# Apex predators and trophic cascades in large marine ecosystems: Learning from serendipity

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The global loss of large predators is undeniable. However, the effects of predator depletion on the structure and functioning of ecosystems are far from resolved, especially as they apply to large pelagic marine ecosystems. Much of what we know about how marine predators function in ecosystems comes from small-scale studies on relatively small, slow-moving, seafloor-feeding predators that are easy to manipulate. Scaling up to consider pelagic (ocean) ecosystem effects from large predatory fish has been challenging for several reasons. For one thing, predators have been functionally removed from many marine ecosystems due to unsustainable fishing that occurred decades or centuries ago. Also, studies often rely on correlations showing increases in prey populations as predators decline, but these correlations can be confounded if coincident oceanographic factors such as ocean warming control prey abundances. What is needed is an ecosystem-scale, large predator addition experiment for which most biotic components of the ecosystem are monitored before and after predator addition. Such an experiment is exactly what Casini et al. (1) report in PNAS.

Casini et al. (1) document a rare but important "natural experiment" of predator addition into a relatively isolated 18,000-km$^2$ branch of the Baltic Sea called the Gulf of Riga. The apex predator in the Baltic, Atlantic cod (*Gadus morhua*), is a large generalist carnivore that before fishing was widespread, abundant, and possibly the most important predator throughout coastal regions of the North Atlantic (2, 3). Casini et al. (1) describe a pulse infusion of juvenile and adult cod into the Gulf where cod fed and grew for about a decade but, for environmental reasons, they could not reproduce or sustain their population. Importantly, cod and all other key players in this pelagic ecosystem such as herring, herbivorous zooplankton, and phytoplankton have been continuously monitored since 1973. Thus, when Baltic cod populations swelled and spilled over into the Gulf of Riga in 1977, they effectively initiated a predator addition natural experiment into a system that had well-established baseline conditions. The predator pulse lasted a decade during which time cod's prey, herring, declined in abundance, releasing zooplankton from herring predation pressure. The rise in herbivorous zooplankton resulted in a decline in phytoplankton, increasing water clarity during the decade cod were abundant. What the authors describe is called a "trophic cascade" in which higher-order consumers significantly affect how organisms interact at three or more lower trophic levels of the food web.

Fig. 1. Ghosts of apex predators past. Photo of Atlantic cod from coastal Maine circa 1880. (Image is in the public domain.)

The Casini et al. study illustrates and reaffirms three important points: (*i*) Apex predators can affect large pelagic marine ecosystems. (*ii*) Cod were a foundation species for the North Atlantic before its fisheries-induced extirpation (2) and it hints at why this species often fails to recover from very low population densities (3). And (*iii*) perhaps the overarching message is that complex ecological interactions among and between managed species can drive dynamics of local populations in demographically significant ways that profoundly affect entire ecosystems. I briefly expand on each of these three points.

There is little doubt that before fishing pressure, Atlantic cod were abundant, large, and important benthic predators throughout cold temperate to subarctic regions of the North Atlantic (Fig. 1) (2, 3). In the western North Atlantic prehistoric fishing targeted cod not only because of their abundance and size but also because they are easy to catch and preserve (2, 4). Cod became the first important export from the New World and as fishing technology and effort escalated, serial depletion progressed from coastal regions to the final collapse of Canada and US cod stocks in the 1990s. The resulting decline in cod predation relaxed population limitations on several invertebrate prey species that live on or near the sea floor such as American lobsters, large crab species (e.g., Jonah and snow crabs), and shrimp (2, 3, 5, 6). In addition to those benthic invertebrate carnivores, the predator decline also relaxed demographic limits on herbivorous sea urchins in a trophic cascading of widespread grazing down of kelp forests (7).

Trophic cascades are most common and clearly evident in low-diversity benthic marine ecosystems (8, 9). Whereas top–down (consumer-driven) effects in benthic food webs are widely accepted, their application to large pelagic marine ecosystems is more contentious. The well-documented decline of predatory cod along Canada's Scotian Shelf was determined to have resulted in increased herring and other small pelagic fish, causing their zooplankton prey to decline, ultimately increasing the region's phytoplankton (10). However, the zooplankton and phytoplankton changes were also coincident with an oceanographic regime shift resulting from climate changes in the Arctic (11). That example illustrates confounding vulnerabilities associated with drawing conclusions from single-trend correlations. The Casini et al. study, however, has a stronger case for a trophic cascade by having quantitative data for the entire food web before and after the addition of cod in this large marine ecosystem. Thus, evidence is growing that Atlantic cod may have the unique capacity to trigger large-scale trophic cascades

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in both benthic and pelagic marine ecosystems.

The cod influx into the Gulf of Riga also informs us about how subpopulations of this species expand to colonize new areas. New colonization by cod may seem unremarkable but it stands in stark contrast to most previous studies on spatial dynamics of this species that focused on how and why cod stocks have declined, contracted, or gone locally extinct (12). Further, it is particularly frustrating for managers and policymakers that this species, when fished to low population densities, recovers slowly or apparently not at all even after all fishing has ceased (13, 14). For example, after Atlantic cod stocks collapsed, both Canada and the United States closed large areas to fishing in the early 1990s. Fisheries managers expected full recovery within a decade but after nearly two decades cod stocks remain at historically low levels of abundance (15). Such protracted lags in population or ecosystem recovery often result from reinforcing ecological feedbacks (14).

Several different, but not mutually exclusive, feedback mechanisms reducing reproductive success or increasing mortality of eggs, larvae, or young of the year cod may interfere with or prevent the recovery of cod stocks. One theory gaining support in both the eastern and the western North Atlantic is predator–prey reversal between cod and forage fish. Forage fish examples include herring (15) or caplin (16) in the Atlantic and sprat in the Baltic (17). Large cod feed predominantly on forage fish but when cod are fished to low abundance, forage fish feed on cod eggs and/or larvae.

Reproductive efficiency of Atlantic cod could be compromised by the loss of spawning aggregations. Cod form spawning aggregations (similar to those known for tropical groupers and snapper). Such aggregations will result in higher fertilization success than that of a single pair mating in isolation. Numerous spawning aggregation sites along coastal Maine in the 1920s were targeted by fishers and eliminated over the next several decades (12, 18). Today there are no known spawning aggregation sites in coastal Maine despite low or zero fishing pressure in many regions over the past half century. Thus, local reproductive and population dynamics could be extremely important to the regional success of this species.

**The local cod stock colonization in the Gulf of Riga provides us with a clue to how cod populations proliferate.**

The local cod stock colonization in the Gulf of Riga (1) provides us with a clue to how cod populations proliferate. Although cod are broadly distributed throughout the North Atlantic, their population structure is effectively a mosaic of substocks or local stocks that complete their life cycle within a relatively small area. Cod tagging studies, genetics, and long-term fisheries independent monitoring indicate this species is a large-scale "metapopulation" composed of numerous loosely connected local stocks, each with its own birth, growth, and death characteristics (18, 19).

The influx of cod to the Gulf of Riga was due to a unique population increase and expansion from the Baltic's adjacent main basin. That increase resulted from favorable conditions and low fishing pressure, but importantly it resulted from an in-migration of juvenile and adult cod. These older cod thus escaped the mortality bottlenecks befalling those 1 y old and less by avoiding limiting feedback mechanisms such as the reverse predator–prey dynamics described above. As a result, the older recruits had no difficulty surviving and growing in the Gulf of Riga. Recruitment by older cod stands in stark contrast to the widely held concept that fish population expansion is driven by the early life sequences leading to recruitment (known as "The Recruitment Limitation Hypothesis," *sensu* ref. 20). Perhaps cod uniquely establish new local stocks as larger adults. If so, this colonization process needs to be considered by managers and policymakers. Perhaps local stocks at low but not dysfunctional reproductive levels should be allowed to recover enough not only to restore the depleted local stock but also to colonize adjacent areas where past stocks have been extirpated.

We learn from these recent studies that Atlantic cod can affect entire food webs in both the benthic and the pelagic realms. Not only are they strong interactors capable of limiting the abundance of their prey and their prey's prey (i.e., trophic cascade), but also the prey themselves may limit the recovery of this predator. In most countries where fisheries management exists, the focus is on the dynamics of single species and often there is no consideration of how two or more managed species interact or how such interactions can affect the entire ecosystem including affecting the turbidity and productivity of the water in the entire ecosystem. If managers or policymakers need an example of why ecosystem-based management is necessary, they need look no further than the Casini et al. study and the lessons we have learned from the serendipitous events they describe.


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