COMMENTARY

Salmon, seabirds, and ecosystem dynamics

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Most of what ocean scientists know or believe to be true about ecological process in the open sea is necessarily based on correlative inferences, the interpretation of time series without direct evidence for cause and effect. This situation arises in part from the near impossibility of studying ocean ecosystems experimentally at appropriate scales of space and time. Freshwater ecology is a study of extreme contrast. Although the principal biotic elements of lakes and oceans are broadly similar (i.e., both support food webs containing phytoplankton, zooplankton, and fish), lakes are comparatively small and sharply defined by surrounding land, thereby making them amenable to whole-ecosystem manipulative experiments. The resulting difference in approach—inference from correlative evidence in the sea and inference from experimental evidence in lakes—sets lakes apart from the oceans as some of the most carefully studied and best-understood ecosystems on earth. However, studies of open ocean ecology are beginning to explore complex interactions among species in interesting new ways. Analyses of long and detailed time series, such as those presented by Springer and van Vliet (1) on the ecological interplay between pink salmon and seabirds in the subarctic North Pacific, are providing an expanded view of ecological process in the world's oceans.

Understanding Oceanic Ecosystems

Much of ocean ecology has focused on one of two general themes—food web dynamics in response to physical oceanographic change associated with ocean basin-wide regime shifts [e.g., the North Atlantic Oscillation and Pacific Decadal Oscillation (PDO)], and depletion of fishes and other species of high trophic status by human exploitation. Although there are many purported effects of both regime shifts and the depletion of higher trophic-level species, the strength of inference in both cases is commonly limited by the long periods of time over which these events occur in nature. Ocean regimes shift over decades, making the search for recurrent patterns (the gold standard of inference in any scientific study) extremely difficult and time consuming. Understanding the ecological consequences of fish stock depletions is limited by the typically one-off nature of these events and a common lack of information on the associated ecosystem. The difficulties have been exacerbated in both instances by a general lack of attention to alternative hypotheses that fall outside a widely held view of bottom-up forcing (i.e., population control by production and trophic transfer efficiency).

Pacific salmon numbers have waxed and waned over the past century with only limited understanding of the causes or consequences. The added challenges of understanding salmon fluctuations stem from a complex life history in which populations are potentially influenced by events in both their riverine spawning and rearing habitats and the open ocean environments where they grow to maturity. Impairment of spawning migrations by dams and destruction of spawning habitat by logging, agriculture, and other forms of development have clearly led to stock declines (2). Furthermore, there is strong evidence that run strengths of sockeye salmon in Alaska have fluctuated on cycles that coincide in period with those of the PDO (3), thus implicating physical oceanography and bottom-up forcing as important drivers of salmon abundance. Although such patterns and their causal mechanisms are often clear in retrospect, the ability of fisheries biologists to forecast salmon run strength with any degree of confidence is largely limited to extrapolations from population assessments of earlier life stages. Environmental influences on salmon abundance and population trends remain vague and controversial.

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Why Pink Salmon Are Informative

Pink salmon, by virtue of their 2-y life cycle and typically odd/even year variation in run strength, provide a potentially edifying exception to unraveling the mysteries of salmon ecology. In contrast with nearly all other trajectories of salmon population change, the odd/even year variation in wild pink salmon run strength is both extreme and highly predictable at regional levels. For example, the difference in spawning biomass between odd and even years in the odd-year–dominated stocks of eastern Kamchatka and the western Bering Sea has varied over the past four decades from about 3- to more than 10-fold. Similar 2-y population cycles occur elsewhere in the North Pacific region, except that dominant runs in some places occur in even years. Occasionally, the pattern of odd/even year stock domination has even switched.

Although the underlying reason for this distinct odd/even year cycle in pink salmon biomass is currently unknown, it is almost certainly not a consequence of biennial variation in physical forcing. There is simply no evidence or reason to believe that physical oceanographic patterns cycle on a 2-y period. Instead, the cycle is probably an epiphenomenon of salmon demography and density-dependent interactions with some aspect of their environment, such as at-sea food availability, in-stream spawning habitat, the per capita effect of predators, and intercohort competition or cannibalism. That is, more-abundant populations realize some advantage over less-abundant populations in environments that are otherwise similar. This general mechanism would work if sequential years were, on average, similar to one another. However, regardless of the cause, the phenomenon by itself provides an interesting window into the ecological effects of pink salmon on their ocean ecosystem.

Nearly two decades ago, Shiomoto et al. (4) recognized both the pattern and the power of this approach, which they then used to explore oceanic food web dynamics

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in the subarctic North Pacific region. These authors found that chlorophyll concentration (a proxy for phytoplankton abundance) was positively correlated with the high years in pink salmon abundance, whereas zooplankton biomass showed the opposite pattern, from which they concluded that the associated ocean food web operated under the influence of a pink salmon-initiated trophic cascade (a chain of interactions that begin with predators and spread downward through food webs). The underlying idea is just this: In years when salmon are abundant, their zooplankton prey are relatively rare and, as a consequence, the zooplankton's prey (phytoplankton) are relatively abundant. Similar open-ocean trophic cascades have since been shown or suggested in the western North Atlantic Ocean (5), the North Sea (6), and the Black Sea (7). These latter three examples were all derived from time-series analyses of fish stocks as they declined from human exploitation (or in some cases recovered following protection), and concurrent measurements of phytoplankton, zooplankton, and forage fish abundance in the associated food webs. Although the evidence for a fishery-driven trophic cascade is reasonably compelling in each of the three cases, alternative interpretations have been advanced because the strength of inference was limited by the typically one-off nature of the purported driver (the decline or recovery of exploited fish stocks). Shiomoto et al.'s (4) initial study, because of the recurrent nature of the rise and fall of pink salmon biomass, stands alone as being largely impervious to alternative interpretations.

Alan Springer and Gus van Vliet (1) have taken the pink salmon's story a large step forward by demonstrating a link between the salmon and breeding seabirds. Virtually every step in the seabirds' reproductive process, from nesting effort to hatching and fledging success, anticorrelates with the pink salmon cycle; seabird reproductive success is therefore higher during the cycles' low years. The repetitive nature of Shiomoto et al.'s (4) data strengthened their inference for a trophic cascade. The even longer time series and more extensive replication of Springer and van Vliet's (1) study make the contrasts in seabird reproductive performance between contiguous high/low pink salmon years difficult to explain in the absence of an indirect interaction between pink salmon and seabirds. Although the cause of this negative association between salmon and seabirds remains somewhat uncertain, the likely explanation is that salmon are outcompeting seabirds for an otherwise limiting food resource. Whether or not the seabirds reciprocate with a negative effect on salmon is an intriguing issue that remains to be explored.

Competitive interactions between salmon and seabirds might have been predicted from an assessment of dietary overlap between these groups of consumers. However, the strong tendency of most seabird and salmon biologists to relate variation in reproductive success and changing population size to bottom-up forcing by physical oceanographic processes may have blinded them to the alternatives. Springer and van Vliet's (1) findings argue persuasively that indirect species interactions are the best available explanation for the coupled fluctuations of pink salmon and seabirds, and in general, deserve more attention as alternative hypotheses to bottom-up forcing as explanations for change in other ocean populations (8).

Springer and van Vliet (1) were able to explore several alternative hypotheses for time trends in pink salmon and seabirds because of a visionary decision in the 1970s by the Alaska Maritime National Wildlife Refuge to design and put in place a seabird monitoring program. Springer and van Vliet's insightful interpretations could never have been made without these data. More comprehensive long-term monitoring programs of this quality would greatly enhance our understanding of marine ecosystem dynamics.

1 Springer AM, van Vliet GB (2014) Climate change, pink salmon, and the nexus between bottom-up and top-down forcing in the subarctic Pacific Ocean and Bering Sea. *Proc Natl Acad Sci USA* 111:E1880–E1888.

2 Montgomery DR (2003) *King of Fish. The Thousand-Year Run of Salmon* (Westview Press, Cambridge, MA).

3 Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull Am Meteorol Soc* 78(6):1069–1079.

4 Shiomoto A, Tadakoro K, Nagasawa K, Ishida Y (1997) Trophic relations in the subarctic North Pacific ecosystem: Possible feeding effect from pink salmon. *Mar Ecol Prog Ser* 150:75–85.

5 Frank KT, Petrie B, Choi JS, Leggett WC (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308(5728): 1621–1623.

6 Casini M, et al. (2008) Multi-level trophic cascades in a heavily exploited open marine ecosystem. *Proc Biol Sci* 275(1644): 1793–1801.

7 Daskalov GM, Grishin AN, Rodionov S, Mihneva V (2007) Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proc Natl Acad Sci USA* 104(25): 10518–10523.

8 Travis J, et al. (2014) Integrating the invisible fabric of nature into fisheries management. *Proc Natl Acad Sci USA* 111(2): 581–584.