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Trend data *do* support the sequential nature of pinniped
and sea otter declines in the North Pacific Ocean,
but does it really matter?

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The Sequential Megafaunal Collapse Hypothesis (SMCH) posits that decimation of great whales in the North Pacific Ocean in the 1950s and 1960s, by Russia and Japan following the end of World War II, removed an important source of prey for marine mammal eating killer whales in southwest Alaska (the Aleutian Islands, southern Bering Sea, and western and central Gulf of Alaska). The killer whales subsequently broadened their diets to include a larger proportion of other, much smaller species—harbor seals, Steller sea lions, fur seals, and sea otters—driving them into steep decline. In the preceding letter, Wade, Ver Hoef, and DeMaster present information and analyses that purportedly refute the SMCH. But, as explained below, we take exception to their analytical procedures, use of data, and the strong claims they have employed in their continuing attempts to discredit the hypothesis.

Editor's Note: The Letter of response by Wade et al. on pages 737–747 was limited by me to addressing only the new analysis presented in the Letter by Springer et al. (2008). The Letter by Estes et al. above is the opportunity to rebut this response. These two Letters, which stem from responses to the original paper by Springer et al. 2003 and rebuttals to the responses will be the last Letters published in *Marine Mammal Science* in this string of responses. The Journal will look forward to papers that provide new data that address the hypotheses and questions raised by these various publications.

This interchange has been limited to details of one contended point—the “sequential” nature of the sea otter and pinniped declines and Wade *et al.*'s view that it represents the core element of the SMCH. However, it is important to recognize that this is largely a side issue, which concerns only a minor piece of the SMCH argument we originally made.

As we previously emphasized (Springer *et al.* 2003) and reemphasized (Springer *et al.* 2008), the SMCH is a hypothesis founded on multiple lines of evidence and reason (Estes *et al.* 1998, Williams *et al.* 2004, Springer *et al.* 2006*a, b*). The singular focus on the rather minor issue addressed here weakens and detracts from the persuasiveness and utility of the debate. This, and the failure of Wade *et al.* to advance a synthetic, explanatory argument of their own, retards the application of the SMCH to inform management considerations for these and other species of marine mammals in the North Pacific.

In considering whether the declines of sea otters and the various pinniped species were evenly spaced in time (as initially assumed in the statistical null model used by DeMaster *et al.* 2006), Wade *et al.* state that “. . . Springer *et al.* (2008) argue this is not a logical extension of their idea, but we believe it is.” Yet they provide no support for their belief. We still can think of no reason why predation-induced declines of any multispecies prey field should be *uniformly* spaced due to predation effects, especially given the markedly different starting biomasses of the various species in this particular case, their different vulnerabilities to predation, and their different values to killer whales based on vulnerabilities and nutritional content—the energetic cost-benefit ratio. Indeed, it is difficult to imagine uniformly spaced population declines arising from any natural process.

In furthering their argument on this point, Wade *et al.* maintain that we have used a statistical null model that is tautological (*i.e.*, false by its logical form alone) by assuming that the time intervals between the declines were independent. That contention is no more valid than its complement—that is, the claim that Wade *et al.*'s null model is logically true due to the assumption of temporal uniformity. Moreover, our analyses actually do not have a formal null hypothesis at all—we fit trends to separate populations and species and compared the overlap in the probability envelopes of decline midpoints. Wade *et al.*, in contrast, have attempted to formalize this process *via* a constraint that is both unrealistic and unreasonably restrictive.

Armed with a statistical construct that favors accepting the null hypothesis, Wade *et al.* erred further by basing their analyses and conclusions on a weak and inappropriate body of supporting evidence. Their first mistake was to use counts from just three closely spaced large islands (Tanaga, Kanaga, and Adak) in just three closely spaced years (1959, 1962, and 1965) to suggest that sea otter numbers were already in decline in southwest Alaska by the early 1960s. Wade *et al.* failed to mention that the post-fur trade recolonization of these particular islands occurred shortly before the first survey in 1959 *via* a surge of population outgrowth from the Delarof Islands (see Kenyon 1969 for details), which lie immediately west of Tanaga. The subsequent declines at Tanaga, Kanaga, and Adak in the early 1960s are not the beginnings of the larger-scale collapse, as suggested by Wade *et al.*, but the result of local buildups and redistributions, as the then recovering sea otter population spread

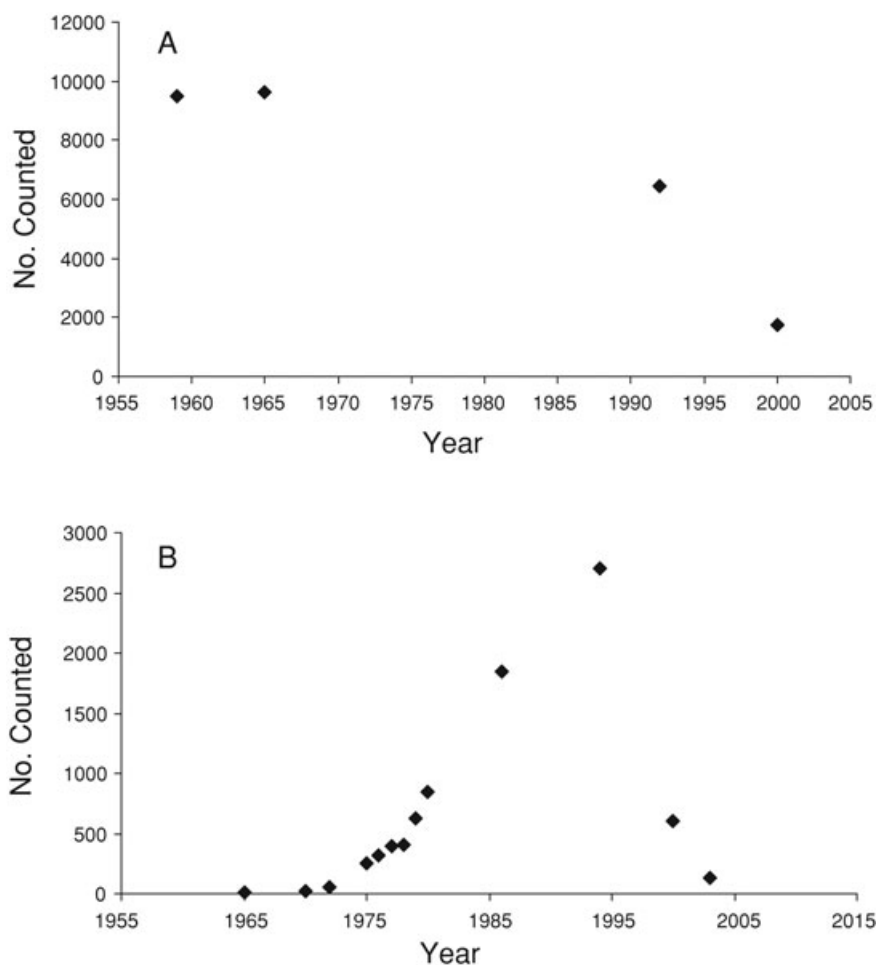


Figure 1. Sea otter survey data from the Aleutian archipelago. (A) Aerial counts from the 31 islands that were surveyed in 1959, 1965, 1992, and 2000; (B) Skiff counts from Attu Island.

eastward across this region (Kenyon 1969). A more comprehensive examination of the data from the 31 islands in the Aleutian archipelago that were surveyed in 1959, 1965, 1992, and 2000 (Fig. 1A) shows a slight increase from 1959 to 1965, a decline of about 33% between 1965 and 1992 (indicating only that the decline had indeed begun sometime prior to 1992), and a further decline of about 49% from 1992 to 2000 (indicating that most of the overall decline occurred after 1992). The only detailed time series of sea otter counts in the Aleutians during the mid-1970s through the early 2000s is from Attu Island (Fig. 1B), data which show that the decline at Attu did not begin until sometime after 1986. Unlike the earlier declines at Tanaga, Kanaga, and Adak, this abrupt collapse was not the result of redistribution because none of the nearby islands showed increases and the distances from Attu to

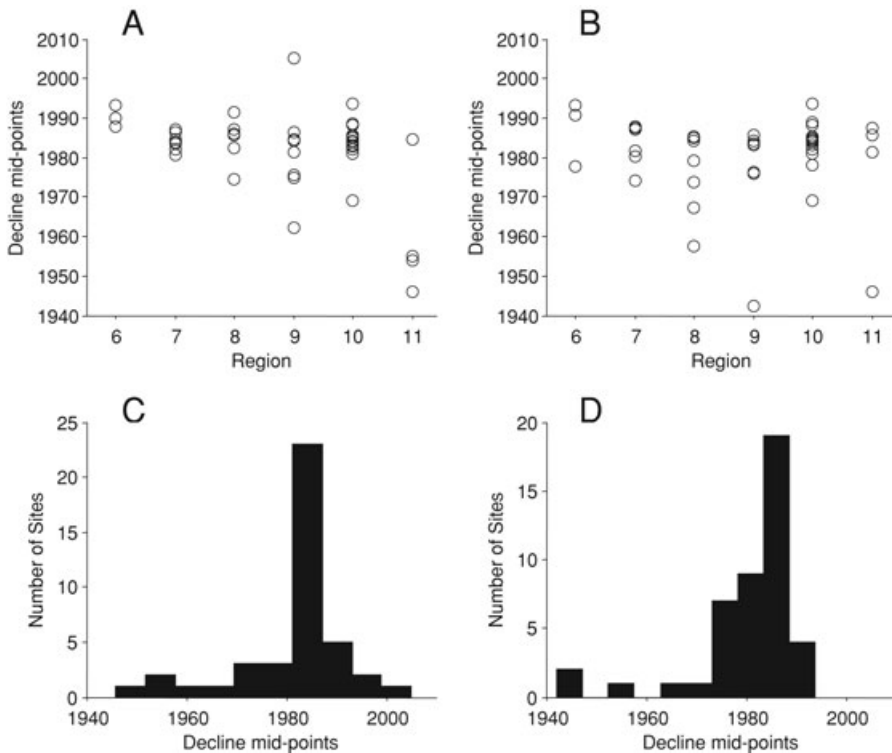


Figure 2. Characterizations of estimated regional midpoints of the Steller sea lion decline in southwest Alaska. Left panels are based on data from Fritz *et al.* (2008), and used in Wade *et al.*'s analyses; right panels include data from earlier counts (see Appendix S1 for all of the raw data and descriptions of regions). Panels A and B show the computed midpoints for each rookery or haul-out. Panels C and D show the overall frequency distributions of computed midpoints.

other potential areas are too great. Hindcast analyses of more recent time series of sea otter surveys from several other islands in the central/western Aleutians provide similar conclusions (Doroff *et al.* 2003).

Although the Steller sea lion, harbor seal, and northern fur seal declines clearly preceded the sea otter decline, their temporal interrelationships are less certain. The essential difficulty for Steller sea lions is a spotty survey effort at many locations until the decline was nearly over. Wade *et al.*'s analysis of these data (from Fritz *et al.* 2008) indicates substantial variation in the midpoint years (ranging from the early 1950s to about 1990) among six survey regions from the eastern Gulf of Alaska through the western Aleutian Islands (Fig. 2A). However, the data in Fritz *et al.* do not include a number of earlier, comparable counts at several rookeries and haul-outs (see Appendix S1). When these data are included, the estimated midpoints take on much more similar averages among the six regions (Fig. 2B). Moreover, the range and variation of estimated midpoints for the sites do not differ strikingly across these

regions, the distinct overall majority of which occurred during the 1980s (Fig. 2C, D). This exercise indicates that (1) the algorithm we all used to compute the decline midpoints is highly sensitive to the early data, (2) Wade *et al.*'s interpretation of regional variation in the timing of the sea lion declines is in all likelihood driven by sampling errors rather than true differences in decline times, and (3) there is no basis for their conclusion that sea lion population declines occurred at markedly different times in different regions across southwest Alaska.

Wade *et al.* claim that the data for harbor seal population trends preclude any overall assessment of when the declines occurred, but here again we see it differently. The two available time series (Tugidak and Otter islands) used by Springer *et al.* (2008) and in Wade *et al.*'s analysis show declines that were nearly coincident with one another and essentially over by 1980, thus indicating midpoints in the 1970s. Although we agree that the data on harbor seals at other sites are limited, and insufficient for a similarly rigorous assessment of population change, there was indeed a broad scale decline in harbor seal abundance in western Alaska in the 1970s and 1980s, as we pointed out earlier (Springer *et al.* 2008). Furthermore, harbor seal counts from 106 islands/haul-outs conducted in 1977–1982 and again in 1999 across the Aleutian archipelago (Small *et al.* 2008) help to clarify the timing of their decline. The raw counts declined by 67% during this period, which on the surface does not seem to indicate a decline that was grossly different in timing from that of the sea lions. However, the 1977–1982 data are from skiff counts, the 1999 data are from aerial counts, and information from eight islands for which both aerial and skiff counts exist in the same or nearly the same years indicate that skiff counts exceed aerial counts by a factor of 1.45 in the Aleutian Islands. Using this value to correct the survey results for methodological differences reduces the post 1977–1982 decline estimate from 67% to about 50%. If the harbor seal decline in the Aleutians was of a comparable magnitude to that which occurred at Tugidak and Otter islands (>90%) and to the declines of sea otters and Steller sea lions, then the harbor seal decline was well along before the first surveys were even begun in 1977. We interpret the evidence, in aggregate, to mean that the bulk of the overall harbor seal decline in southwest Alaska occurred prior to 1980.

A selective use of data and model assumptions can almost always be employed to turn the results of statistical hypothesis testing in whatever direction one might wish. It is our contention that Wade and colleagues, under the pretense of rigorous and objective analysis, have done exactly that. Although the data are deficient in certain respects, we stand by our initial view that the most reasonable interpretation of the available evidence is that harbor seal, Steller sea lion, and sea otter populations collapsed sequentially—that is, one after another—over a period of several decades.

A most unfortunate aspect to this particular exchange is that the contended issue is not even particularly relevant to whether the SMCH is true or false. Given the small number of transient killer whales needed to drive each of the declines (Williams *et al.* 2004), the collapse could just as easily have happened in synchrony as in sequence without compromising the proposed mechanisms or countermanding the logic of the SMCH.

There are two reasons for not embracing new ideas in science. One is philosophical—an opinion that the supporting evidence/arguments are not sufficiently compelling to challenge the status quo; the other is empirical—an assertion that the supporting evidence/arguments are flawed. We can understand and even respect those who object to the SMCH on philosophical grounds; it is much more difficult to sympathize with criticisms that are founded on flawed reasoning and inappropriate analyses. We will say again (for the third time in print) that the SMCH is a hypothesis, not an established fact. Critics have attacked it while simultaneously failing to provide convincing alternatives, much less subject them to the same standards of scrutiny. From our perspective, they seem more intent on proving us wrong than on searching for where the truth really lies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Counts of Steller sea lion non-pups used in the analyses presented in Figure 2. Data from Fritz *et al.* (2008), National Marine Mammal Laboratory (NMML, unpublished data). Shaded values were not reported by Fritz *et al.*, but are included in the NMML raw data set and were taken on comparable dates to the counts reported by Fritz *et al.* Values of 99 = unknown. Regions, as defined by NMML, in Figure 2: 6 = Eastern Gulf of Alaska; 7 = Central Gulf of Alaska; 8 = Western Gulf of Alaska; 9 = Eastern Aleutian Islands; 10 = Central Aleutian Islands; 11 = Western Aleutian Islands.