evenly spaced, pattern. Most critically in evaluating different hypotheses for the population declines, our results demonstrate that these declines did not occur in any approximation to close synchrony in either broad or narrow geographic regions.

POINT 3: THE DECLINES WERE CAUSED BY NUTRITIONAL LIMITATION

Most people have long thought that the various pinniped declines in southwest Alaska were caused by nutritional limitation, either directly or indirectly, as argued by Trites and Donnelly (2003) and Trites *et al.* (2007a, b). This view, in our opinion, is not founded on a fair and comprehensive interpretation of the available data. The sea

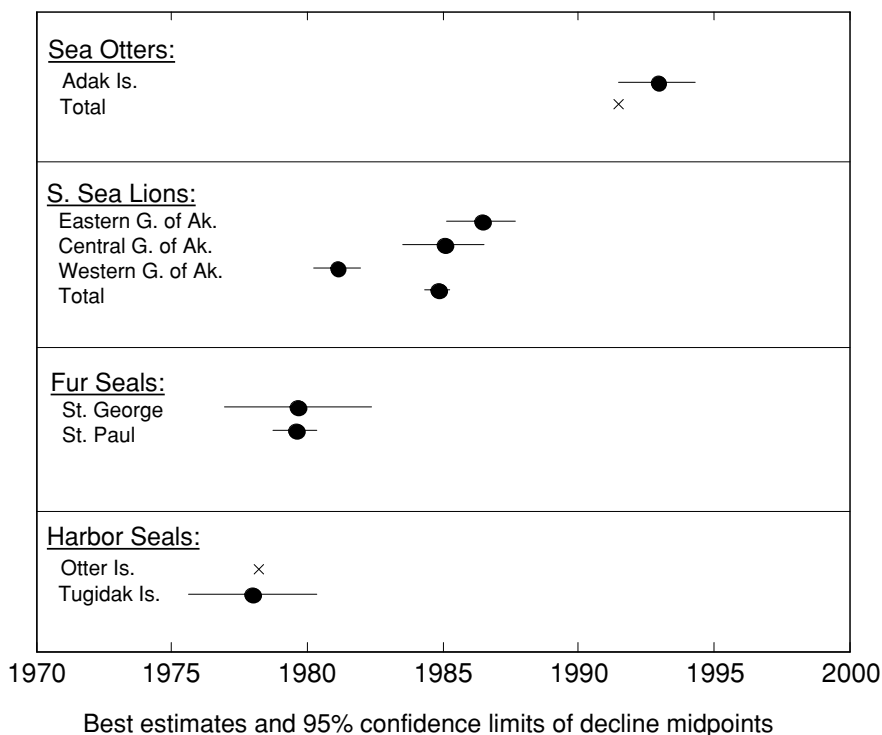


Figure 1. Best estimates and 95% confidence limits of the midpoints (timing of 50% reduction in numbers) of population declines for harbor seals, fur seals, Steller sea lions, and sea otters. Only three relevant data points were available for the total Aleutian Islands sea otter population and the Otter Island (Pribilof Islands) harbor seal population. Such limited data make fitting of the five-parameter model used for the other data sets, or estimation of uncertainty in a decline midpoint, impossible. Therefore, we fitted these declines with a second-order polynomial regression (to account for the clear non-linearity in both data sets) and show only the best estimate of the time of 50% decline from the first to the last population estimate (marked with crosses on the figure). For all other data sets, we fitted a five-parameter model that is nearly identical to that used by DeMaster *et al.*: $\hat{N}_t = \beta_1 + (\beta_2 - \beta_1)/(1 + \exp(-\beta_3(t - \beta_4)))$, where \hat{N}_t is the estimated population size at time t , β_1 is the estimated minimum following the decline, β_2 is the estimated maximum before the decline, β_3 is the rate of decline, β_4 is the midpoint of the decline, and a final fitted parameter, β_5 , is the residual variance estimate. As with DeMaster *et al.*, we assumed normally distributed variances, but unlike them, we did not assume that the sampling variance for each estimate was linearly related to the observed population size, as we saw little evidence in the data sets to support this strong assumption. Confidence limits for the decline midpoint parameters were estimated assuming normally distributed errors, and checked by fitting one-dimensional likelihood profiles by direct search (which did not differ significantly from the parametric estimates). These estimates were made for the following data sets: harbor seals: Tugidak Island data (Jemison *et al.* 2006); fur seals: pup counts from St. Paul Island and St. George Island from 1970 (following the cessation of female culling) to 2000 (after which renewed and separate declines have occurred); Steller sea lions: western rookery counts (Clubbing Rock, Pinnacle, Chernabura, and Atkins), central rookery counts (Chowiet and Chirikof), eastern rookery counts (Marmot, Sugarloaf, Outer Pye, and Chiswells), and combined data from all rookeries (only years with counts from all rookeries were used); sea otters: Adak Island counts and total Aleutian Islands population.

otter decline surely did not result from nutritional limitation (Estes *et al.* 2004, Laidre *et al.* 2006). Although a significant ocean climate change event occurred in the mid 1970s that affected the abundances of some marine species, community organization, and other relationships between organisms and the environment in the North Pacific Ocean (Francis and Hare 1994; Mantua *et al.* 1997; Springer 1998, 2004; Anderson and Piatt 1999; Hare and Mantua 2000; Mueter *et al.* 2007), and various fisheries have extracted large quantities of fish from the North Pacific Ocean and southern Bering Sea (NMFS 2006), there are reasons to question whether these events led to nutritional limitation of pinnipeds. To summarize, the overall abundance of prey actually increased in many areas during the period of decline (Fritz and Hinckley 2005, Brown 2007); diets of sea lions have not varied substantially since the late 1940s (Sinclair and Zeppelin 2002, Springer *et al.* 2007); several indices of the physiological condition of sea lion females and pups have shown convincingly that those in southwest Alaska are nutritionally better off than those in southeast Alaska (Merrick *et al.* 1995; Davis *et al.* 1996, 2002; Adams 2000; Rea *et al.* 1998, 2003); within the declining stock, sea lions in the central Aleutian Islands are the fattest of all, likely owing to a diet rich in energy-dense Atka mackerel (Sinclair and Zeppelin 2002, Logerwell and Schauffler 2005), and notwithstanding claims that these fish are junk food (Trites *et al.* 2007a); sea lion maternal attendance patterns and foraging trip durations in summer and attendance patterns at haul outs in winter in southwest Alaska are similar to those in southeast Alaska (Brandon 2000, Milette and Trites 2003); and harbor seal pups in Prince William Sound, where the population was in decline, were exceptionally fat (Iverson *et al.* 2003).

Despite these observations, the underlying belief in bottom-up forcing and nutritional limitation during the 1980s and early 1990s has led to unlikely scenarios. This includes the junk food hypothesis (Alverson 1992), which has been largely dismissed by the National Research Council (2003) and by Fritz and Hinckley (2005), but in various iterations continues to be used as a means of reconciling abundant prey with nutritional limitation (Trites *et al.* 2007a, b). This is despite the fact that it is based in large measure on extrapolations from captive studies (Trites and Donnelly 2003) that do not mimic natural pinniped prey consumption patterns.

The junk food hypothesis posits that the regime shift of the mid-1970s led to declines in the abundance of various species of lipid-rich forage fishes that were critical to seals and sea lions, and that those species were replaced by junk food—low fat forage species that are insufficient to support the nutritional needs of pinniped populations. As Trites *et al.* (2007a) summarized it, the changes in community structure documented in the very near-shore environment of the Gulf of Alaska by Anderson and Piatt (1999) “included declines of shrimp, crabs and possibly small pelagic fishes (herring and sand lance).” The only evidence presented by Anderson and Piatt of a decline in fatty forage fishes of relevance to pinnipeds, and that might have been precipitated by the mid 1970s regime shift, was for capelin, which declined in the near-shore environment in the early 1980s, after sea lions had already begun to collapse and well after harbor seals had collapsed. The decline in herring abundance in the 1980s, also reported by Anderson and Piatt, followed an increase in abundance of an order of magnitude in the 1970s, as they showed. Gulf-wide, herring increased

substantially from the early 1970s through the 1980s (Brown 2007), as harbor seal and sea lion populations were crashing, owing to the positive relationship between herring production in the Gulf of Alaska and warm phases of the Pacific Decadal Oscillation (Hollowed and Wooster 1995, Brown 2007). Likewise, there is no empirical evidence for wide spread declines of sand lance in the Gulf of Alaska during this period (Golet *et al.* 2002), although Kuletz *et al.* (1997) did suggest that they declined in Prince William Sound. Thus, the implication by Trites *et al.* that declines of herring and sand lance were responsible for the pinniped declines is not credible.

Empirical evidence our critics have cited in support of nutritional limitation includes a decline in length at age of Steller sea lions just prior to, and in the initial stages of, the population collapse, between the mid-1970s and mid-1980s (Calkins *et al.* 1998, Trites and Donnelly 2003). However, this trend began long before the onset of the collapse—adult female sea lions in the late 1950s in the central Gulf of Alaska were significantly larger than they were by the mid-1970s, and they had attained most of their growth years earlier in an era when diets were apparently very similar to those during the collapse and following decades (Calkins *et al.* 1998, Springer *et al.* 2007). This observation appears to have been discounted by those who use the change in body size, and its purported relationship to the mid-1970s climate regime shift, to support the food limitation hypothesis as the cause of the population collapse.

Changes in pinniped body condition also cannot be assumed to necessarily have demographic correlates. This is clear from the detailed data on northern elephant seals that were obtained over this same time period (Le Boeuf and Crocker 2005). This example provides what we consider to be unequivocal evidence for ocean climate effects on behavior and body condition in pinnipeds. With the onset of the climate regime shift in the mid 1970s, the rate of mass gain of foraging females and suckling pups declined, the weaning mass of suckling pups declined, and the foraging trip durations of females increased (all by as much as 20%). These patterns reversed with the climate reversal in 1989–1990. Yet throughout this period of oceanographic change and apparent nutritional stress, northern elephant seal numbers marched steadily upward. There was no noticeable connection between behavior, body condition, and demography. As noted above, a wide range of other data indicate that foraging conditions and the nutritional status of sea lions were actually quite good over the course of their decline and since.

Recently, an analysis of changes in Steller sea lion age structure by Holmes and York (2003) has been used to support the view that the western stock of Steller sea lions has experienced a reduction in fertility. However, the most recent and best iteration of this work (Holmes *et al.*, in press), which uses changes in size structure to infer demographic changes, provides another important challenge to the nutritional limitation hypothesis. Holmes *et al.* show that the initial decline of western Steller sea lion populations was accompanied by an extreme depression of survival rates of adults and especially juveniles, but little or no depression of fertility. Following this initial period, survival rates have risen while fertility rates have declined. It is difficult to reconcile these patterns with nutritional limitation, especially given the observations that the lowered fertility rates are not accompanied by any evidence of starvation or malnutrition (Holmes *et al.*, in press).

While the patterns that Holmes *et al.* show do not match our expectations from nutritional limitation, they accord well with the expected direct and indirect effects of predation and prey learning behaviors (Berger *et al.* 2001). In particular, the rapid initial decline in survival, accompanied by subsequent rises in survival, are the predicted changes in prey demography following the arrival of a novel predator—or dramatic increase in predation risk—and then the subsequent learning by surviving prey to avoid that risk. Likewise, the decline in reproductive success with increasing vigilance and stress is a predicted and observed consequence of prey efforts to avoid death at the teeth of a predator. These patterns match the demographic changes that Holmes *et al.* document, and they have been observed in other systems where newly arrived predators are attacking intelligent mammalian prey species (Berger *et al.* 2001, Creel *et al.* 2007). Such trait-mediated effects of predation (Werner and Peacor 2003) occur widely in nature (Peckarsky *et al.* 1993, Schmitz *et al.* 1997, Boonstra *et al.* 1998, Nelson *et al.* 2004, Preisser *et al.* 2005), equaling or exceeding density-mediated effects in some instances (Trussell *et al.* 2003, Pangle *et al.* 2007). Perhaps even more important to the current debate, these risk effects of predation can lead to patterns that might easily be mistaken as evidence for bottom-up forcing (Creel and Christianson, in press). There is also growing evidence for risk effects of predation on several species of marine mammals (Heithaus and Dill 2002; Frid *et al.* 2007; Wirsing *et al.* 2008, in press) that closely matches the observed patterns in Steller sea lions.

Other data that have been used to argue for the nutritional limitation hypothesis also offer only dubious support. For example, estimates of contrasting survival rates of sea lions at Marmot Island in the northern Gulf of Alaska compared to Forrester Island in southeast Alaska (*i.e.*, declining *vs.* increasing populations) have been taken as additional evidence of nutritional limitation of sea lions in southwest Alaska (Pendleton *et al.* 2006). However, all of the differences noted between these two groups of animals could just as easily be explained by differential predation rates on the most vulnerable juveniles (age classes 2 and 3) in particular, and secondarily on adult females.

Finally, there is no evidence in the seabird record of a generalized shortage of forage fishes in the Bering Sea, Aleutian Islands, and western Gulf of Alaska, as invoked by the nutritional limitation theory. Several species of abundant, widespread avian piscivores in southwest Alaska depend on adults and juveniles of the very forage fishes, the lack of which are being used as explanations for the pinniped declines, yet there are no broad patterns in population change as there are for marine mammals (Springer 2007, Dragoo *et al.* 2007). The only exception is that of the enigmatic marbled murrelet (*Brachyramphus marmoratus*) that has declined conspicuously throughout its range from California to the western Aleutian Islands for various known and unknown reasons (Piatt *et al.* 2007).

In summary, there is little doubt that ocean climate has a large influence on marine ecology in the North Pacific, especially at lower trophic levels. However, higher trophic level species, such as pinnipeds and sea otters, are buffered from this environmental variability by life-history strategies that have evolved to manage uncertainty, such as large size, longevity, and parental investment in offspring that attenuate population-scale responses compared to species at lower trophic levels such as plankton and fishes (Iverson *et al.* 2007). This is not to say that they would not

register some measure of change in the environment, as for example the apparent decline in growth rates and near-term pregnancy rates of sea lions or variability in pupping dates of harbor seals, all of which might be caused by food shortage (Calkins *et al.* 1998, Pitcher *et al.* 2000, Jemison and Kelly 2001). However, one does not expect, nor is there a precedent for, the kinds of population collapses that have occurred in southwest Alaska in the absence of compelling evidence of starvation, or other agents such as disease or slaughter by people. In our view a fair assessment of the available evidence argues against nutritional limitation as a singular or even the primary cause of the multispecies collapse.

POINT 4: THE TIMING OF THE MULTISPECIES COLLAPSE IS INCONSISTENT WITH THE TIMING OF THE GREAT WHALE DEPLETIONS

Our critics claim that most of the removal of great whale biomass in the North Pacific occurred in the 1800s and first half of the 1900s and was not as significant, in terms of biomass reduction, as we suggest (DeMaster *et al.* 2006, Wade *et al.* 2007). This argument fails on several counts. First, the geographic context of our hypothesis is not the whole of the North Pacific, as discussed further in response to Point 5 below. Commercial whaling did begin in Alaska in the middle of the 19th century and two species, bowhead and right whales, were severely depleted shortly thereafter. Also in the same era, gray whales that migrate to Alaska in summer were slaughtered on their breeding grounds in southern California and northern Mexico. In light of what we know about the current importance of bowhead and gray whales to many killer whales, the loss of all three species might well have caused killer whales to shift their attention to other species of large whales that were still numerous.

Most of the harvest of blue and humpback whales occurred in the early part of the 20th century. Yet the magnitude of biomass lost in southwestern Alaska pales by comparison to that lost when sperm, fin, and sei whales were depleted after WWII (Springer *et al.* 2006 and papers cited therein). Indeed, the true magnitude of loss of great whales from the North Pacific in the most recent era was much greater than the "official" data indicate because catches were underreported by the former Soviet Union (Brownell *et al.* 2000, Clapham 2006), and was likely greater in the more distant past as well as indicated by genetic analyses (Alter *et al.* 2007).

Our critics further argue that the great whale population declines occurred gradually during the industrial whaling era, that the losses were not as great as we believe, that some species have recovered following the cessation of industrial whaling, and thus if the pinniped declines are linked to the abundance of great whales, it is difficult to understand how and why these declines occurred when they did. In fact, the major declines of great whales in southwestern Alaska occurred during very short intervals of about 3–5 yr, when the *coup de grace* was applied to humpback and blue whales in the early 1960s, to 10–15 yr at most for fin, sei, and sperm whales, which were depleted sequentially through the early 1970s (Danner *et al.* 2006, Springer *et al.* 2006).

In this regard, Wade *et al.* (2007) pointed out that the estimate of the magnitude of the decline in great whale biomass made by Pfister (2004), and which we used

in Springer *et al.* (2003; fig. 3), was wrong because of an error in the calculation of the decline in sperm whales, and instead implied that sperm whale abundance in the Bering Sea and Aleutian Islands declined by just 2,000 animals—from 17,000 to 15,000. Yet despite the error by Pfister, huge numbers of sperm whales were in fact harvested from this region during the mid 1950s and 1960s: 4,500 or more sperm whales per year were killed in the Aleutian Islands and Bering Sea, and the total harvest in 1955–1967 (the peak years) was at least 37,000 animals, over 27,000 of which came from the Aleutians. A sense of the scale of the resulting decline of sperm whales is given by the fact that Japanese fisheries stopped hunting them in the Bering Sea in 1972 because they were so scarce (only 87 were reported taken), even though they were not protected until 1979 (Kasuya 1991). The overall scarcity of great whales in this region is reflected in a 1980 census in the northern Gulf of Alaska, which reported just 159 fins, 364 humpbacks, 36 sperms, and no blues or seis in an area of 2.2×10^5 km² that formerly supported thousands of great whales (Rice and Wolman 1982).

Thus, importantly, and contrary to the claims of Wade *et al.* (2007), the magnitude of great whale removals in the 1950s and 1960s was extreme in both temporal and spatial contexts. The removal of at least a 1,000,000 t of sperm whale biomass alone from such a small region as the Aleutian Archipelago and rim of the eastern Aleutian Basin in the Bering Sea over a span of just 13 yr must surely have altered a variety of food web relationships, including those between sperm whales and their predators.

The effect on the predatory behavior of killer whales by the loss of living great whale prey might have been exacerbated by their loss as dead meals that could be readily scavenged. Whitehead and Reeves (2005) have pointed out that industrial whaling on the high seas utilized exploding harpoons that would have alerted foraging killer whales to the location of whale kills, just as the sounds of winches and motors on long line fishing boats attract fish-eating killer whales to easy meals as gear is retrieved (Yano and Dahlheim 1995). The whale carcasses, which normally sink, were buoyed with gas injections so that the processing vessels could later retrieve them. Industrial whaling thus may have temporarily benefited transient killer whales by providing large and defenseless nutritional resources, advertising the location of these resources, and keeping them on the ocean's surface for sufficient lengths of time that they could be more effectively consumed by the killer whales. Whales that were struck and lost would have further contributed to this larder. The abrupt end to most industrial whaling in the 1970s immediately eliminated these potential benefits. If such scavenging behavior was important to killer whales in the North Pacific, the cessation of industrial whaling, which closely coincided with the onset of the multispecies collapse, could have resulted in an abrupt shift in the killer whales' foraging behavior.

POINT 5: THE GEOGRAPHY DOES NOT WORK

The geographic range of the multispecies collapse varies little among the species and in general extends from about the Kodiak archipelago through the western Aleutian Islands and southern Bering Sea. The overall geographic range of great

whales, whaling, killer whales, pinnipeds, and sea otters is much greater than this. Our critics thus ask, if the Springer *et al.* hypothesis is correct, why did the population declines not occur more broadly? This is a fair question, but one that needs to be considered for all potential explanations of the declines.

At the spatial scale of southwest Alaska, DeMaster *et al.* (2006) and then Wade *et al.* (2007) asserted that there is scant evidence for declines of harbor seals in the Bering Sea, citing a single report by Hoover-Miller (1994), or anywhere else in southwestern Alaska except Tugidak Island. However, other information on harbor seal trends from Kodiak Island and Tugidak Island in the Gulf of Alaska, and Bristol Bay, the Pribilof Islands, and the Alaska Peninsula in the Bering Sea, leaves little doubt that there were indeed widespread, substantial declines in this region during the 1970s–1980s (Withrow and Loughlin 1996, Small *et al.* 2003, Jemison *et al.* 2006). More recent information, that DeMaster *et al.* and Wade *et al.* did not have access to reveals that harbor seal declines in the Aleutian Islands were substantial as well (Small *et al.* 2008).

At the scale of the North Pacific Ocean, the fact that the multispecies collapse is a geographically restricted phenomenon is important and may be a critical clue to its causes. The occurrence of key species or events in different regions is not sufficient to reject or accept any of the competing hypotheses. In this general context, it is important to recognize that ecosystem dynamics and behavior are seldom simple, deterministic phenomena—in fact, similar suites of species and general perturbations often lead to different outcomes (Sutherland 1974, Scheffer *et al.* 2001). For example, we now have an extensive database showing that the removal of sea otters from rocky reef systems predictably results in increased sea urchin and reduced kelp populations. Nonetheless, the time course of ecosystem recovery following the reestablishment of sea otters varies markedly among different geographic regions, from just months in British Columbia and southeast Alaska to decades in the western Aleutian archipelago (Watson 1993, Estes and Duggins 1995, Soulé *et al.* 2003).

This principle is not lost on our critics, as they invoke the conspicuous east-west phase difference between meteorological forcing and ecosystem response in the North Pacific (*e.g.*, Hare *et al.* 1999) as the cause of contrasting population trajectories of pinnipeds and sea otters (Trites *et al.* 2007*a, b*). Their premise is that the prominent climate regime shift of the mid-1970s was received positively by ecosystem processes important to marine mammals in the northeastern North Pacific (*i.e.*, southeast Alaska through British Columbia where sea lions, harbor seals, and sea otters have been increasing in the past several decades), whereas this perturbation was received negatively in the northern and western Gulf of Alaska, Aleutian Islands, and Bering Sea. They maintain that this differential ecosystem behavior led to opposite trends in the abundance of pinnipeds and sea otters by way of general bottom-up processes. However, more than just oceanographic patterns differ across these areas.

Industrial whaling also occurred over a much wider region than that presently circumscribed by the multispecies collapse. But the magnitude of removals of whales from foraging/predation hot spots, and the likely effects that had on community structure and predator–prey relationships, differed greatly among regions (Springer *et al.* 2006). Moreover, coastal marine ecosystems of southwest Alaska and of southeast Alaska and British Columbia had been conditioned much differently during the era of industrial whaling by commercial harvests and bounty programs that severely

depleted sea lion and harbor seal populations in the east, but minimally in the west (Pitcher *et al.* 2007, Springer *et al.* 2007). Furthermore, sea otters, which had been exterminated by the fur trade in southeast Alaska, were not reintroduced into this area until the late 1960s (Jameson *et al.* 1982, Estes 1990). Thus, by the early 1970s when large whales were depleted to their lowest levels, options for diet diversification by killer whales were much different in southeast Alaska and British Columbia than in southwest Alaska. In southwest Alaska, pinniped and sea otter populations were still at high abundances and densities that far surpassed even historical sizes and densities in southeast Alaska and British Columbia, and dwarfed the levels to which those populations had fallen by the end of the whaling era.

In like manner, our critics argue that our hypothesis fails because similar patterns were not observed in the Commander Islands, the western most island group in the Aleutian Archipelago (Wade *et al.* 2007). By their own accounting, the Commander Islands are much different in many respects from the rest of the island chain, and there are additional important biogeographic and ecosystem distinctions that uniquely separate them, just as there are other, albeit less pronounced, ecoregional boundaries elsewhere in the Aleutian Islands (Schumacher *et al.* 2005, Piatt and Springer 2007). However, this may now be changing—Mamaev and Burkanov (2006) have documented a rapid rise in the incidence of killer whale attacks on fur seals in the Commander Islands since 2000, after observing none in the prior decade.

What would have been surprising is if population dynamics, food web dynamics, and predator–prey relationships among all of these species had been the same in all of the regions. First, the most parsimonious explanation for increasing abundances of pinnipeds and sea otters in southeast Alaska and British Columbia is simply the protections from wanton human killing that were enacted in the early 1970s (Pitcher *et al.* 2007, Springer *et al.* 2007), not complex ecosystem processes driven from the bottom-up by meteorological forcing. Second, given the importance of culture and individuality in the foraging behavior of animals such as killer whales (Whitehead 1998, Bolnick *et al.* 2003), and the broad and largely exclusive ranges of the different transient killer whale populations across the North Pacific Ocean (Barrett-Lennard and Heise 2006, L. G. Barrett-Lennard⁷), killer whale-induced effects on their ecosystems that are both geographically restricted and sharply punctuated are not surprising. Animals capable of diverse behavioral responses through cultural evolution, such as killer whales, should not be expected to respond to environmental changes in consistent or predictable ways. In fact, if unique foraging behaviors developed and spread through regional killer whale populations (as we know they do), but were inhibited from crossing their boundaries by the tendencies of the different populations to avoid one another (as reportedly occurs), then large-scale and sharply punctuated response patterns in their selection of prey species is precisely what one might expect to see.

Wade *et al.* (2007) argued that if large whales were important prey of killer whales in the past, then they should again become more prominent in diets as various

⁷Personal communication from L. Barrett-Lennard, Vancouver Aquarium Marine Science Centre, 845 Avison Way, Vancouver, BC V6G 3E2, 2007.

species recover. Indeed, such a process may now be occurring. Gray and bowhead populations have doubled since the early 1970s (Pfister and DeMaster 2006 and references therein)—grays are preyed upon heavily by killer whales in the eastern Aleutian Islands (Matkin *et al.* 2007) and attacks on bowheads apparently increased during this time as noted above. Humpbacks also have recovered considerably in western Alaska (Zerbini *et al.* 2007) and, as noted above, several attacks on them have been seen in recent years. Because functional feeding responses are seldom if ever linear, but instead exhibit thresholds of prey abundance/availability below which they are not profitable (Piatt and Methven 1992, Piatt *et al.* 2007), it is unlikely that killer whales would have gradually shifted their diets to pinnipeds as great whales declined, as suggested by Trites *et al.* (2007a), but it is reasonable to believe that with increases in some species of great whales in recent years in southwest Alaska, critical population density thresholds may have been met such that they are again targets of killer whales.

Wade *et al.* (2007) further argued that as a result of a shift back to large whales as prey for killer whales, predation pressure on pinnipeds should decrease and their populations should increase. This too might be occurring—in recent years the abundance of sea lions has been stable or increasing in the eastern Aleutians and western Gulf of Alaska, and harbor seals in the western Gulf of Alaska have been increasing slowly but steadily as well (Small *et al.* 2003, Fritz *et al.* 2006). These are regions where increases in the abundance of large whales (gray, fin, and humpback) have been most conspicuous. In contrast, sea lions and sea otters have continued to decline in the western Aleutians (Estes *et al.* 2005, Fritz *et al.* 2006), where evidence of significant recovery of large whales is not apparent.

Finally, there is no reason to believe that killer whales ever relied upon great whales in southeast Alaska and British Columbia to the extent they may have in southwest Alaska. The biomass of great whales in that region was nowhere near as great as it was in southwest Alaska (Springer *et al.* 2006), and many great whales killed in British Columbia were only migrating through the region and were thus available as potential prey during comparatively brief intervals in spring and fall (Gregr *et al.* 2000). With such low abundances of pinnipeds and sea otters available in southeastern Alaska and British Columbia at the time of the great whale removals, it would not be surprising if killer whales were targeting them less also, but instead were preying on other more profitable species, in an energetic cost/benefit sense (Williams *et al.* 2004), such as porpoises, dolphins, and small whales. In southwest Alaska just the opposite would have been expected. Still, it seems unlikely that killer whales in southeastern Alaska and British Columbia would have passed up vulnerable pinnipeds even when they were at low abundance, which may account for the very slow rate of recovery of sea lions throughout this region and of harbor seals in southeast Alaska since they were protected three and a half decades ago (Small *et al.* 2003, Pitcher *et al.* 2007).

In sum, the geographical range and pattern of the multispecies collapse is at least as easily reconcilable by Springer *et al.* as by any of the alternative hypotheses. By applying a “one shoe fits all” logic to ecosystem behavior, our critics have overlooked the key factors driving the unique trophic interactions in these dissimilar ecosystems.

SOME CONCLUDING REMARKS

We acknowledge that Springer *et al.* is a hypothesis, necessarily built around a chain of reasoning that includes several links with little or no direct empirical support. We acknowledge here, as we did initially, that oceanographic change and fisheries both can have important impacts on ocean ecosystems. Furthermore, we recognize a potential for, if not the inevitability of, complexity in the dynamic overall behavior of the North Pacific/Bering Sea ecosystem, including that resulting from interactions among various potential drivers of the multispecies collapse, such as climate change, fisheries, and predation. Like all species, pinnipeds and sea otters are sensitive to environmental variability, and it would thus be surprising if they did not respond to fluctuations in their prey populations. However, the few responses documented in sea lions and harbor seals, and used as evidence of nutritional stress, are, in our view, of the kind that would be expected to keep populations in dynamic equilibrium with prey resources over the long term, but not cause the unprecedented, abrupt population collapses that have been witnessed.

In the end, the Springer *et al.* model may be proved wrong. But despite our critics' claims, we do not believe that this has yet happened. They claim that killer whales rarely eat large whales, but in fact there is a large and rapidly growing body of evidence that this is incorrect. They claim that the multispecies collapse was not sequential, but we have presented evidence to show that this too is incorrect. They claim that there is clear evidence for nutritional limitation in Steller sea lions, but we believe that the evidence in fact is thin at best and actually counter-indicative in many cases. They claim that the timing of industrial whaling is inconsistent with the multispecies collapse whereas we believe the key events line up just as one would expect. They claim geographical inconsistency between the purported drivers of the multispecies collapse and the collapse itself, but we believe this discrepancy actually is more easily reconciled by Springer *et al.*, and with all of the facts, than the regime shift/junk food hypothesis.

It has been over 4 yr since Springer *et al.* was published and we are both surprised and dismayed by how it has polarized a segment of the research and management communities. Much of what has been written to date has been accusatory, with little searching for common ground or a way forward toward further understanding. In closing, therefore, we provide a synopsis of our views on what might be done to put the various hypotheses for the megafaunal collapse to more critical tests.

The first question that must be asked is whether the various views surrounding Springer *et al.* can be resolved or melded to the extent that a reasonably strong consensus view can emerge? The problem is more difficult than, say, the equally contentious debate over historical population sizes of large whales (Roman and Palumbi 2003, Palumbi and Roman 2006, Alter *et al.* 2007). With further development of genetic theory, refined measures of mutation rate and gene flow, and the sequencing of more genes, this latter debate is likely to be resolved. Approaches that might resolve the debate over Springer *et al.* are more problematic. The depletions of great whales, manipulations of fish stocks by fisheries, collapses of pinnipeds and sea otters, and recent trends in climate, have radically altered the larger ecosystem of the northern

North Pacific from its condition of 50 to 100 yr ago, such that explanations about the past based on observations in the present are troublesome. Nonetheless, we believe the following activities will be helpful.

Demographic/Energetic Bookkeeping

The sustainability of any predator–prey system is based on prey production on the one hand and predator removal on the other. The limits to these systems thus can be determined by the consumption needs of the predators and the value and production potential of their prey. Information of this nature cannot inform us of what actually happened, but it can provide “windows of feasibility.” That is, it can be used to assess whether or not predation of great whales is capable of supporting substantial numbers of killer whales, and if so how much of the whale productivity would have been required (*e.g.*, Williams *et al.* 2004, Doak *et al.* 2006, Williams 2006). Similarly, this approach easily could be used to address and potentially resolve the question of whether the predator–prey system defined by transient killer whales and their marine mammal prey in the North Pacific Ocean is sustainable without nutritional input from the great whales. Of course, conclusions from such an exercise could be complicated by behavioral changes—trait-mediated effects, cultural evolution in predatory behavior as prey populations are reduced, and the competing evolution of prey defenses as predation is increased.

The Weight of Evidence

The various hypotheses for the multispecies collapse lead to differing sets of predictions about the predators, the prey, and the ecosystem. For instance, all bottom up forcing scenarios have associated expectations for nutritional limitation—poor body condition, reduced weaning success, increased time spent foraging, increased dive depth, reduced net rates of energy gain, and so on. Although the available data probably are inadequate to conduct a definitive evaluation, considerable information on the animals and their ecosystem has been obtained over the years, and an independent and objective assessment of the extent to which this information tends to support or refute the various hypotheses might prove to be quite insightful. A preliminary effort of this sort was conducted by the National Research Council (2003), but the results of that analysis do not seem to have been widely considered.

A View to the Past

If one could relive the past with the questions in mind that we are now struggling to answer, it might be possible to watch the key events unfold in a manner that would reveal the cause or causes of the multispecies collapse. Although it is of course impossible to relive the past, various clues always are left in the historical record. A more careful look at history, in all of its manifestations, could move us closer to the ideal of actually rerunning the clock. Detailed historical analyses have shown us with reasonable certainty why the dinosaurs became extinct some 65 mya (Alvarez

et al. 1980) and why the New World megafauna suddenly lost so many species at the Pleistocene/Holocene border (Barnosky *et al.* 2004, Koch and Barnosky 2006). Surely the same or greater successes for an event that is only decades old are within reach. For example, a recent retrospective study of stable isotope ratios in fur seal teeth casts doubt on the general notion of a decline in productivity of the North Pacific Ocean and Bering Sea during the past half century (Newsome *et al.* 2007).

A View to the Future

The Springer *et al.* hypothesis centers on the notion that great whale reductions resulting from post WWII industrial whaling led to an extensive multispecies collapse of pinnipeds and sea otters. The specific mechanisms by which this purportedly happened have been specified. Pending upcoming management decisions in the arena of international whaling, all of the great whales in the North Pacific will likely recover, even, perhaps, the extremely depleted right whales—grays, bowheads, and humpbacks already are well on their way. This natural experiment will provide a great opportunity for learning, provided that scientists gather the right information. Although a considerable amount has been learned in recent years about the natural history of transient killer whales in southwest Alaska and elsewhere, much more remains to be revealed. Science will never be able to gauge with empirical data the role of transient killer whales and top-down forcing on dynamics of prey populations and ecosystems without a commitment to expanded field research to discover temporal and spatial patterns in their abundance, movements, behavior, and diets in the area of the megafaunal collapse. Among the current tools available, in addition to expanding shipboard surveys to the central and western Aleutians to further document abundance and distribution, are telemetry⁸ and acoustic monitoring that can provide critical information on movements and behavior (*e.g.*, Deeke *et al.* 2005, Newman and Springer 2007); genetic finger printing that can add necessary details about group and ecotype structure (Barrett-Lennard 2000); stable isotope analyses to provide information on current and historic trophic level and diet (Herman *et al.* 2005; Newsome *et al.* 2007; D. Monson⁹); and fatty acid analysis, that to date has been used merely to identify qualitative dietary differences and similarities among killer whales (Herman *et al.* 2005), but could be substantially expanded to quantitatively estimate their diets as has been done, for example, with polar bears in the Arctic (Iverson *et al.* 2006). While this may not necessarily answer all of the questions about what happened in the past, it will provide a basis for evaluating possible future changes in the context of predator–prey relationships and population and ecosystem change. Together, knowledge gained from these various approaches will be central to understanding ecosystems of the North Pacific and how to manage and conserve many of the valuable species contained in them.

⁸Unpublished data from J. Durban, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

⁹Unpublished data from Dan Monson, U. S. Geological Survey, 4230 University Drive, Suite 201, Anchorage, AK 99580.

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