and oceanographic factors can intervene through effects on the magnitude and timing of primary production or on the distribution by winds and currents of larvae and their prey. A great advantage of an hypothesis of this kind is that it provides the basis for designing and interpreting empirical studies.

See also

Coral Reef and Other Tropical Fisheries. Crustacean Fisheries. Demersal Species Fisheries. Marine Fishery Resources, Global State of. Molluskan Fisheries. Open Ocean Fisheries for Deep Water Species. Open Ocean Fisheries for Large Pelagic Species. Salmon Fisheries: Atlantic. Salmon Fisheries: Pacific. Seabirds and Fisheries Interaction. Small Pelagic Species Fisheries. Southern Ocean Fisheries.

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FISHERIES

Multispecies Dynamics

J. S. Collie, Danish Institute for Fisheries Research, Charlottenlund, Denmark

doi:10.1006/rwos.2001.0456

Introduction

The abundance of marine fish populations is notoriously variable. Much attention has focused on year-to-year fluctuations in the abundance of young fish entering the fisheries (recruitment). Even larger amplitude fluctuations are apparent at timescales of tens to hundreds of years. The species in marine ecosystems have shared patterns of variability because they eat each other, compete for food and space and/or respond to shared variation in the ocean environment. This article examines temporal patterns in the abundances of commercially exploited species along with those of their predator and prey species. The dynamics of entire food webs are considered in other articles. The first part of this article illustrates some of the abundance patterns seen in marine fish communities. Next is a description of the tools available to fisheries ecologists to explain these temporal patterns. This is followed by detailed description of alternate hypotheses and the evidence in support of these hypotheses. The article ends with a general discussion of species interactions in marine fish communities and the implications of these interactions for the conservation and management of marine fishes.

Terminology

The term fish is used broadly here to include exploited invertebrates and marine mammal species. A guild is a group of species that share life-history characteristics and feeding habits. Demersal fishes live on or near the seafloor and feed primarily on benthic animals. Pelagic fishes live in the water column and depend on the planktonic food chain. A species' trophic level is determined by its feeding habits: piscivorous fish feed on forage fish which are themselves planktivorous. The trophic interactions among species in a community are competition and predation. Decadal variations in abundance occur on timescales of 10 to 100 years.

Patterns of Variability in Exploited Fish Communities

Doctor Umberto D'Ancona collected statistics on the fisheries of the Upper Adriatic Sea before, during, and after World War I. Having noticed that the proportion of predators to forage fish in the catches increased following the war, he interested his mathematician father-in-law, Vito Volterra, in studying this phenomenon. They reasoned that the reduction in commercial fishing during the war altered the balance between predator and prey species, allowing the predators to multiply at the expense of their prey. Volterra realized that, although the fish populations are influenced by external forces of periodic nature, there are other intrinsic processes which add their action to the external influences. These observations spurred Volterra to construct mathematic models of interacting species, which included competition, predation, and a carnivore–herbivore–plant food chain.

In many fish communities there have been replacements of one species by another or replacements of one guild by another. In the four eastern boundary current ecosystems, dominance has alternated between a sardine and anchovy species with a period of 40–50 years. Concomitant shifts are also seen in the plankton and in the piscivorous fish species that live in these upwelling systems. From the analysis of fish scales in sediment cores, it is known that these fluctuations occurred before the advent of modern fisheries. Species replacements have also occurred in pelagic communities on the western boundaries of the ocean basins. For example, there have been large-amplitude fluctuations in the catch of Japanese sardine during the past 400 years. During the last century, dominance has alternated between the Pacific sardine and two species groups, one containing anchovy, horse mackerels and Pacific saury, and the other, chub and spotted mackerel (**Figure 1**).

Replacements also occur at the community level between demersal and pelagic fishes. In one regime, much of the primary production is utilized by the benthic community, supporting large populations of demersal fish. In the other regime, a greater proportion of the productivity is consumed in the pelagic zone and the fish community is dominated by pelagic species. Such demersal–pelagic shifts appear to have occurred on Georges Bank, in the North Sea, the Baltic Sea, and off Ivory Coast. On Georges Bank, in the north-west Atlantic, the principal demersal species (cod, haddock, flounder) declined from 1964 to 1993 and were replaced by elasmobranchs (dogfish and skates) and pelagics (herring and mackerel); this pattern seems to be reversing as of the late 1990s (**Figure 2**). The fish community of the Baltic Sea is dominated by three species: one demersal (cod) and two pelagics (herring and sprat). Sprat biomass increased markedly in the late 1980s following the reduction of cod biomass (**Figure 3**).

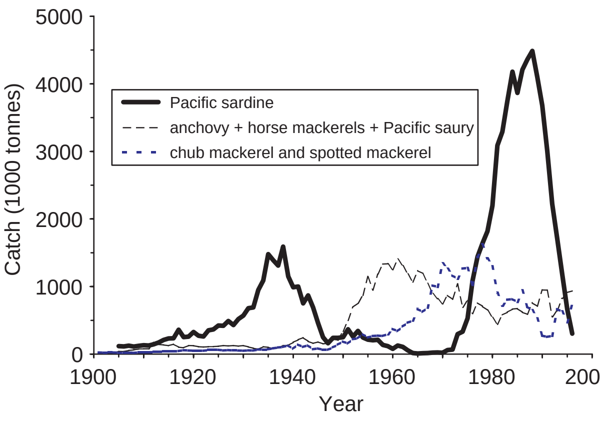

Figure 1 Catches of pelagic fishes off the Japan coast. Adapted with permission from data from Hiroyuki Matsuda (Ocean Research Institute, University of Tokyo).

The patterns illustrated in the preceding **Figures 1**, **2** and **3** represent the types of fluctuations that fisheries ecologists seek to explain. By taking a multispecies perspective, one may see patterns in the abundances that would be missed if each species were studied in isolation: a case of trying to see the whole forest and not just the trees. Patterns of shared variation may give clues to the causes of these fluctuations. The job of explaining fish population dynamics is greatly complicated by the fact that we seldom directly observe fish populations and, instead, must reconstruct their abundance from catch data. Fisheries scientists have been likened to ecological detectives who sift through all the available data to reconstruct the most likely causes of the observed fluctuations.

Tools for Quantifying the Interactions Among Marine Fish Species

Feeding interactions in marine fish communities are determined by diet analysis, in other words by carefully examining the stomach contents of thousands of fish. The degree of diet overlap between species is a measure of potential competition. The rate of food consumption can be estimated either directly by measuring the rate of evacuation of a meal of known size or indirectly with bioenergetic calculations. By combining the food consumption rate with the diet composition, one can estimate the amount of each prey species consumed. Finally, by dividing the amount of each prey species consumed by the biomass of that prey species, predation mortality can be estimated and compared to other sources of mortality such as fishing.

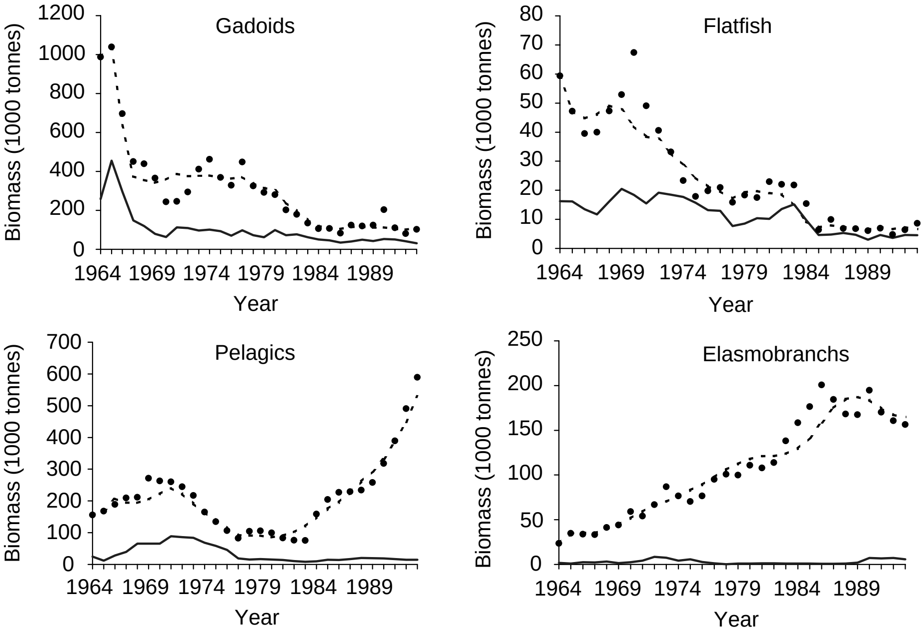

Figure 2 Biomass of species groups on Georges Bank in the north-west Atlantic. The species groups are gadoids (cod, haddock, silver hake), flatfish (yellowtail flounder, winter flounder), pelagics (herring, mackerel), and elasmobranchs (spiny dogfish, winter skate, little skate). The points (●) are the observed biomasses of age two and older fish. The broken lines are biomass estimates from a multispecies production model. The solid lines are the catch in weight. (Adapted with permission from Collie and Delong (1999). In: *Ecosystem Approaches for Fisheries Management.*)

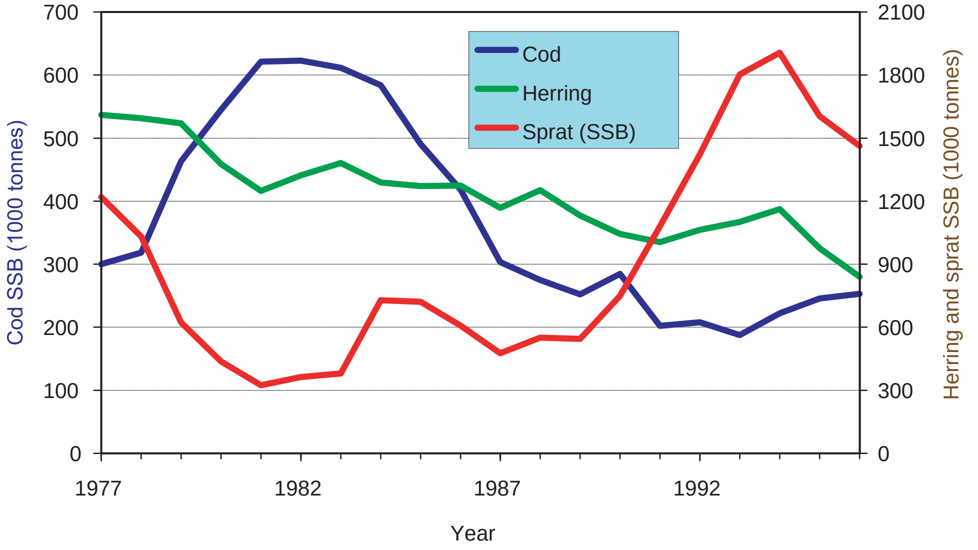

Figure 3 Spawning stock biomasses of cod, herring, and sprat in the Baltic Sea. (Adapted with permission from Gislason H (1999) Single and multispecies reference points for Baltic fish stocks. *ICES Journal of Marine Science* 56: 571–583.)

Multispecies models are used to describe the fluctuations in fish populations while accounting for the interactions among species. The main categories of multispecies models can be distinguished by two important features. One main distinction is between models that encompass the entire food web (e.g. dynamic energy budget models) and those that concentrate only on the fish community. A second distinction is whether the model incorporates the age structure of each species or just describes the total biomass of a species. Multispecies production models are an example of the latter approach. These models have extended the classic Lotka–Volterra equations by incorporating density dependence, fishery removals, and alternative forms of the predator functional response. Multispecies virtual population analysis (MSVPA) is an example of an age-structured multispecies model. MSVPA is used to reconstruct the abundance by age of each fish species while estimating predation mortality from the consumption rates and diet composition. Multispecies models are needed to predict what the future abundance of interacting species might be given differing numbers of predators and prey, and given differing levels of fishing.

Energy budgets trace the flow of energy (or the equivalent units of carbon) through the food web. Fish production is ultimately limited by primary production. The construction of energy budgets for many marine ecosystems has shown that most energy budgets are tightly coupled. After allowing for energy losses at each trophic level (ecological efficiency), there is little excess production that cannot be accounted for by consumption at higher trophic levels. From the tight coupling and variability of these food webs we infer that change in one component of the food web can affect the other components. Species at one trophic level compete to consume the production of lower trophic levels if that production is limited. The abundance of forage fish may limit the growth rates of the predator species that feed on them. Conversely, the rate at which predators consume forage species can limit the overall production of these smaller fish (**Figure 4**). This coupling implies negative feedback within the fish community, which should act to stabilize total biomass.

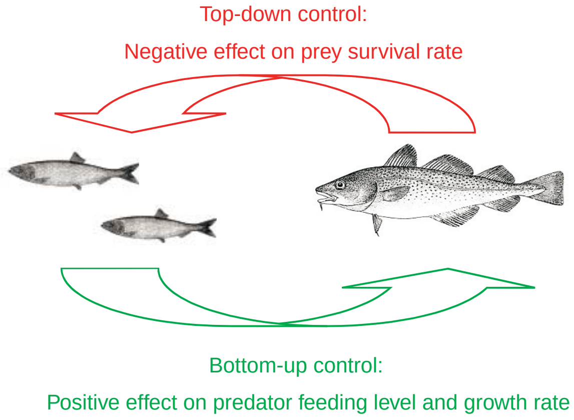

Figure 4 Trophic interactions between predator and prey species, in this example cod feeding on herring.

Another important observation from marine food webs is that most of the production of younger fish is consumed by bigger fish: the mass of fish consumed by fish generally exceeds the amount consumed by seabirds, marine mammals or captured in fisheries. Predation of fish by fish is therefore important for the dynamics of individual fish populations. Energy budgets are generally calculated for equilibrium conditions such that the energy flows are in balance. However, one can easily imagine that energy flow will vary from year-to-year since primary production is not constant. An energy budget can be transformed to a dynamic ecosystem model by specifying the rates of change of each species or guild.

To test the strength of the trophic interactions among fish species one would ideally like to manipulate the abundances of predator and prey species. Such experiments have been conducted in small lakes but are impractical for marine populations, which are open and not subject to direct human control. Area closures, such as the experiments conducted on the north-west Australian shelf, provide a means of experimenting with marine fish populations. To study marine populations, we generally rely on observations and seek informative comparisons between fish communities under different oceanographic conditions and harvest levels. Marine fisheries, overall, can be considered as a sort of unplanned experiment. High levels of fishing mortality perturb marine fish communities, altering the relative abundance of predator and prey species. By studying what happens in response to these perturbations, it is possible to learn about the interactions among species.

Hypotheses and Evidence for Multispecies Interactions

The ocean environment is characterized by high levels of variability at decadal timescales. Marine fish cannot insulate themselves from these changes and hence are adapted to living in a changing environment. Species replacements may occur because the different species are adapted to live under different environmental conditions. As the ocean environment changes, one species may be better able to survive than another. For example, sardine (or pilchard) populations dominate coastal upwelling regions during warm periods when upwelling is less intense. During warm periods, sardine populations expand their range both offshore and toward the poles. Sardine larvae grow more quickly than anchovy larvae and reach metamorphosis at a younger age. Anchovy populations thrive during cooler regimes with intermittent periods of intense upwelling. The reciprocal replacements of anchovies by sardines seem to be in phase in all the major upwelling regions, suggesting that they are driven by global fluctuations in the ocean environment.

Bottom-up Control

How do changes in the ocean environment affect the productivity of marine fish? Apart from the obvious effects of temperature on metabolic rates, it is most likely that changes in the ocean environment manifest themselves through the food web. According to the hypothesis of bottom-up control, productivity at higher trophic levels is limited by primary production. Just as a rising tide floats all boats, one would expect an increase in primary production to benefit all the species that rely on this production. We might expect to find the best evidence for bottom-up control in ecosystems with seasonal production and relatively simple food chains, such as boreal and upwelling ecosystems. In the North Sea there have been parallel changes in abundance of phytoplankton, zooplankton, herring, and seabirds, which can be interpreted as bottom-up control of the pelagic food chain. During the gadoid outburst in the North Sea, recruitment of five demersal species – cod, haddock, whiting, saithe, and Norway pout – increased by a factor of 4 or 5 between the early and late 1960s. The gadoid outburst has been interpreted as bottom-up control of recruitment by zooplankton abundance and availability. Though the gadoid outburst ended in the 1980s, debate continues on the cause of this phenomenon.

Given that primary production limits production at higher trophic levels, species replacements may be caused by competition for limiting resources. According to accepted ecological methods, for species to compete, they must use the same resource, which must be in limiting supply. Removal of one species should result in increased use of the resource by the other species. Because of the difficulty of manipulating marine fish populations it has been very difficult to demonstrate competition, except for some sedentary species such as reef fishes. For many fish species that are mobile and differ in their feeding preferences, opportunities for interference competition are few. However, the species may still compete if one species eats food that the other species would have eaten. The limited energy in a food web may be channeled to one species or another, and this partitioning process can be considered exploitative competition.

For example, sardines and anchovies have a broad diet overlap and may potentially compete. The Japanese sardine fluctuations (**Figure 1**) have been explained with a cyclic advantage hypothesis. A mathematical model of this hypothesis, which incorporates competition between the sardines and the other species groups, is able to reproduce the sequential replacement of the species groups. The replacement of the gadoids on Georges Bank by elasmobranches can also be interpreted as competition

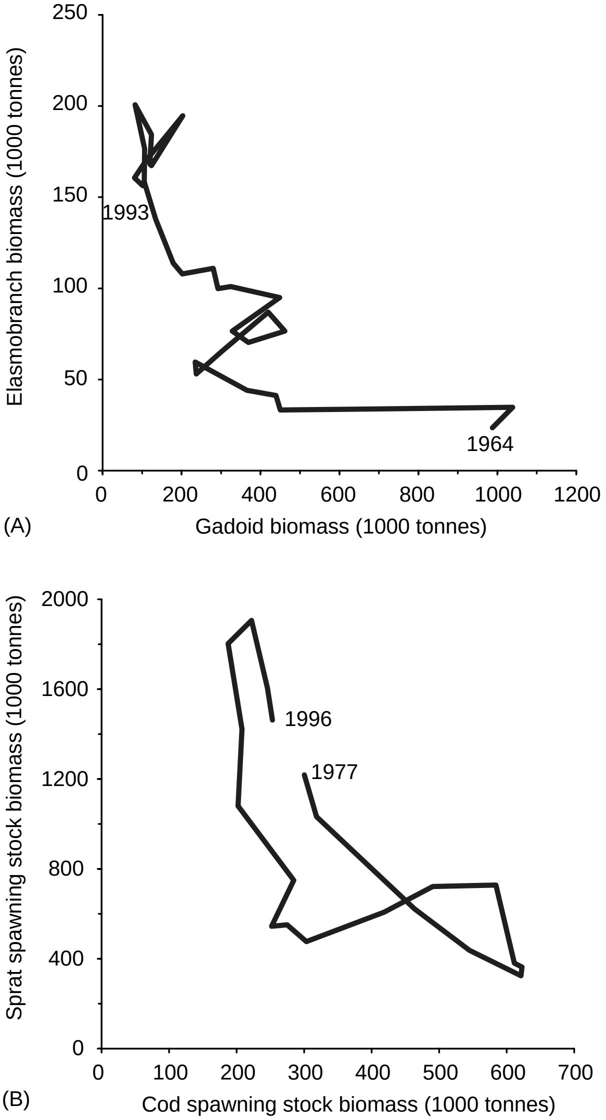

Figure 5 Phase-space plots. (A) Elasmobranch and gadoid biomass on Georges Bank. The species groups are defined as in **Figure 2**. Adapted from Collie and DeLong (1999). (B) Cod and sprat spawning stock biomass in the Baltic Sea. (Adapted with permission from Gislason (1999) Single and multispecies reference points for Baltic fish stocks. *ICES Journal of Marine Science* 56: 571–583.)

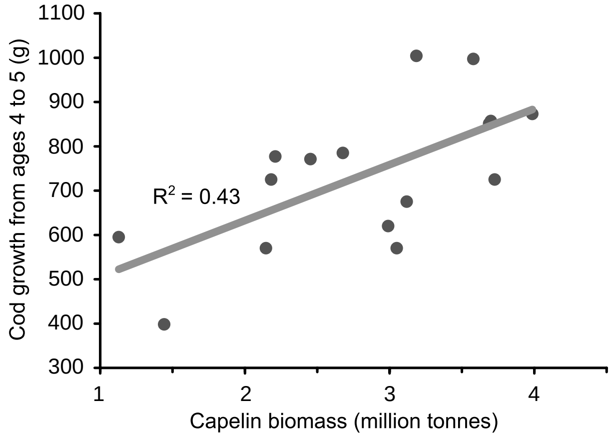

Figure 6 Growth of Icelandic cod in relation to capelin biomass. Cod growth is the increment in mean weight between ages 4 and 5. Capelin biomass is measured with hydroacoustic surveys. The line is the linear regression. (Adapted with permission from Stefánsson *et al.* (1998) *ICES Journal of Marine Science* 55: 859–862.)

between the species groups. The abundance of the two species groups is inversely related in phase space (**Figure 5A**), and reciprocal negative interaction terms were estimated between these groups in a multispecies model. As there is little predation between the gadoids and elasmobranches, the negative interaction terms support the competition hypothesis. An alternative hypothesis is that the different species groups simply respond differently to varying oceanographic conditions. However, this simplistic explanation begs the question of what changes in the environment caused the dramatic fluctuations and whether these changes occurred in the food web.

The bottom-up hypothesis implies that prey density limits the feeding rate, growth and production of predators. The best evidence of this limitation is shifts in the mean size at age of predator species in response to changing prey abundance. For example, the growth rate of Icelandic cod was significantly related to the biomass of capelin, one of its primary prey species (**Figure 6**). Faster-growing cod mature at a younger age and larger females produce more eggs; hence faster growth rates should translate to higher per capita fecundity. However, care must be taken when interpreting size-at-age data because growth rates are influenced by factors in addition to food availability, such as temperature.

Top-down Control

According to the hypothesis of top-down control, the abundance of marine fish populations is controlled by predation from top predators. Predation is easier to demonstrate than competition because evidence of it can be found in the predators' stomachs. However, to demonstrate that predation regulates production at lower trophic levels requires more than the simple observation that big fish eat smaller ones. Firstly, the predation rates must be high enough to account for the observed changes of prey abundance. Predation is certainly the main cause of death, especially for young fish. High levels of predation have been estimated for age-0 and age-1 fish with multispecies models such as MSVPA. For Georges Bank haddock and Baltic Sea cod, about 60% of the age-0 fish and 20% of the age-1 fish are eaten by other fish each year. These high predation mortality rates support the hypothesis of top-down control by predators.

As further evidence for the predation hypothesis, we would expect predator and prey populations to vary in phase with a time lag. When viewed in predator–prey phase space (**Figure 5B**), a clockwise trajectory is expected; the prey increase when predator abundance is low and vice versa. In the Baltic example, when cod abundance was reduced by fishing, sprat biomass increased due to lower predation mortality. Predation mortality of sprat, as estimated with MSVPA, is linearly related to cod biomass (**Figure 7**). In the Georges Bank example, the predation hypothesis is supported by the feeding habits of cod and silver hake, predation mortalities estimated with MSVPA and the interaction terms estimated with a multispecies production model. The interaction term was negative for the pelagics and

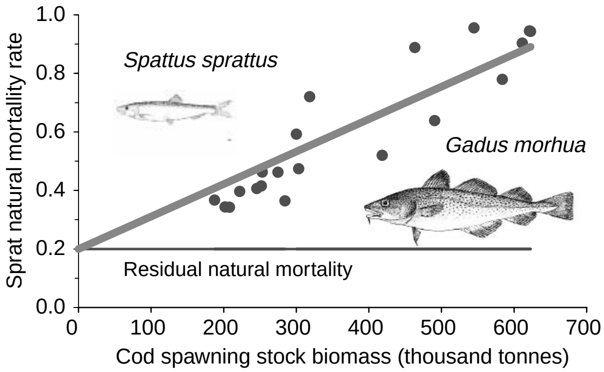

Figure 7 The natural mortality rate of Baltic Sea sprat depends on the abundance of its main predator, cod. Natural mortality rate was estimated with Multispecies Virtual Population Analysis. (Adapted with permission from Gislason H (1999) Single and multispecies reference points for Baltic fish stocks. *ICES Journal of Marine Science* 56: 571–583.)

positive for the gadoids, which is consistent with predation on the pelagics by gadoids. There are several other examples of predator–prey interactions with cod as the predator and herring, sprat, or capelin as prey.

The top-down control hypothesis emphasizes the role of predation in structuring fish communities. In closed ecosystems, such as lakes, removal of the top predators can have indirect effects on the lower trophic levels. For example, piscivores (e.g., pike, walleye) can control the abundance of planktivorous forage fish (e.g., sunfish). With low predation, the zooplankton flourish and are able to crop the phytoplankton. When the top predators are fished out, planktivorous fish can increase and crop the zooplankton. With reduced grazing pressure, phytoplankton proliferate and may cause blooms, resulting in reduced water clarity. This mechanism, known as a trophic cascade, has been demonstrated with elegant experiments on whole lakes. A classic example of a trophic cascade involves the sea otters on the west coast of North America. Sea otters eat sea urchins, which graze on kelp. Harvesting the sea otters for their fur apparently allowed the sea urchins to proliferate and to graze down the kelp beds. Trophic cascades are less likely to occur in pelagic communities where trophic responses are attenuated by dispersal and the complexity of marine food webs.

In many boreal and upwelling ecosystems, the middle of the food web is dominated by one or two species of planktivorous fish. Such food webs are said to have ‘waists’ because there are more species at lower and higher trophic levels than in the middle. For example, walleye pollock is the dominant forage species in the Bering Sea and capelin is the dominant planktivore in the North Atlantic. In coastal upwelling systems, the waist position is occupied by anchovies or sardines. Most of the energy in the food web is filtered through these planktivorous species because there are few alternative pathways. The waist species therefore occupy a very important trophic position and can exert both bottom-up control of their predators and top-down control on the zooplankton.

Given the trophic linkages that exist in marine food webs, we should expect harvesting one component of the food web to have indirect effects on the interacting species. In simple two-species, predator–prey systems (e.g., Vito Volterra’s equations) it has been shown that harvesting the predator benefits the prey and conversely, that harvesting the prey limits predator production. In the Southern Ocean, the depletion of the baleen whales is thought to have created a ‘surplus’ of krill. In the Georges Bank ecosystem harvesting the pelagic species in the 1960s and 1970s may have reduced the prey available to the gadoid predators. However, in the Southern Ocean there are other predators (penguins, seals) to consume the ‘surplus’ krill, and on Georges Bank there are other prey species to feed the gadoids. Provided that the trophic interactions can be quantified, multispecies models can be used to predict the indirect effects of fishing. However, the outcomes or predictions of these models can be very sensitive to the assumptions made in their formulation. We do expect fishing to have indirect effects on the food web but it will always be easier to rationalize past patterns than to predict the consequences of future fishing activities.

Discussion

The hypotheses concerning the regulation of multispecies fish communities are not mutually exclusive. Therefore, as ecological detectives, we should not expect to definitively disprove any of the hypotheses and emerge with a single explanation of the observed population patterns. Instead we should evaluate the relative credibility of the alternative explanations.

The major fluctuations in population abundance occur on timescales of 20–40 years. These timescales are more than twice the generation spans of most fish species; hence it is likely that the fluctuations are environmentally driven. However, simply attributing the fluctuations to environmental variability just pushes the explanation up or down one level in the food chain. A full explanation requires understanding how ocean variability affects marine food webs.

Plotting the abundance of interacting species in phase space helps to distinguish the mechanisms of interaction. In the prey–predator example (**Figure 5B**), a clockwise trajectory is expected, not the opposite. Observational data alone are insufficient for demonstrating the mechanisms of interaction. The magnitude of the interaction needs to be measured with diet studies and multispecies population models.

Generalizations can be made about the strength of species interactions in different types of ecosystems. Boreal fish communities are characterized by having a small number of species with strong interactions. Large fluctuations in abundance of forage species (e.g., capelin) may be caused both by bottom-up control and by predation mortality. Prey limitation of predator growth rates is apparent in boreal fish communities. Upwelling systems have several features in common with boreal fish communities. Production is highly seasonal and bottom-up control of the forage fish may be apparent. Upwelling and boreal food webs both have 'narrow waists' such that much of the productivity is filtered through a small number of forage fish species with large numbers of individuals.

In contrast, temperate food webs have a larger number of species with weaker levels of interaction. The predators are opportunistic and may feed at more than one trophic level. The interactions may become more apparent when species are aggregated into trophic guilds. Within the guilds, individual species may be interchangeable in their trophic roles. Temperate fish communities have less pronounced seasonal cycles, and bottom-up control of fish production is less evident than in boreal communities. Tropical fish communities are subject to even less seasonality and are even more species rich. Some degree of species aggregation is necessary for fitting multispecies population models. Habitat features are particularly important for structuring tropical fish communities. For example, on the north-west Australian shelf, composition of the demersal fish community is most strongly associated with the density of large epibenthos – sponges and gorgonian corals.

What are the implications of multispecies dynamics for the management and conservation of marine fish populations? The main conclusion is that there are trade-offs in the harvests of interacting species. In upwelling systems there may be large fisheries for anchovies or for sardines but not both simultaneously. The fisheries and fishery managers need to respond at the same timescales as the changes in the ocean environment that cause the population fluctuations.

The trade-offs in yield are influenced by the relative fishing pressure on interacting species. Even gradual changes in fishing effort can interact with ocean variability to cause rapid shifts in species dominance. Whether we are concerned with safe levels of harvesting or with maximizing the yield, fishing rates of predators and prey must depend on the abundance of the other species. The trade-off inherent in predator–prey complexes is whether to harvest a lower volume of the higher valued predator (e.g., cod) or a higher volume of the lower valued prey. Economically, the prey species may be more valuable as prey for the high-value predators. However, as the top predator populations have been depleted, fisheries have switched to harvesting prey species such as squid, sand lance and sprat. Industrial fisheries for forage fish can compete directly with piscivorous fish, seabirds and marine mammals. This global trend of 'fishing down the food web' may hinder efforts to rebuild stocks of depleted predator species.

See also

Coral Reef and Other Tropical Fisheries. Crustacean Fisheries. Demersal Species Fisheries. Marine Fishery Resources, Global State of. Molluskan Fisheries. Open Ocean Fisheries for Deep Water Species. Open Ocean Fisheries for Large Pelagic Species. Salmon Fisheries: Atlantic. Salmon Fisheries: Pacific. Seabirds and Fisheries Interaction. Small Pelagic Species Fisheries. Southern Ocean Fisheries.

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FISHERIES OVERVIEW

M. J. Fogarty, NOAA, Woods Hole, MA, USA

doi:10.1006/rwos.2001.0444

Introduction

The long-standing importance of fishing as a human enterprise can be traced through the diversity of