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Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems

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In upwelling ecosystems, there is often a crucial intermediate trophic level, occupied by small, plankton-feeding pelagic fish dominated by one or a few schooling species. Their massive populations may vary radically in size under intensive exploitation. We have used decadal-scale time series to explore patterns of interactions between these fish, their prey, and their predators so as to quantify functional roles of small pelagic fish in those ecosystems. Top-down control of zooplankton is detected off South Africa, Ghana, Japan, and in the Black Sea. Conversely, bottom-up control of predators, such as predatory fish and marine birds, is observed in the Benguela, Guinea, and Humboldt currents. Thus small pelagic fish exert a major control on the trophic dynamics of upwelling ecosystems and constitute midtrophic-level "wasp-waist" populations. Ecosystem effects of fishing are addressed by considering potential structural changes at different scales of observation, ranging from individuals, via school dynamics, to food webs. The overall impact is explored using a trophic model (Ecosim) given different types of food web control. Ecosystem dynamics can be entirely different depending on how the food web is controlled (bottom-up, top-down or wasp-waist). The threat of eroding intra-specific diversity is emphasized because it may lead to a long-term decline in the productivity of the pelagic fish resources. School composition is shown to reflect the relative species abundance within the pelagic community and functions as a "school trap" that could maintain a collapsed population in a depleted state for lengthy periods, and affect spatial dynamics such as migrations. As a result, overfishing can alter the abundance, composition, and distribution in pelagic communities, and may induce drastic changes of state. Predation on zooplankton by the jack mackerel (*Trachurus symmetricus murphyi*) population in the South Pacific provides an example of the alteration of matter fluxes in trophic webs caused by fishery removals. In conclusion, it is doubtful that pelagic fisheries will continue to increase without major disruptions to ecosystems.

Key words: dominant fish species, eastern boundary currents, ecosystems, effects of fishing, food web, marine birds, pelagic fisheries, plankton, predator-prey relationships, schooling behaviour, small pelagic fish, trophic models.

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Introduction

Many marine ecosystems typically contain a large number of species at the lower (e.g. planktonic) trophic levels. They also contain a substantial number of predatory fish, seabirds, or marine mammals that feed at the upper apex and near-apex trophic levels. However, in many of the highly productive ecosystems of the world, and particularly in upwelling regions, there tends to be a crucial intermediate trophic level occupied by small, plankton-feeding pelagic fish that is typically dominated by only one, or at most a few, species (Bakun, 1996). For example, in South Africa's marine fauna, which is particularly rich and well documented, the three phyla Mollusca, Crustacea, and Chordata are represented by 3062, 2333, and 2492 species, respectively (Gibbons *et al.*, 1999). Among the 2000 marine fish species recorded, about 70% are demersal, benthic, or reef species; in contrast, only 6.1% large and 3.7% small pelagic fish species are found (Fig. 1). Species diversity is relatively high at the bottom of the food chain (e.g. 429 copepods, 2262 gastropods) and at its top (92 species of marine birds and 41 species of marine mammals). This "wasp-waist" richness pattern appears to be a common characteristic of upwelling systems as well as of many other types of marine ecosystems.

The contribution of pelagic fisheries to the total marine fish catch has ranged from about 50% in 1950 to over 64% in 1994. Just six species (anchoveta, Atlantic herring, Japanese and South American pilchard, chub mackerel, capelin, and Chilean jack mackerel) among the 186 pelagic species exploited (FAO, 1997a) represent about half of the catch. These small pelagic fish are mainly planktivorous (Blaxter and Hunter, 1982) and are themselves an important source of food for predators (Anon., 1997). Schooling behaviour is a salient characteristic. A large biomass of small fish implies huge numbers of individuals and consequently a high level of intra-specific genetic diversity (Ryman *et al.*, 1995). Thus, the pelagic domain is a distinctive one, characterized by a crucial intermediate trophic level occupied by small pelagic fish whose behaviour, life-history traits, and dynamics differ in many ways from those of other species. It is reasonable to expect such differences to play an important role in the functioning of ecosystems.

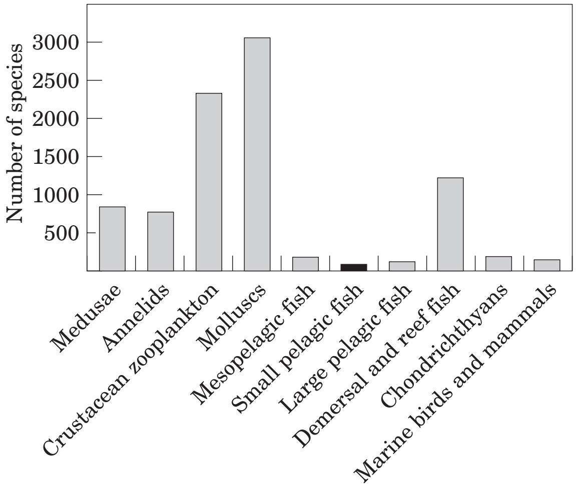


Figure 1. Species diversity for different fauna groups off South Africa (after Gibbons *et al.* (1999) and Fishbase (1997)).

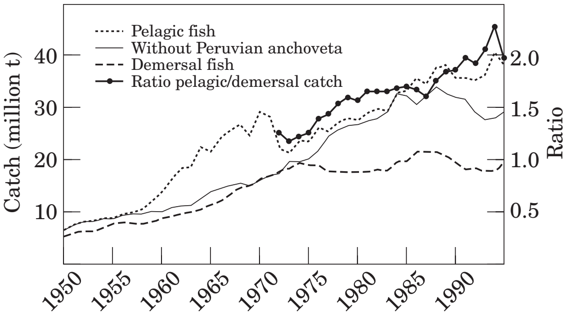


Figure 2. World annual pelagic (with and without Peruvian anchoveta) and demersal marine fish catch from 1950 to 1995 (FAO, 1997b), and ratio between pelagic and demersal catches.

Twenty years ago, in view of the overexploitation of many conventional fish stocks and the growing interest in harvesting new kinds of food from the sea, May *et al.* (1979) stressed the need for fisheries managers to take account of interactions among species. This appears even more important today because of the sustained increasing trend in the catches of pelagic fish since the 1950s (Fig. 2). Although the continued existence of these intensively exploited resources may not yet be threatened, collapses of major populations may affect the biological structure of the community or ecosystem (Beverton, 1990). In upwelling systems, patterns of interaction between pelagic fish and other organisms have received little attention, because scientists have focused more on the effect of the environment on fish population dynamics. How does the removal of millions of tonnes of pelagic fish affect the functioning of ecosystems? What are the effects of pelagic fish collapse on the other species? What are the implications of each removal or collapse for predators, as well as for prey species? What structural changes can be expected in the community or the ecosystem? These are the types of questions we address here.

Patterns of instability and change in pelagic fish populations

A central scientific question for ecosystem management is whether the effects of harvesting or changes in the physical environment are responsible for major changes in fish abundance (Larkin, 1996). This is particularly important when considering small pelagic fish, because population crashes and sudden recoveries have been observed in almost all of the world's pelagic fisheries (Durand *et al*., 1998; Schwartzlose *et al*., 1999). Pelagic fish stocks have been studied intensively, and, since the classic work of Hjort (1914), environmental factors are recognized as a determinant of recruitment success. Food availability (Cushing, 1996) and physical processes (Bakun, 1996) exert a significant role on larval survival, which determines subsequent fish abundance (Cury and Roy, 1989). Records of scale deposition from anaerobic sediments show that large-amplitude fluctuations occurred even in the absence of any fishery (Baumgartner *et al*., 1992). Moreover, an emerging pattern of decadal-scale variation in pelagic fish populations has exhibited a substantial degree of global synchrony (Crawford *et al*., 1991) that is believed to be driven by global climatic teleconnections (Klyashtorin, 1997). However, reviewing the collapse of 10 major fisheries on small pelagic species, Beverton (1990) concluded that fishing was the main cause of collapse in most, but not all, cases. Therefore, the impact of fisheries on pelagic resources remains controversial. Another perspective has been added recently. Using two-species competition models, Ferrière and Cazelles (1999) showed that phases of extremely low abundance followed by short peaks in abundance could arise in a simple community model as a result of competitive interactions within and between species. This reinforces the importance of considering pelagic fish interactions.

Competition

The fish biomass of upwelling systems tends to be dominated by one species of sardine (or sardinella) and one species of anchovy, and most often only one of the two is dominant at any particular time. Alternating patterns of abundance between these species have been observed in most upwelling ecosystems during recent decades (Bakun, 1998). The mechanisms that are generally invoked in direct competition are not completely satisfactory in explaining replacement. Sardine and anchovy usually do not occupy the same space (sardine are usually found farther offshore) and do not eat the same type of food (e.g. Van der Lingen, 1994). Skud (1982) concluded that dominant species respond to environmental factors, and subordinate species respond to the abundance of the dominant one. Thus, from an ecosystem perspective, climatic factors are thought to affect fluctuations in abundance of a species, whereas its absolute density is rather controlled by intra-specific competition (Serra *et al*., 1998). These multi-year patterns of alternation are important for long-term management, because exploitation reduces the biomass of the target (usually the dominant) species and sometimes precipitates its collapse. Within a pelagic community, the removal of the dominant species should favour the subordinate species, provided that the latter is only lightly exploited.

Top predators

Patterns that relate the abundance of two interacting populations are more numerous in theoretical ecology than in the real world (Bascompte and Solé, 1998). In predator-prey systems, it is difficult to establish any clear links particularly when several prey and predator species are involved (May *et al*., 1979). Small pelagic fish function as forage fish in marine systems (Anon., 1997), representing an important food resource for numerous top predators such as large pelagic fish, demersal fish and marine birds and mammals. In the four major eastern boundary current (Canary, Benguela, California, and Humboldt) ecosystems, natural mortality of small pelagic fish (1.1–2.1 year^{-1}) is much higher than fishing mortality (0.1–0.7 year^{-1}; Jarre-Teichmann and Christensen, 1998). For example, almost 55% of all small pelagic fish in the Benguela Current region are eaten by top predators. Comparing trophic flows in these four large upwelling systems and for four pelagic species, these authors found that large pelagic fish were the strongest predator group in 31%, fisheries in 27%, demersal fish in 23%, and marine mammals and birds in 19% of cases. These values emphasize the relative importance of predation versus removal by fisheries.

A succession in the abundance of five fish species – sardine (*Sardinops sagax*), horse mackerel (*Trachurus symmetricus*), bonito (*Sarda chiliensis*), anchovy (*Engraulis mordax*), and chub mackerel (*Scomber japonicus*) – have been observed off California during recent decades (MacCall, 1996). The peaks in abundance of the more predatory species (bonito, chub mackerel) follow those of the planktivorous sardine, horse mackerel, and anchovy. Similarly, off South Africa, mackerel peaked after horse mackerel and sardine became plentiful (Crawford *et al*., 1987). Thus, predatory fish may undergo large changes in abundance owing to natural fluctuations in the availability of forage fish. Predators may also influence the size of the populations on which they prey. For example, an increased mortality rate of anchovy owing to predation by chub mackerel was considered a likely cause of a severe reduction in anchovy biomass off California (MacCall *et al*., 1985). Off South Africa, low predation on anchovy by snoek (*Thyrsites atun*) during 1969–1972 was followed by an increase in the anchovy resource (Crawford and de Villiers, 1985). Dramatic impacts on predatory fish have followed collapses of forage resources. After the Chilean anchoveta (*Engraulis ringens*) population collapsed in 1973, the snoek

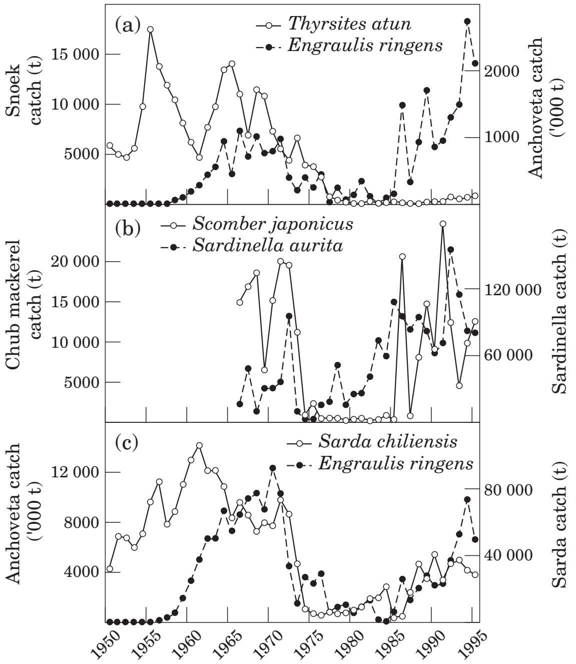


Figure 3. Annual catches of fish predators and their prey: (a) *Thyrsites atun* (predator) and *Engraulis ringens* (prey) in Chile, 1950–1995 (FAO, 1997b); (b) *Scomber japonicus* (predator) and *Sardinella aurita* (prey) in Côte d'Ivoire and Ghana, 1966–1993 (data source CROA and MFRD); and (c) *Sarda chiliensis* (predator) and *E. ringens* (prey) in Peru, 1950–1995 (FAO, 1997b).

collapsed 4 years later; the prey recovered in 1986 but the catch of snoek remained very low (Fig. 3a). In the Gulf of Guinea, large fluctuations of the local *Sardinella aurita* population have been related to major environmental fluctuations between the 1960s and the 1990s (Pezennec and Koranteng, 1998). Chub mackerel is found temporally and spatially in the same area as sardinella and feeds on juveniles as well as on their larvae. After the collapse of the sardinella stock in 1973, the chub mackerel stock collapsed 2 years later, suggesting cause and effect (Fig. 3b). Despite the recovery of sardinella in 1976, chub mackerel apparently experienced difficulty in recovering from its depleted state and did not rebound until 10 years later. In Peru, bonito (*sarda chiliensis*) appears to have a modest impact on the anchoveta, their main prey (Pauly *et al.*, 1987). However, the opposite was not true: 1 year after anchoveta collapsed, bonito did, too; bonito re-appeared with the outburst of anchoveta in the mid-1980s (Fig. 3c). These examples illustrate that predatory fish suffer from the collapse of their prey. Once food again becomes abundant, their recovery may be almost immediate, or markedly delayed, highlighting the complex interactions.

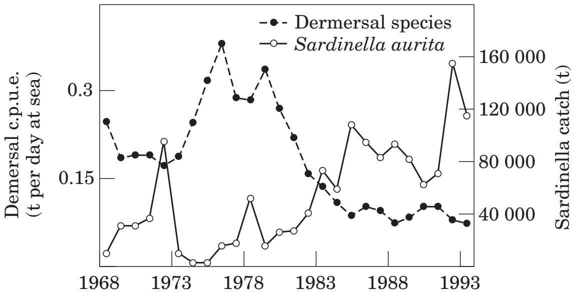


Figure 4. Annual catch of *Sardinella aurita* and catch per unit of effort (tonnes per day at sea) of demersal species off Côte d'Ivoire, 1968–1993 (data source CROA).

Only a few examples of demersal-pelagic interactions have been documented in the literature, and these exhibit contradictory empirical patterns (Anon., 1997). In Côte d'Ivoire, sardinella may be present alternatingly as demersal schools at or near the edge of the continental shelf, and as surface shoals closer to the coast during upwelling seasons (Longhurst and Pauly, 1987). When abundance of demersal fish species was high, the sardinella stock was small, suggesting a possible predator–prey relationship between the two communities (Fig. 4).

Upwelling ecosystems support a wide diversity of predators, ranging from piscivorous fish to seabirds and mammals. The numbers of the latter sometimes attain very high levels. In 1954, there were more than 20 million guanay cormorants (*Phalacrocorax bougainvillii*) along a segment of the Peruvian coast that stretched over 8° of latitude (Tovar *et al.*, 1987). Such high numbers of predators can only be sustained by large populations of forage fish. However, year-class strength of the usually short-lived forage fish may vary substantially (e.g. Cury and Roy, 1989). Many predators have life-history characteristics that buffer them against fluctuations in their food supply. In seabirds, these include high annual survivorship, protracted longevity, delayed sexual maturity, and a relatively low reproductive rate (Hunt *et al.*, 1996). As a consequence, breeding populations often comprise many year classes and they are not unduly affected if a weak cohort results intermittently from reproductive failure or low juvenile survival in a particular year.

However, many predator populations may not be buffered against the effects of longer-term fluctuations in prey resources (Crawford, 1999). For example, alternating regimes of sardine and anchovy frequently result in changes in prey distribution (Lluch-Belda *et al.*, 1989) and consequently in food availability (Crawford, 1998). Predators not tied to specific geographical locations and able to feed throughout the water column (such as predatory fish) are least affected. For example, snoek in the Benguela system are displaced to the north or south depending on whether prey populations are abundant off Namibia or South Africa, respectively (Crawford *et al.*, 1990). In contrast, species that are constrained to a particular area and have a limited foraging range may be strongly affected. These include the African penguins (*Spheniscus demersus*), which on account of their fidelity to mates return to the same breeding localities year after year. Being flightless, they have a restricted feeding range during the breeding season. Intermediate between these two extremes are animals that show fidelity to breeding sites, yet have substantial foraging ranges, such as Cape fur seal (*Arctocephalus pusillus pusillus*) and Cape gannet (*Morus capensis*), and those with a more restricted feeding range that are able to move between breeding sites, e.g. Cape cormorant (*Phalacrocorax capensis*) (Crawford *et al.*, 1994; Crawford, 1999).

Predators in upwelling ecosystems have adapted to long-term changes in their food resources by switching from one prey species to another as their relative abundance changes. Such changes in diet of predators between anchovy and sardine have been observed off South Africa in Cape gannets (Crawford, 1999) as well as in several seabird species in the Gulf of California (Velarde *et al.*, 1994). However, predators may not always be able to switch diet successfully. Off Namibia, sardine was replaced in the 1970s as a forage fish mainly by horse mackerel and pelagic goby (*Sufflogobius bibarbatus*). These species were either distributed too far to the north or occurred too deep in the water column to be available to penguin and gannet colonies situated south of Lüderitz and massive declines in seabird populations were observed (Crawford *et al.*, 1985; Crawford, 1999).

Another mechanism to cope with changes in prey resources is for first-time breeders to emigrate to colonies where food is plentiful at the time. For example, there has been little or no recruitment of young breeders to several colonies of African penguins (e.g. at Dyer Island since 1986, Fig. 5a) and Cape gannets (Crawford, 1999) over extended periods, leading to enormous decreases in populations at these colonies. Conversely, some colonies (e.g. penguins at Dyer Island before 1979 (Fig. 5a) and at Robben Island more recently (Fig. 5b)) have expanded at rates too rapid to be explained in the absence of immigration.

Superimposed on natural, long-term cycles in forage fish species abundance, fishing may be expected to reduce and shorten peaks during periods of high abundance, and deepen and lengthen troughs during periods of scarcity. This would result in less food for, and hence reduced populations of, predators. Off Peru, numbers of guanay cormorants have shown large fluctuations, decreasing following strong El Niño events that reduced availability of anchovy, and then increasing again (Tovar, 1983). However, bird numbers failed to recover after the 1965 El Niño, and have not subsequently attained previous levels. Evidently, by that time the anchovy fishery had increased to such an extent as to considerably reduce the food availability to birds (Crawford and Jahncke, 1999). Off South Africa, commercial fishing for sardine had the effect of first removing peaks in guano production, followed by a decline in average yield (Crawford and Shelton, 1978).

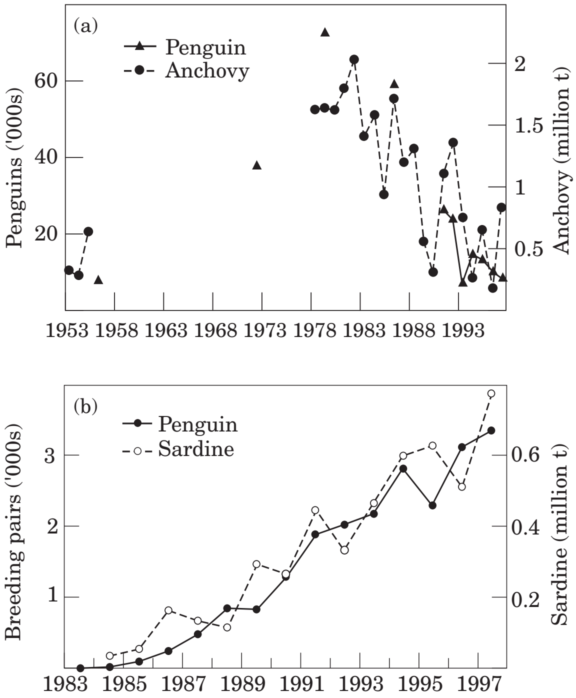
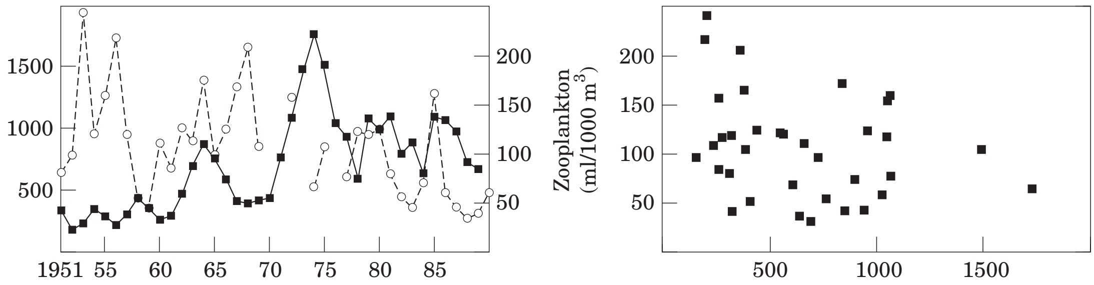


Figure 5. Changes in the breeding population of African penguins at (a) Dyer Island and (b) Robben Island, compared with biomass off South Africa of anchovy, 1953–1997 and of sardine off South Africa, 1983–1997, respectively (after Crawford, 1999).

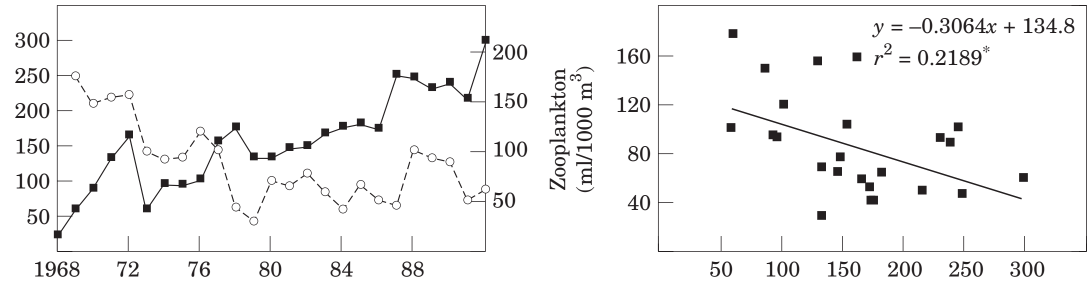
Whereas commercial extraction of foraging fish reduces the food for predators, discarding practices may increase food availability. Off South Africa, a substantial part of the diet of Cape gannets consists of hakes *Merluccius* spp. discarded by bottom trawlers (Berruti *et al.*, 1993). More generally, fisheries targeted at large piscivorous predators (including cannibalistic species) may benefit seabirds by increasing the abundance of small fish and crustaceans (Hunt *et al.*, 1996).

There may be several reasons why seabirds provide the clearest examples of how exploitation of forage fish affects predators in upwelling systems. Firstly, foraging strategies of seabirds are usually less flexible than those of other predators, especially because they are often restricted to the upper parts of the water column. Secondly, seabirds are accessible to study and changes in their populations are usually better monitored than those of predatory fish. Thirdly, many marine mammal populations have been recovering during the latter part

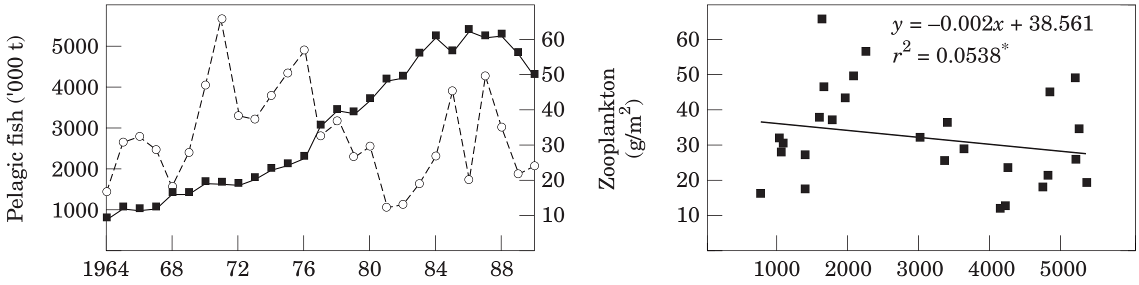
(a) California



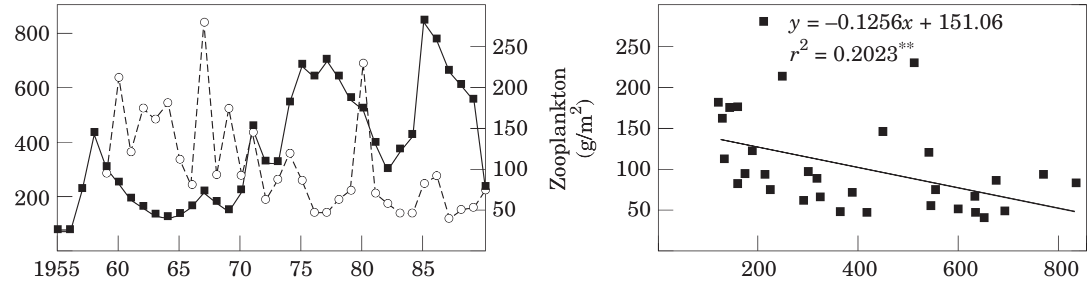
(b) Ghana and Ivory Coast



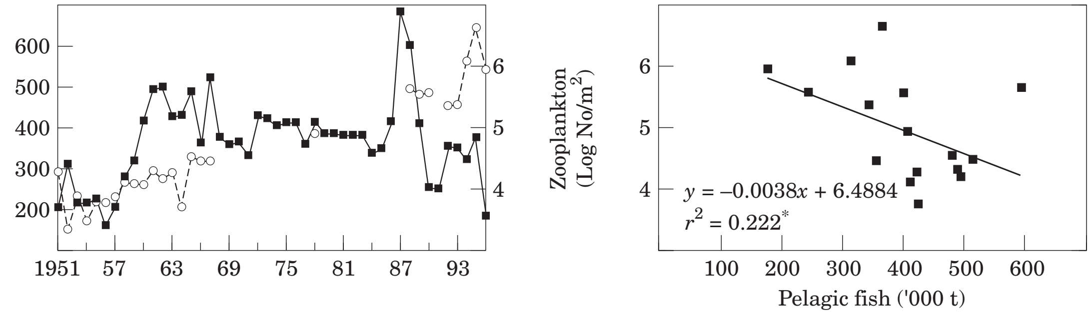
(c) Oyashio (Japan)



(d) Black Sea



(e) Southern Benguela



of the 20th century after having been greatly reduced previously (e.g. David, 1989). They may not have reached a size yet at which exploitation of their prey results in food limitation, although some may be close. In 1994, widespread mortality from starvation of Cape fur seal pups was observed off Namibia. Food scarcity was attributed to unfavourable environmental conditions (Crawford *et al*., 1999).

Although there is some limited evidence for top-down control of forage fish by predator populations, overall many observations suggest bottom-up control of predator populations by forage fish. Consequently, impacts of fishing on the abundance of prey resources can be expected to affect top predators.

Prey

Primary production and fish production in upwelling systems are tightly linked and about 25% of primary production may be required to sustain the fisheries (Pauly and Christensen, 1995). Jarre-Teichmann and Christensen (1998) estimated that between 15% and 30% of total primary production is necessary to sustain the major pelagic fish component in the four main upwelling areas of the world. *A priori*, one might expect to observe strong interactions between primary production and pelagic fish, mediated through the zooplankton component.

Long-term trends in zooplankton abundance in the California and Guinea current systems, the Oyashio system off Japan, and the Black Sea (Fig. 6a–d: left panels), as well as in the Humboldt Current off Peru (Carrasco and Lozano, 1989), are characterized by significant declines over the past three to five decades. In contrast, zooplankton abundance in the southern Benguela region has increased by two orders of magnitude since the 1950s (Fig. 6e). This increase was accompanied by a shift in the crustacean zooplankton community structure, from one dominated by relatively large zooplankters (>900 μm) during 1951–1967 to one of mainly cyclopoid copepods (<900 μm) during 1988–1996 (Verheye and Richardson, 1998; Verheye *et al*., 1998). The shift coincided with a change in dominance in the pelagic fish stocks from sardine to anchovy. Using decadal-scale time-series data from different trophic levels, Verheye *et al*. (1998) proposed several mechanisms that may contribute to the observed long-term changes in the zooplankton. From a bottom-up perspective, the increase in zooplankton abundance could be related to a long-term increase in upwelling-favourable windstress and associated processes (Verheye, 2000). From a top-down perspective, however, it could be related to a long-term reduction in predation pressure by pelagic fish abundance (Fig. 6e shows the commercial catches, which may be taken as a proxy of pelagic fish abundance since 1960 when the fishery for both anchovy and sardine was well established). The reduction in pelagic stocks may have been caused by increased fishing effort, but also by increased predation by apex predators. Snoek and Cape fur seal, for example, appear to have become increasingly abundant over the past decades (Crawford *et al*., 1995).

The observed shift in composition of crustacean zooplankton, the main food source of pelagic fish (Van der Lingen, 1994), may reflect the top-down effects of differential size-selective predation by sardine and anchovy (Verheye and Richardson, 1998; Verheye *et al*., 1998). It may also provide evidence for the bottom-up influence that food limitation, *inter alia*, may have on specific fish population characteristics over time. For instance, it is conceivable that the progressive increase in ovary mass and ovary-free condition in sardine, observed between the 1950s and the 1980s (Armstrong *et al*., 1989), is related in a density-dependent manner to the long-term increase in both the absolute and relative abundance of cyclopoid copepods. Cyclopoids are the preferred prey of sardine (Van der Lingen, 1994); their increasing abundance since 1950 may have arisen from diminishing predation as the sardine stock declined over that period, leaving increasingly more prey to be apportioned among fewer predators (Verheye, 2000).

Based on the arguments for top-down control, it is not surprising that a negative relationship exists between zooplankton abundance and pelagic fish catch in the Benguela system. However, although interannual variability within all systems is considerable, a negative relationship between predator and prey appears to be a feature common to most systems (Fig. 6a–e; right panels). The regressions explain between 5% and 22% of the variance. Top-down control of zooplankton populations by pelagic fish has been described in other marine (e.g. for herring [*Clupea harengus*] in the Northern Baltic; Arrhenius, 1997) as well as freshwater ecosystems (Cyr and Pace, 1993).

The apparent long-term decline in biomass of large zooplankton in the Humboldt Current system off

Figure 6. Time-series of (left panels) annual catches of pelagic fish (solid squares) and annual mean abundance, or biomass, of zooplankton (open circles), and (right panels) the relationship between the two: (a) California Current (data from Roemmich and McGowan (1995) and CA1COFI), (b) Guinea Current off Ghana and Côte d'Ivoire (data from Mensah (1995), and CROA/MFRD), (c) Oyashio district of the Tohoku Sea area off Japan (data from Odate (1994) and FAO (1997b)), (d) Black Sea (data from Daskalov (1998)), and (e) southern Benguela Current off South Africa (redrawn from Verheye and Richardson (1998) and Verheye *et al*. (1998). Lines in right panels indicate significant regressions (*p<0.05, **p<0.01).

Peru between the mid-1960s and mid-1980s, following the well-documented collapse of the local anchoveta population (Alheit and Bernal, 1993), appears to be an exception. From a food-chain perspective, the enormous reduction in anchoveta biomass should have reduced predation on zooplankton populations and also reduced competition for phytoplankton between zooplankton and anchoveta. Accordingly, zooplankton standing stocks might have been expected to increase. The opposite effect suggests a basic change in ecosystem functioning, concomitant with a switch in the diet of pelagic predators (horse mackerel [*Trachurus symmetricus murphyi*] and chub mackerel) from anchoveta to zooplankton (Carrasco and Lozano, 1989). The expanding sardine population may also have grazed down phytoplankton, leading to less food for copepods and fewer zooplankton.

In summary, ecosystem components may exert bottom-up or top-down control on pelagic fish depending on their position in the food web. Often, such control mechanisms may act in concert rather than singly, and their relative importance may not be easily discernible (Verheye *et al*., 1998).

Trophic flow models

Rose *et al*. (1996) classified multi-species models into three types: budget models, coupled single-species models, and holistic models. Budget models describe the flows of energy or biomass between species groups, and include, *inter alia*, those developed for upwelling ecosystems during different time periods (Jarre-Teichmann, 1998). A widely used ecosystem model is Ecopath (Christensen and Pauly, 1992), a steady-state model recently extended to a dynamic simulation model called Ecosim (Walters *et al*., 1997). Using Ecopath with Ecosim, increased fishing mortality of the three most abundant small pelagic fish in the southern Benguela upwelling region was modelled and effects on ecosystem components were simulated, assuming different types of control between trophic components (for details see Shannon *et al*., 2000).

Bottom-up control of small pelagic fish (sardine, anchovy, and redeye) occurs when zooplankton availability is a limiting factor for pelagic fish. In this case, there is intense competition between small pelagic fish for zooplankton prey, and modelled effects of changes in fishing mortality on small pelagics are small. Increases by a factor of four for anchovy and sardine were sustainable and stocks stabilized at smaller sizes.

However, the effects were larger when "wasp-waist" control is assumed. "Wasp-waist" control (Rice, 1995) describes the trophic linkages when there is top-down control of zooplankton by the intermediate small pelagic fish component, which also exerts bottom-up control on top predators (pelagic fish, marine birds, marine mammals, and fishers). Under "wasp-waist" control, zooplankton is highly vulnerable to small pelagic fish and therefore competition for zooplankton prey is reduced when fishing is increased. This allows the ecosystem components to respond more readily to changes in stock sizes of small pelagic fish. Modelling heavy fishing on small pelagic fish caused stocks of anchovy and sardine to collapse and favoured groups such as chub mackerel and horse mackerel, which compete for zooplankton prey. The increase in biomass of these competitors delayed recovery of anchovy and sardine once heavy fishing was alleviated and it took populations longer to recovery when "wasp-waist" control was assumed than under bottom-up control (Shannon *et al*., 2000).

The simulations thus strongly indicate that assumptions on the type of control of different trophic components are important in determining the projected effects of fishing on ecosystems.

"Fishing down" intra-specific diversity

The life histories of marine species have been shaped by strong selective pressures (Cury and Pauly, 1999). Present levels of fishing mortality could act as an additional selection pressure producing genetic (Sutherland, 1990) and structural changes within exploited populations. This leads to questions of whether and how current harvesting practices may affect long-term yields. The need to protect biodiversity in the terrestrial environment has become increasingly appreciated and is slowly becoming a topic for consideration in the marine environment, too (Roberts and Hawkins, 1999). The loss of small pelagic fish species diversity has not been, and is not currently, an issue in biological conservation (Beverton, 1990). However, the presence of genetic variation within species (between as well as within populations) is essential for their survival, and for adequate responses to short- and long-term changes. Thus, threats to intra-specific genetic diversity need particular attention in large and highly fluctuating populations (Ryman *et al*., 1995). Pelagic fish populations are known to vary enormously in year-class strength (Pauly and Tsukayama, 1987) and total population abundance. Beverton (1990) estimated that the ratio between the lowest and highest recorded stock size varied between 1/20 and 1/3000 for the 10 major fisheries during the past few decades. Using theoretical arguments, Ryman *et al.* (1995) emphasized that the long-term genetic effects of reduced population sizes with regard to allelic diversity are more dramatic for large populations than for small ones. However, they cautioned that the immediate biological implications of excessive losses of alleles are not clear and most likely would remain undetected in a typical genetic study. Nevertheless, they concluded that population crashes could represent a considerable change in genetic constitution.

How such changes will affect pelagic fisheries in the long term is still an open question. Apparently, populations reduced to the order of one-thousandth of their peak sizes for extended periods (e.g. >20 years in the case of the Californian sardine) can still provide a nucleus for subsequent revival when conditions become favourable again (Beverton, 1990). In this sense, reduction of intra-specific diversity does not represent the same kind of threat that species extinction does. However, long-term sustainability of the fisheries could still be affected (Sinclair *et al*., 1985; Cury and Anneville, 1998). Beverton (1990) noted "the possibility that the collapsed population may never be able to fully regain its former status in the ecosystem": of the nine stocks for which collapse has been documented, only one has fully regained its original size.

At a stock level, the extinction of one or a few constituting sub-populations might pass unnoticed if others had greater productivity, and some could go extinct before any signs of their overfishing became apparent. Consequently, even if appropriate regulation of fisheries were to be established, total stock biomass might fluctuate at a lower long-term level. In ecological modelling, it is common to assume demographic interchangeability of individuals (two individuals are equivalent), but this assumption may be unwarranted. Cury (1994) proposed a generalization of "natal homing", under which homing is viewed as part of a continuum of reproductive strategies, all relying on imprinting. This generalization postulates that a newborn individual memorizes early environmental cues, which later determine the choice of its reproductive environment. This way of looking at fish population dynamics implies that inertia is a driving force in the functioning of natural systems. Because every individual is able to explore a specific environmental possibility and in some way to transmit it to its descendants, each specimen is unique in terms of its reproductive behaviour. In other words, once a spawning site or a subpopulation adapted to specific imprinted environmental conditions has been fished out, it takes a long time for subsequent generations to re-occupy or re-employ the area (Corten, 1993). The resilience of marine fish populations is potentially enormous and this allows fisheries to be successful, but mechanisms that lead to discrete spawning groups may tend to thwart the renewal process in its duration and intensity. Therefore, the erosion by fisheries of intra-specific diversity could lead to a long-term decline in the productivity of marine pelagic resources.

Effects of fishing on schooling behaviour

Schools of clupeoid fish are highly adaptive structures. Their sizes, shapes, and dynamics are related to predator avoidance, feeding, migration, energy conservation, and reproduction (Blaxter and Hunter, 1982), as well as to abundance (Fréon and Misund, 1999). Fisheries generate directional and differential harvesting that modifies total abundance, but can also alter school dynamics, which in turn affects migration behaviour and geographical distribution.

A vivid illustration of the schooling imperative may be seen in the marked tendency for small pelagic fish of similar size and body form to school together regardless of species. For example, Radovich (1979) pointed out that as the sardine population in California declined, pure schools became less frequent and sardines were found mixed with anchovy or mackerel. Likewise, off Peru, large sardines have been found in mixed schools with horse mackerel and chub mackerel of similar size, whereas smaller sardines have been observed nearer the coast mixed with anchoveta (e.g. Jordán *et al*., 1978). The predominance of mixed-species schools of similarly sized fish is the most commonly observed situation in the Peru system as well in the Canary system (Fréon, 1984).

Estimates of school composition with respect to the main constituting species (sardine, sardinellas, and anchovy) were derived from fisheries as the ratio of the catch of a given species to the total catch for each set (Fig. 7). In addition, relative population abundance for each species was derived from total biomass estimates derived from acoustic research surveys or catch-per-unit-effort data. The results reveal a clear pattern. When sardine, sardinellas, or anchovy are abundant, they tend to form pure schools, whereas when their relative abundance is diminishing they mix with other species. The variations in mean percentages of pelagic species contained in sampled schools track remarkably well the overall relative population abundance. These results imply that the urge to become a member of a school of similarly sized fish of similar body form, regardless of species, is a dominating aspect of the schooling impulse (Fréon and Misund, 1999).

These findings appear to be fraught with implications regarding potential effects of exploitation patterns on species interactions, competition, changes in species dominance, alterations in migration habits, etc. Fish of a species that are driven to join schools of another more abundant species must effectively subordinate their specific needs and preferences to the "corporate volition" of the school that is largely driven by a different set of needs and preferences (Bakun and Cury, 1999). A filter-feeding clupeoid such as sardine that must attempt to survive and prosper in a school dominated by a voracious predatory mackerel would seem to face severe difficulties. Moreover, in view of the pelagic mode of spawning of these fish, spawning success of a minor component of a mixed species school might be severely limited. This introduces a mechanism for population instability: a less-abundant species tends to be adversely affected and so becomes even less abundant; and a dominant species tends to become even more dominant.

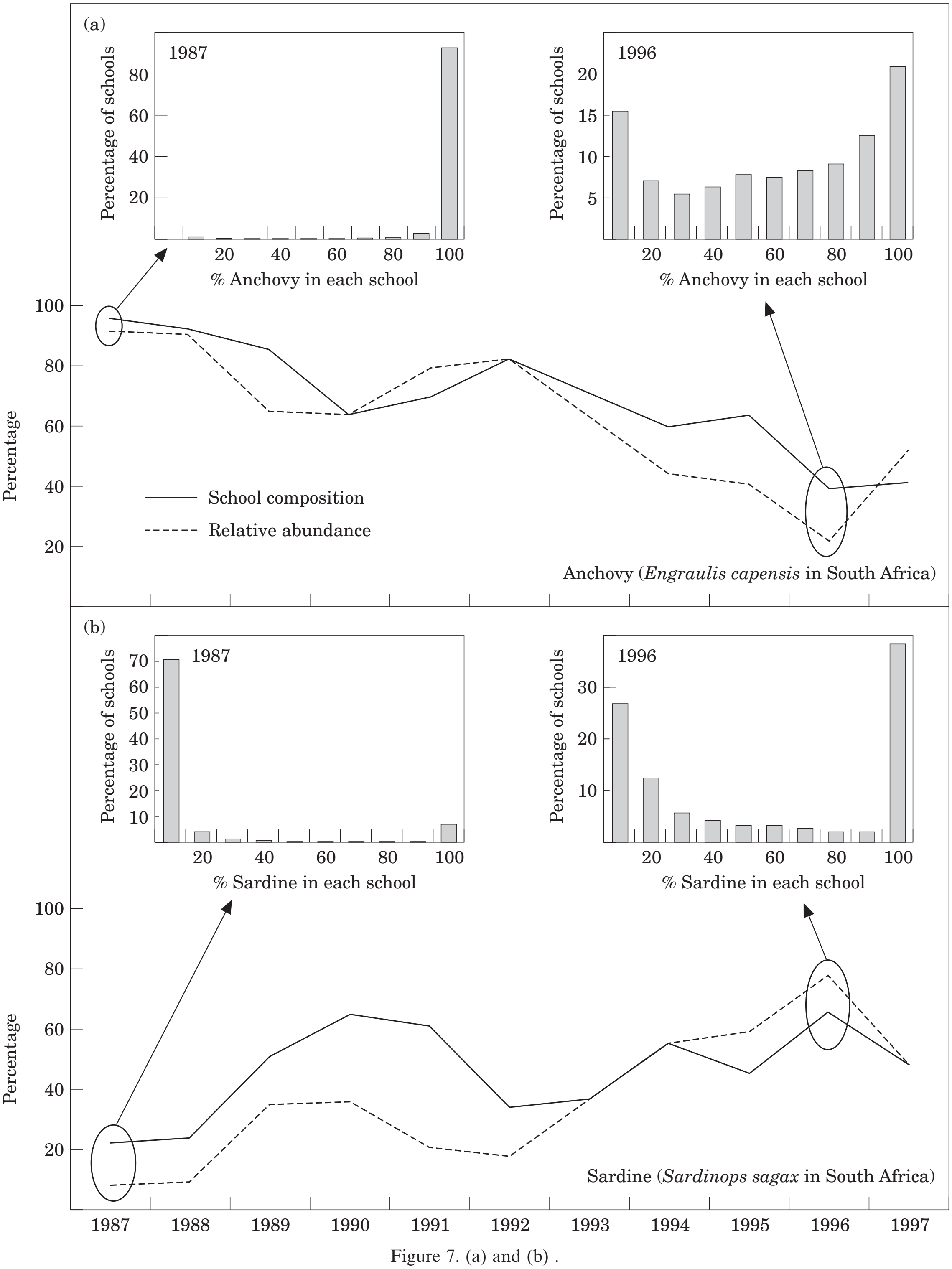


Figure 7. (a) and (b) .

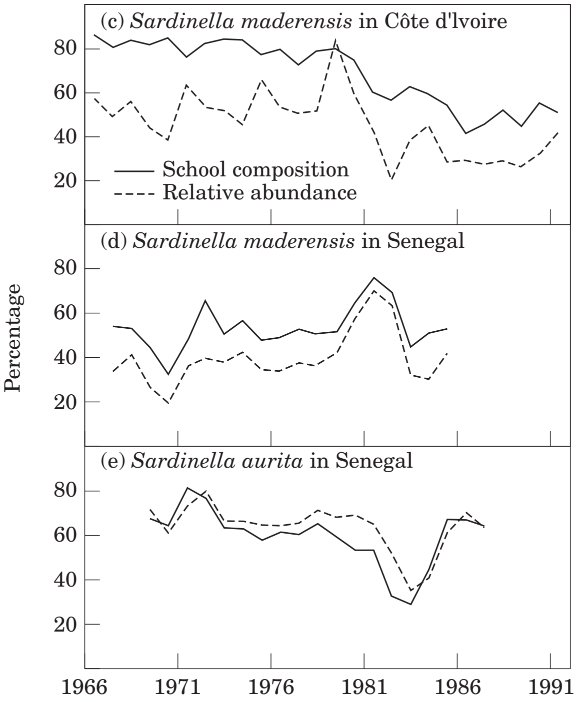


Figure 7. (c)–(e).

Figure 7. Pelagic fish school composition per species expressed as the percentage of the biomass of a species in the school in which this species was observed relative to the total biomass of the school (solid line; data extracted from the purse-seine fisheries) and relative abundance of the species in the ecosystem (dashed line; derived from acoustic data or catch statistics): (a) anchovy (*Engraulis capensis*) and (b) sardine (*Sardinops sagax*) in South Africa, 1987–1997 (catch-per-set analysed (130690); M&CM, Cape Town; relative abundance from acoustic surveys, Barange *et al.* (1999)). Insets: frequency distributions of the schools with different fractions of the two species for 1987 and 1996; (c) flat sardinella (*Sardinella maderensis*) off Côte d'Ivoire, 1966–1991 (catch-per-set analysed 7167; relative abundance from catch-per-unit-effort data; CROA); (d) flat sardinella (*S. maderensis*), 1967–1985; and (e) round sardinella (*Sardinella aurita*) off Senegal, 1969–1987 (relative abundance from catch-per-unit-effort data; CRODT, P. Fréon).

Accordingly, once such a change is initiated by a fishery or by an ecosystem event, the consequence might extend far beyond the initial change.

The "school trap" may also constitute a mechansim for abrupt changes in migration paths and effective habitat sizes. For example, pure schools of adult sardines often migrate long distances between their feeding and spawning grounds, whereas schools of anchovies tend to remain resident in or near the habitat for reproduction (Parrish *et al.*, 1981). The situation in schools of mixed species with differing degrees of inherent migration traditions might become even more pronounced when fisheries target a particular species. Indeed, changes in migration patterns have been recorded in several instances after the collapse of established fishing industries (Do Chi and Kiefer, 1996). We conclude that overfishing of one particular pelagic fish can alter the abundance, composition, and distribution in pelagic communities, and thus induce drastic and lasting changes of state.

Carbon cycling in the pelagic food web

Although the classic food web and the microbial food web are both present in upwelling systems (Stockner, 1988), it is generally accepted that the former is the predominant pathway of biomass transfer in this type of ecosystem (Ryther, 1969). Primary production is fuelled largely by nutrient inputs from below the thermocline and, consequently, new production is expected to be much higher than regenerated production. Large or colonial phytoplankton cells are generally abundant and form the basis of the food web. Fish production is based on short food chains: the large phytoplankton cells are grazed efficiently by crustacean zooplankton and these organisms are eaten by fish. However, this scheme is oversimplified and a wide spectrum of trophodynamic scenarios may be observed during upwelling as well as relaxation periods. For example, during pre-El Niño and El Niño conditions, the microbial food web in the coastal and oceanic zones of the Humboldt Current system off northern Chile was very active. Pico- and nanoplankton size fractions dominated the total primary production (González *et al.*, 1998), microplankton respiration amounted to 40–200% of the total primary production (Eissler and Quiñones, 1999), and secondary production by bacteria was higher than that of chitinous zooplankton (González *et al.*, 1998). A large proportion of phytoplankton production may also be channelled through the microbial food web in the Benguela upwelling ecosystem (Probyn, 1992). In addition the gelatinous food web can be significant in marine ecosystems (e.g. Shiganova, 1998), including upwelling systems (González *et al.*, 1998).

In lake ecosystems, the removal or addition of fish biomass cascades down through the food web, regulating production and consumption of lower trophic levels and altering the availability of nutrients (e.g. Carpenter and Kitchell, 1988). In marine ecosystems, a cascade of events produced by the increase (e.g. immigration) or decrease (e.g. emigration, fishing) of fish biomass might also be expected, although "clear-cut" evidence for such effects at the community level is lacking (Steele, 1998). One example of the possible effect of removal of fish biomass on the carbon fluxes of an upwelling ecosystem was provided by Walsh (1981) for the Peruvian zone. He estimated that when the anchovy population was not overfished the carbon fixed by primary producers was channelled through the trophic web equally through the anchovy and copepod populations. In contrast, when the anchovy population was depleted, the carbon flux to copepods increased, but copepod production was taken care of mostly by euphausiids and sardines. Also, a higher proportion of primary production reached the bottom, enhancing the benthic food chain. The transfer of carbon towards bacterioplankton decreased by an order of magnitude and the carbon buried and/or exported increased sevenfold.

The jack mackerel, a pelagic species that is widely distributed in the South Pacific from the coast of South America to New Zealand and Australia, and its predation on zooplankton, provides another example. The total adult biomass for 1990–1995 was estimated as 14 million tonnes (Cerda *et al*., 1997). Considering the typical dietary composition in stomach contents from the SE Pacific and a consumption-to-biomass ratio of 0.59 (Arancibia *et al*., 1995), the adult stock consumes about 100 million tonnes of zooplankton (or 14 million tonnes of C) per year. Euphausiids make up 65–95% of the diet (Arancibia *et al*., 1995). Quiñones *et al*. (1997) showed a strong local impact on euphausiid abundance in areas where high aggregations of jack mackerel were present for 10 days. The total annual catch of jack mackerel in the SE Pacific (Chile, Peru, and Ecuador) for 1990–1995 ranged between 2.6 and 4.9 million tonnes (FAO, 1997b). The estimated potential annual consumption of zooplankton by jack mackerel removed by fishing is equivalent to about 2.7–5 million tonnes C y^{-1}. The scale of this particular fishery, one of the largest in the world during the early 1990s, provides a perspective on the high productivity of eastern boundary current systems and the role of large-scale fishing on carbon fluxes. Uncertainty about the fate of this flux, depending on whether there is a fishery for jack mackerel or not, exemplifies the need for an interdisciplinary framework between fisheries and biogeochemistry.

“Wasp-waist” ecosystems: fisheries implications

Ecosystem management presumes a reasonable understanding of the interactions among and between species complexes as well as their environment (Larkin, 1996). Today, we are far from fully understanding the role of small pelagic fish in food-web dynamics and in the functioning of ecosystems. Moreover, the role of non-exploited fish, such as myctophids, is almost unknown (Tsarin, 1997). Nevertheless, small pelagic fish do act as dominant species and have a significant role in shaping the structure of the marine ecosystems. Apparent control exerted on the other components of the systems, and as described based on retrospective analyses, is different from what would have been expected. Top-down control on zooplankton and bottom-up control on top predators are not conventional ways of viewing predator–prey interactions.

Fishing commonly changes the relative abundance of fish species (Larkin, 1996), but may also change the structure and functioning of the ecosystem. The contemporary importance of fisheries places humans in a central position in the exploitation of marine resources, and we do not know what changes are to be expected because they have never been experienced before on this scale. As fisheries continue to fish down the food web (Pauly *et al*., 1998), one must carefully consider the implications for other species. It is doubtful that pelagic fisheries will continue to increase at an annual rate of 4.3%, as has been the case since the 1950s, without major ecosystem disruptions. As stated by Beddington (1984), there is an obvious danger that the perturbation caused by a fishery could be irreversible if there are alternative system states. The effect of crashes of pelagic fish stocks on the loss of intra-specific diversity and on ecosystem structure is a valid concern but has only started to receive the attention it deserves. Overfishing may induce drastic changes of state in the pelagic communities because it presumably releases competing species from competitive control by the targeted species. School dynamics appear to play a fundamental role in alternating predominance of species such as sardine and anchovy. The “school trap” may exacerbate the effects of exploitation of target species and thereby have a strong impact on ecosystem structure. Effects of fishing on ecosystems may be more subtle in essence than commonly appreciated (Jennings and Kaiser, 1998). In this regard, the role of weak trophic interactions in promoting community persistence and stability (McCann *et al*., 1998) should be viewed as a new but important concern for fishery management. In view of the paramount role of the pelagics in marine food webs (Stephenson, 1997), the patterns presented hold several cautionary lessons regarding management of these resources. One lesson is that viewing the habitat of a resource stock as being some fixed ocean volume with a given “carrying capacity”, etc., may be too simplistic and lead to unexpected pitfalls. Another lesson is that whatever impact is exerted upon a natural ecosystem has inevitable effects. Although marine ecosystems exhibit a considerable resilience, drastic responses have been observed and many more are to be expected. As it becomes even more clear that there are major uncertainites regarding the continued exploitation of the main renewable resources, the need for an increased focus on ecosystem issues becomes more urgent.

In 1978, FAO’s ACMRR (1979) formally advocated the development of an ecosystem approach to fisheries management. Some 20 years later, one can say that significant progress has been made. A scientific basis for ecosystem management has been suggested (Christensen *et al*., 1996) and an operational framework, based on defined ecological units, has been proposed (Grimm, 1998). This being said, the ability of marine ecology to contribute multi-species and ecosystem information useful to fisheries management has remained limited

(Botsford *et al.*, 1997). There are several reasons for this. One is the lack of detailed knowledge of most of the dynamic interactions that might underlie multi-species modelling efforts (Rose *et al.*, 1996). Another is the intrinsic complexity of ecological systems (Jennings and Kaiser, 1998), which usually have no clear boundaries and lack the sort of clear reasons for existence that can be ascribed, through evolutionary theory, to organisms. Rather, their dynamics are driven by interactions (Grimm, 1998) at multiple levels and scales, potentially leading to a high degree of complexity. Medawar (1967) called science the art of the soluble, because one secret of successful science is to ask important questions that can be answered. According to Peters (1991), ecologists have ignored this advice and have continued to ask seemingly important questions that can never be answered. Valid ways to narrow the breadth of possibilities and focus on some soluble issues will be profitable. Comparative ecosystem studies may be helpful in this regard. In any case, a view of fishing in terms of its ecosystem effects seems on the verge of becoming an efficient and operational paradigm, and we scientists must find ways to play our role by addressing soluble relevant questions. Ecosystem management represents a paradigm shift, as well as a new attitude towards the exploitation of renewable marine resources (Christensen *et al.*, 1996; Jennings and Kaiser, 1998). The ecosystem should be viewed as an integrative level for ecological studies. For scientific and management purposes, this will give new and refreshing insights, which will be essential for achieving political and management goals.

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