might, however, be a cheap and effective alternative to conventional pesticides for vector control, and one that could preserve the effective use of proven, life-saving, compounds, such as pyrethroids.

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Cascading effects of overfishing marine systems

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Profound indirect ecosystem effects of overfishing have been shown for coastal systems such as coral reefs and kelp forests. A new study from the ecosystem off the Canadian east coast now reveals that the elimination of large predatory fish can also cause marked cascading effects on the pelagic food web. Overall, the view emerges that, in a range of marine ecosystems, the effects of fisheries extend well beyond the collapse of fish exploited stocks.

Introduction

Although the role of fishing in the collapse of exploited stocks is beyond doubt, it has been less easy to determine whether there are indirect effects on other ecosystem components. Fish are the main predators in most marine systems and one would expect that removing them might have an impact on lower trophic levels. However, assessing the relative impact of predators has long been a difficult problem in ecology.

When do predators make a difference?

The classic dilemma is nicely illustrated by the account of the Italian scientist Lorenzo Camerano published in 1880 [1] explaining how naturalists in those days were divided in two categories. According to Camerano, the first category reasoned: 'Birds feed to a great extent on insects; so if we increase the numbers of birds, the number of insects will decrease'. This is what we now call top-down regulation. The second category had a 'bottom-up' perspective: 'the number of birds is high particularly in those places where insects are very abundant. The number of insects in a region depends essentially on the amount of food found in it. In general, birds have only a small role in destroying insects that might damage crops.'

The difficulty with bottom-up and top-down regulation is that they can both be strong at the same time and that

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their relative roles are not easily inferred from field patterns. Much of the variation in abundances that we see in nature is bottom-up regulated and marine systems are no exception. This is illustrated by a recent study [2] showing a strong correlation between chlorophyll concentration and fish yields along the American west coast. However, although this suggests that primary production largely determines what can be harvested from higher trophic levels, such empirical relationships cannot tell us much about the importance of top-down forces. For instance, correlations between nutrient richness and abundance at all trophic levels are commonly found in lakes [3]. Nonetheless, top-down effects are strong in these ecosystems [4]. This has been convincingly demonstrated by the experimental removal of fish from lakes, and has important management implications [5]. Lake managers have found that such 'biomanipulation' can boost large-bodied zooplankton, which then filters the water clear of excessive phytoplankton.

Given that we deplete many marine fish stocks so dramatically, could top-down forces in the oceans be strong enough to imply similar cascading effects? It has been shown that ecosystem effects of overfishing can be strong in coral reefs [6] and other coastal systems [7]. However, with the exception of the replacement of exploited stocks by competing species [8], evidence for indirect effects of overfishing in the open ocean has remained illusive. A recent analysis of historical data from the Scotian Shelf by Kenneth Frank and colleagues [9] changes this situation. The authors have now shown how effects of the decline of cod *Gadus morhua* and other large predators can cascade down the food web, through small fish, crab and shrimp, zooplankton and phytoplankton to the level of nutrients (Figure 1).

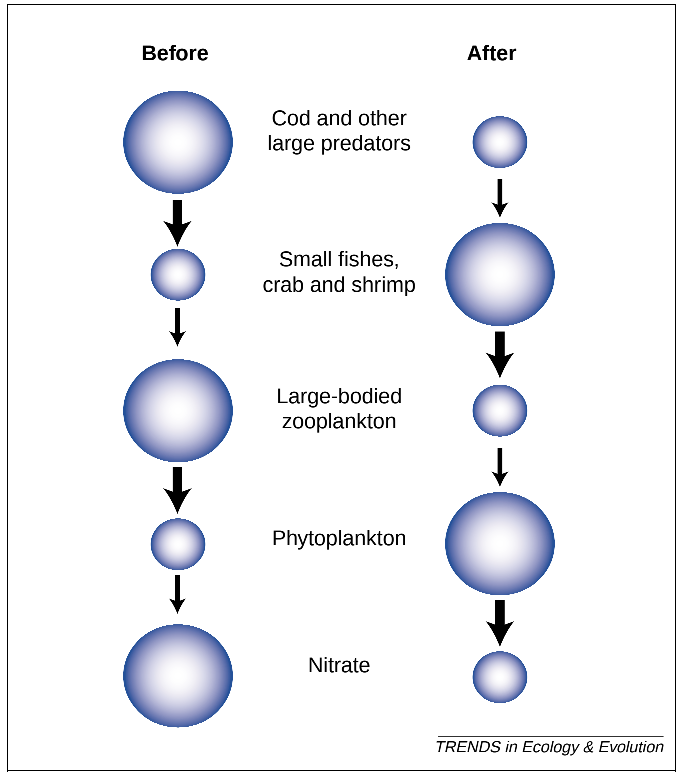

Figure 1. The cascading effect of the collapse of cod and other large predatory fishes on the Scotian Shelf ecosystem during the late 1980s and early 1990s. The size of the spheres represents the relative abundance of the corresponding trophic level. The arrows depict the inferred top-down effects.

Cascading effects of a Canadian cod collapse

The findings of Frank *et al.* are based on the analysis of a time series that shows a remarkable coincidence of changes in the Atlantic shelf ecosystem off the coast of Nova Scotia, Canada. During the late 1980s and early 1990s, numbers of cod and other large-bodied predators in the benthic fish community declined sharply. This appeared to result in the near elimination of the ecological role of this group in the ecosystem (i.e. as top predators). Indeed, the biomass of benthic invertebrates, such as the northern shrimp *Pandalus borealis* and the snow crab *Chionoecetes opilio*, and of small pelagic fishes increased markedly following the collapse of their former predators. The structure of the zooplankton community also changed in a way that is consistent with a top-down effect: large-bodied zooplankton species (>2 mm), which are the preferred food of pelagic planktivores and early stages of shrimp and crab, declined, whereas the abundance of small-bodied species remained unaltered. By contrast, phytoplankton has become more abundant, which is consistent with the effect of reduced grazing pressure by zooplankton. Finally, the concentration of one of the major limiting nutrients, nitrate, is now lower, suggesting that it is being depleted more strongly by the increased phytoplankton populations.

One might suggest that the observation of correlated changes can be a tricky basis for inferring causal links. Indeed, as Frank and colleagues show, there have been simultaneous changes in the ocean climate on the Scotian shelf. The water temperature close to the seabed declined steadily during the years preceding the crash of cod. Also, although these temperatures have returned to 'normal', stratification continued to intensify during the 1990s. It seems likely that these changes would also have influenced the biology of the system to some extent.

Clearly, experimental fish removal as is done in lakes, monitoring non-manipulated similar lakes as 'controls', is easier to interpret. But although the controlled experimental approach is convincing, it cannot be used to unravel the forces that drive vast open ecosystems such as the oceans. One alternative is to compare case studies in different places. Such a meta-analysis of cod–shrimp studies has revealed that an increase in benthic invertebrates, such as shrimp and crab, has occurred almost everywhere where cod stocks collapsed on both sides of the Atlantic under different climatic conditions [8]. Although Frank and colleagues were unable to compare case studies, the change in zooplankton size and the decrease in nitrate with increasing phytoplankton in their study do look very much like the 'smoking gun' of a top-down cascade.

Future questions

Unraveling the interplay of bottom-up and top-down forces will remain a major challenge in marine research over the coming years. Intensive fishing and ongoing climatic change imply that we are heavily modifying both forces, and good management should be based on an understanding of how this affects the ecosystem. The issue is a difficult one as there is much at stake and it is not easy to get the balance right. For instance, some have argued that fishermen should be 'let off the hook' because some stock collapses appear to be related to climatic changes [10], even though most scientists agree that overfishing is an overwhelmingly dominant force driving stock collapse [11]. Although the mechanisms that drive stock collapse can be difficult to unravel, the cascading effects shown by Frank *et al.* imply that we should look beyond the stock collapse itself. Their work also suggests two important questions for future research:

Where should we expect cascading effects of stock decline?

Do the findings of Frank *et al.* highlight an exceptional case or would similar cascading effects occur in other open ocean systems? It is important to keep in mind that fishing is already known to be a major driver of change in many coastal ecosystems [7]. A particularly striking example is the role of fishing in the collapse of Caribbean coral reef ecosystems [6,12]. Depletion of herbivorous fish left sea urchins as the only grazer to control macro algae. When a disease affected the sea urchins during the early 1980s, brown fleshy algae rapidly encrusted the reefs, replacing the corals and inducing radical change of the ecosystem at all levels.

When may marine ecosystem shifts be irreversible?

In both the Scotian shelf and the coral example, there are indications that the changes observed might not be easy to reverse. Although sea urchins have recolonized the Caribbean coral reefs in small numbers, the algae remain dominant. Similarly, the Scotian shelf system shows no signs of recovery despite the near-elimination of cod exploitation and the return to normal seawater temperatures. Although the question of reversibility remains open, the persistence of the new state is striking.

Conclusions

Overall, the observations on the Scotian shelf and the Caribbean reefs are in line with the emerging view that marine communities are characterized by strong non-linearities [13,14]. Such an ecosystem view [15] suggests that there is a need to look differently at management of marine ecosystems. It implies that sharp irreversible change can sometimes result from gradually increasing fishery pressure, and that the critical threshold for such change will vary with climatic conditions. Although the task of unraveling the functioning of ocean ecosystems is daunting, many will agree that a true ecosystem approach is needed if we want to predict, and eventually avoid, adverse shifts in marine communities.

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The darting game in snails and slugs

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Love darts are hard 'needles' that many snails and slugs use to pierce their partner during mating. In a few species, darts have been shown to play a role in sperm competition. Two new papers, by Davison *et al.*, and Koene and Schulenburg, might further pique researchers' interest, because they show how the full potential of

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