THE EFFECTS OF FISHING ON NON-TARGET SPECIES AND ECOSYSTEM STRUCTURE AND FUNCTION

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ABSTRACT

Marine fisheries landings increased through most of the 1900s, at the same time as their composition has shifted from larger, fish-eating species towards smaller, plankton-eating fishes. Fishing can affect the composition of the fauna by changing the relative abundance and size distribution of target and by-catch species, by affecting the habitat or by providing discards to scavenging populations such as seabirds. This can lead to changes in species interactions that can affect other parts of the ecosystem. In some cases, fisheries-generated reductions in populations of important forage fish has been reported to affect the growth, abundance and distribution of populations of fish, seabirds and marine mammals that depend on these species for food. Other studies have shown that fisheries-generated habitat changes have had knock-on effects on the local fauna. However, most of the cases where changes in species interactions have been linked to fishing come from relatively simple ecosystems, where a major part of the energy has to pass one or a few species positioned at an intermediate level in the food web. In the more complex systems, the effects of fishing are difficult to separate from natural changes in species abundance due to environmental changes in, for example, temperature and currents, or from man-made changes, such as increases in nutrients. For most of these systems, it is therefore unknown how fishing affects their overall structure and function. Although attempts have been made to develop overall indicators of the impact of fishing on marine food webs, the performance of these indicators has not yet been sufficiently studied to allow them to be used in fisheries management.

INTRODUCTION

[1] Marine fisheries have expanded considerably during the second half of the twentieth century, and on a global scale the annual catch of fish and shellfish now amounts to more than 100 million tonnes. In heavily fished areas, such as the North Sea, this means that of the order of one-third of the fish biomass is removed each year, and on a global scale most commercially targeted fish stocks are now either fully exploited or overfished.

[2] The expansion has been accompanied by a shift in the composition of the landings, from large, fish-eating fishes towards smaller, plankton-eating fishes and invertebrates (Pauly *et al.* 1998). Ecologists use the term ‘trophic level’ to characterize the number of links in the food web from the species in question to the primary producers (level 1) at the bottom of the web. Figure 1 shows how the mean trophic level of the global marine landings has changed over the last 45 years. In the 1960s and early 1970s, the large landings from the fishery for Peruvian anchoveta, which feeds at low trophic levels, caused a temporary dip in the average trophic level

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of the global landings, but from 1972 onwards the mean trophic level has shown a steady decline. Part of this decline may have been caused by developments in markets and technology, but the fact remains that, on a global scale, fishing is now extracting fish further down the food chain than previously.

[3] Approximately 75% of the world's fish catch is taken on the continental shelf or in coastal and estuarine areas where the primary production is high (Pauly and Christensen, 1995). Estimates of the transfer of energy through the food web suggest that between 25 and 35% of the energy fixed by the primary producers in these areas is needed to sustain the current fisheries. When such a high fraction of the production is removed from the system it is likely that species that compete with the fishery for resources will be affected. It is also likely that fishing will influence production at the lower levels of the food web.

[4] It is, however, difficult to quantify these effects. Marine ecosystems are complex and subject to large natural fluctuations caused by changes in temperature and currents for example. The natural changes and the changes caused by other human impacts, such as input of nutrients, interfere with the effects of fishing and make them difficult to isolate. Thus, even in situations where major exploited stocks have collapsed, the cause cannot always be attributed exclusively to fishing. In most cases, a combination of high fishing pressure and unfavourable environmental conditions has been involved. To show that a change in the abundance of a target species affects another species requires that both species are monitored, that a causal mechanism (e.g. predation or competition) can be established and, not least, that other likely causes can be excluded. For more than a century, fisheries biologists have struggled to separate the contribution of species interaction, the physical environment and the size of the parent stock to fluctuations in recruitment, so far with only modest success. It is therefore not surprising that a full answer to the more general question of how fishing affects the function and structure of marine ecosystems cannot yet be provided and that many of the cases where fishing has been found to be involved in ecosystem change are based on circumstantial evidence rather than proof.

[5] The rarity of data from unexploited marine ecosystems constitutes an additional problem. In most cases, little information was collected before a fishery developed, and although historical and palaeoecological information can provide insights (e.g. Baumgartner *et al.,* 1992, Jackson, 1997, Quero, 1998), it is often impossible to know how a system looked prior to exploitation. Without knowledge about the unexploited situation it is difficult to evaluate the present, and fisheries biologists run the risk of using a situation already influenced by fishing as their baseline for evaluating further change (Pauly, 1995).

[6] One of first attempts to quantify how fishing affects the structure and function of marine ecosystems dates back to the Italian scientist, Vito Volterra, who tried to explain the apparent increase in sharks and other predators and the decline in their fish prey in the Adriatic Sea during World War I (Gasca, 1996). His son-in-law, Umberto D'Ancona, had noticed a change in the landings in Venice, Trieste and Fiume after the war. The species composition had changed, even though the total landings had remained the same. According to D'Ancona, the cessation of the fishery during the war changed the species composition in favour of fish-eating fishes, and Volterra developed a simple theoretical model where the observations were explained as a result of changes in species interactions. Since then, a large number of case studies have examined how fishing affects the structure and functioning of marine ecosystems. In this paper I will review a number of these case studies, describe a couple of the indices that have been proposed to capture the overall impact of fishing, and end by briefly summarizing the general patterns that emerge.

THE IMPACT OF FISHING ON MARINE ECOSYSTEMS

Coastal and estuarine systems

[7] Due to the growing interest in establishing marine protected areas, a large number of studies have been undertaken recently to demonstrate the effects of marine reserves on the fauna. Mosquera *et al.* (2000) reviewed empirical studies of the effect of marine reserves on the fish fauna and found that fish abundance was on average more than three times higher within the reserves than outside. Most of the difference was, however, due to an increase in large-bodied target species, while non-target species were generally equally abundant inside and outside the reserves. This suggests that any indirect effects of a change in the abundance of the target species had only a minor or no impact on the abundance of the non-target species. Similar observations have been made in coral reefs, where the indirect effects of removing fish predators on the abundance of their fish prey have been subtle (Jennings and Kaiser, 1998).

[8] Coastal fishermen use a various gear that can disturb the habitat either directly or indirectly, and effects have been noticeable where fishing has affected species providing a structural habitat such as corals, sea-grasses or seaweed. In coral areas, where destructive fishing methods, such as explosives, cyanide or heavy trawling gear, have destroyed the corals, the associated fauna has disappeared. In less impacted areas, the changes are often not as dramatic. On reefs where the abundance of fish eating fish species has been reduced, herbivorous fishes will range farther from their coral shelter and/or become more abundant (McManus *et al.*, 1992). This has been suggested to increase the areas on adjacent reef flats devoid of seagrass (Miller and Hay, 1998; Jennings and Polunin, 1997). However, when fishing affects ‘keystone’ species either directly or indirectly, the effects on the reefs can be pronounced. Widespread changes were thus observed in the coral reefs of Jamaica when the algal-grazing sea urchin *Diadema antillarum* suffered mass mortalities from a species-specific disease from 1982 to 1984. This resulted in a massive bloom of fleshy macro-algae that overgrew the corals and produced a dramatic decline in coral cover (Hughes, 1994). The change in coral cover was brought about by a sequence of events that included a hurricane that struck the island in 1980, and overfishing of the sea urchin’s natural fish predators and the algal grazing fishes with which they competed. This left *Diadema* in control of algal growth. By removing the competitors and predators of the sea urchins, fishing set the stage for the shift to algae that followed the sea urchin collapse. Similar effects have been observed elsewhere. On the Great Barrier Reef, the removal of a number of fish species that feed on young starfish has been implicated in outbreaks of a coral-eating starfish (*Acanthaster*) (Bradbury and Seymour, 1997), and in Kenya the removal of triggerfish by fishing has caused an increase in the abundance of a burrowing sea urchin (*Echinometra*) leading to extensive bio-erosion of the reefs (McClanahan and Muthiga, 1988; McClanahan *et al.*, 1996).

[9] In colder waters, productive kelp forests supports a highly diverse fauna. Kelp forests are variable and influenced by grazing, storms and El Niño events. Among the animals that feed on kelp, sea urchins are by far the most important (Dayton, 1985). When sea urchins are abundant they are able to graze down the kelp and create “barren grounds,” resulting in a dramatic change in the fauna. The abundance of sea urchins is influenced by recruitment, predation, disease and immigration of adults: factors that vary greatly over time and space. The abundance and types of sea urchin predators also vary from area to area. In the North Pacific, along the coasts of Alaska and Canada, sea otters function as keystone predators. When sea otters are abundant, they reduce the abundance of sea urchins. In the absence of sea otters, dense populations of sea urchins develop and graze down the kelp (Estes and Duggins, 1995). Along the coast of California, the situation is more complex, but two sea urchin predators, spiny lobster and the sheaphead, a labrid fish, are likely to play a similar role as sea otters further north. Both of these predators are subject to intense fishing and it has been suggested that fishing may lead to more abundant grazing outbreaks (Tegner and Dayton, 2000). A similar interaction between fishing and sea urchin grazing may exist in other areas where commercially exploited predators affect sea urchin

abundance. In the northwestern Atlantic, a range of large, commercially exploited fish prey on sea urchins (Steneck, 1997); off South Africa, rock lobster is the most important sea urchin predator (Anderson *et al.,* 1997); and in northern New Zealand, spiny lobsters and snappers predate sea-urchins (Babcock *et al.,* 1999).

Semi-enclosed seas

[10] Many semi-enclosed seas, such as the Baltic, the Black Sea and the Mediterranean, support important fisheries. The fauna in these areas have undergone marked changes over time. However, fishing is unlikely to be the only driving force behind these changes. In many areas, nutrient enrichment seems also to be involved (Caddy, 1993). The most dramatic example of the combined effects of nutrient enrichment, overfishing, decreases in freshwater input, and the introduction of alien species has been observed in the Black Sea (Shiganova and Bulgakova, 2000). In the 1970s, increases in nutrient input produced an increase in primary and secondary production at the same time as fishing reduced the biomass and changed the species composition of the fish fauna. The larger, fish-eating fishes declined, while small pelagics increased. In the early 1980s, the increasing production at lower trophic levels led to an explosive development of jellyfish and to a rapid growth of the population of an invading ctenophore *Mneniopsis.* During the 1980s and in the early 1990s, jellyfish and *Mneniopsis* reduced the biomass of zooplankton to a level that led to a reduction in the recruitment of the fish populations, in particular anchovy, after which the fish populations and fisheries collapsed. In the late 1990s, the situation started to reverse after the invasion of another ctenophore, *Beroe*. This species feeds on *Mnemiopsis* and has apparently reduced its biomass in the most recent years.

[11] Despite general increases in nutrient input, quite as dramatic changes have not been observed in other semi-enclosed seas. In the Baltic Sea, the large reduction in cod biomass following intensive exploitation in the late 1970s and 1980s was accompanied by an increase in the biomass of sprat. The fish fauna in the Baltic is dominated by three commercially exploited species: cod, herring and sprat. The interactions between these species are well studied (Sparholt, 1994). Cod is the major predator of sprat and herring, and the reduction in cod biomass in the 1980s coincided with an increase in the biomass of sprat, and was followed by a subsequent increase in the growth rate of cod (Figure 2). Since sprat also feeds on the eggs and larvae of cod, it has been suggested that the fishery has driven the system from a cod-dominated state with low biomasses of sprat, to a sprat-dominated state in which the recruitment to the cod stock is limited by sprat predation (Rudstam *et al.,* 1994). However, the story is complicated by the fact that the changes have been observed in a period where nutrients concentrations increased concurrently with decline in the salinity and oxygen content of the water in spawning areas of cod over the deep parts of the Baltic, partly as a result of a reduced inflow of saline waters from the Atlantic. Thus, both changes in environmental conditions and a high fishing pressure reducing the spawning biomass of adult cod are likely to be implicated.

Boreal shelf areas

[12] The Barents Sea north of Norway and Russia is subject to large variations in climatic conditions, with changes between cold and warm periods (Loeng, 1989). Capelin, juvenile herring and polar cod are the most important plankton-eating fish, while cod and a variety of seabirds and marine mammals constitute the main predators (Hamre, 1994). After hatching, juvenile herring from the Atlanto-Scandian herring stock drifts along the west coast of Norway and eventually enters the Barents Sea, where they stay until they mature. When the Atlanto-Scandian herring stock collapsed in the late 1960s due to heavy fishing, the inflow of juvenile herring to the Barents Sea ceased. Herring is a predator of larval and juvenile capelin, and after the collapse of the Atlanto-Scandian herring stock the capelin stock in the Barents Sea increased and became the target of a directed fishery. Capelin biomass remained high in the 1970s despite heavy fishing. At the same time, the cod population, a predator on both herring and capelin, continued a long-term decline caused by fishing. When recruitment to the Atlanto-Scandian

herring stock improved and the influx of juvenile herring increased again, the predation on capelin increased. The increased predation and heavy fishing made the capelin stock collapse in the mid-1980s (Gjøsæter, 1998). Following the capelin collapse, the growth and fecundity of cod decreased and cod cannibalism increased (Bogstad and Mehl, 1997) (Figure 3). Seabirds and marine mammals feeding on capelin were also strongly affected. Harp seals migrated down the coast of Norway in 1987 and high unintentional catches occurred in fishing nets along the coast, while guillemots suffered winter kills of thousands of individuals in the Barents Sea (Livingston and Tjelmeland, 2000). The capelin stock recovered as a result of the large 1989 year class, only to collapse again when the large 1991 and 1992 year classes of herring entered the area. This time, however, the guillemot population did not decline, perhaps because the birds were able to switch to herring as an alternative food (Anker-Nilssen *et al.,* 1997). The changes in the relatively simple ecosystem of the Barents Sea demonstrate the importance of the links between capelin, cod and herring. The overfishing of herring in the adjacent Norwegian Sea and changes in the inflow of warm water from the Atlantic (Skjoldahl *et al.*, 1992) triggered a sequence of changes in which fishing seems to have played a significant role.

[13] In the Bering Sea between Alaska and Russia, recent declines in populations of marine mammals and seabirds have attracted attention. The various hypotheses explaining these declines are discussed in a report from the USA National Research Council (NRC, 1999). As in the Barents Sea, the environmental conditions are variable, with interdecadal changes in sea surface temperature and ice cover. The biomass and composition of the demersal fish community has undergone large changes over time (Livingston and Tjelmeland, 2000). Over the last 20 years, the stock of walleye pollock has increased, and in the beginning of the 1990s it accounted for half the biomass of demersal fish. The causes for the increase are not well known. It may be related to a number of warm years, where pollock cannibalism was reduced because the adults and juveniles were spatially separated (Wespestad *et al.,* 2000), but it may also be linked to increases in the food supply to pollock caused by a reduction in the abundance of other fishes and whales competing for the same resources as pollock. In the 1950s, 1960s and early 1970s, whales were intensively exploited. At the same time, trawl fisheries severely reduced the stocks of eastern Bering Sea shelf flatfishes and herring as well as the stocks of rockfishes found on the upper continental slope. In addition, ocean climate changed as sea surface temperatures increased and ice cover reduced. The increase in pollock biomass was accompanied by an apparent decline in a number of smaller fish species that serve as food for Pollock. Seabirds, seals and other top predators declined as well. In the Pribiloff Islands, juvenile and adult female fur seals declined from the mid-1970s to the early 1980s. Harbour seals declined rapidly in the late 1970s in the Gulf of Alaska and have remained low since then. Steller sea lions declined in the eastern Aleutians in the early 1970s and in the central and western Aleutians and western Gulf of Alaska in the 1980s. The evidence available to explain these declines is mainly circumstantial, but for Steller sea lions they have been explained as a result of a fisheries-generated lack of food. Steller sea lions eat pollock in addition to other forage fish, and as the pollock fishery overlapped with the foraging areas of the sea lions it may have reduced the biomass of pollock in these areas sufficiently to reduce the growth of the mammals. The decline in sea lions and seals may have had knock-on effects in nearshore kelp forests, where declines in sea otter populations have recently been observed (Estes *et al.,* 1998). These declines have been suggested to be a result of increases in killer whale predation on sea otters, and hypothesized to be linked to changes in the foraging area of the killer whales caused by the reduction in the abundance of the sea lions and seals that they normally would eat.

Temperate shelf areas

[14] The North Sea is one of the most intensively studied marine systems in the world and several analyses of long-term trends in the species composition of fish and other biota are available. For fish, the analysis of long-term survey time series of the composition of the demersal fish fauna of the northern North Sea has remained surprisingly stable. Greenstreet *et al.*

(1999) studied the species composition in bottom trawl survey data from 1925 to 1996. Comparing different periods, they found only small changes in the relative species composition. The most apparent was an increase in Norway pout, a small gadoid, for which an industrial fishery developed in the 1960s. Examination of the size composition of the catches revealed a shift towards smaller fish in the whole assemblage, but this shift was not significant for the non-target species. The fish fauna in the southern North Sea has shown a larger change. Rijnsdorp *et al.* (1996) compared catches from bottom trawl surveys in 1906-1909 with data from 1990-1995, and found a reduction in overall abundance as well a decrease in diversity caused by an increase in dominance of a few of the target species.

[15] Some of the exploited species have also exhibited changes in growth and size at maturity. During the Second World War, the North Sea fishery declined. Studies of North Sea plaice show that growth was reduced during the war and in the period immediately after, coinciding with a three-fold increase in the plaice stock. Length at first maturity has decreased in both male and female plaice since 1900 (Rijnsdorp and Leeuwen, 1992). While part of the decrease in length at first maturity can be explained by phenotypic plasticity and differences in water temperature, the authors suggest that the remaining part could be linked to genetic selection of a smaller size at first maturity caused by size selective fishing.

[16] The results referred to above considered the long-term changes. Over shorter time spans, considerable changes in the fish fauna have been observed. One of the most apparent was the gadoid outburst that started in the beginning of the 1960s (Cushing, 1980). Over the next 20 years the main commercially exploited gadoid species – cod, whiting, haddock and Norway pout – all produced one or more outstanding year-classes. The outburst has been explained by fisheries-generated changes in species interactions (Andersen and Ursin, 1977), while others have correlated gadoid recruitment to various environmental parameters such as salinity anomalies (Dickson *et al.*, 1988a), the prevalence of westerly (Aebisher *et al.*, 1990) or northerly winds (Dickson *et al.*, 1988b) and wind stress and winter cooling (Svendsen and Magnusson, 1991). At the same time as gadoid recruitment increased, the mackerel and herring stocks declined due to heavy fishing. In the second half of the 1960s, the stock of North Sea mackerel dropped from almost 3 million tonnes to 0.5 million tonnes, while herring declined from 2 to 1 million tonnes. Andersen and Ursin (1977) built an extensive model of the North Sea ecosystem in an attempt to explain the gadoid outburst. The model included primary production, two functional groups of zooplankton, three benthos groups, detritus and 11 interacting fish species. The model was able to mimic the general increase in the gadoid biomass as a result of reductions in mackerel and herring predation on juvenile gadoids, but did not allow the authors to exclude the possibility of a general upward recruitment trend due to other environmental factors. In a later analysis of the timing of the events, Hislop (1996) concluded that none of the explanations offered have provided a satisfactory explanation. The first large year-class of haddock occurred in 1962 at a time when the stocks of both herring and mackerel were high. According to Hislop (1996), we are still – almost 40 years after it began – no closer to understanding the causes of the outburst.

[17] Some 1 million tonnes of fish, offal and benthic invertebrates is presently discarded annually by commercial fisheries in the North Sea (Tasker *et al.*, 2000). A number of seabird species feed on these discards and many of these have shown large increases over most of the twentieth century. The increases have been linked to improved food resources, in particular discards, but are also related to the decrease in seabird hunting that took place in the early part of the century. The birds are unable to eat all of the discarded material. A part will sink outside their feeding range or be composed of flatfish and other items that are difficult to swallow. However, a link between increases in discards and overall changes in the abundance of scavenging species of fish and invertebrates on the seabed has not yet been established.

[18] When the mackerel and herring stocks declined in the North Sea, a fishery for sandeels developed. Mackerel and herring include sandeel in their diet and an increase in sandeel biomass was predicted by the model of Andersen and Ursin (1977). However, no data on sandeel

abundance from the 1960s and early 1970s are available to show whether such an increase did in fact take place. On Georges Bank, on the other side of the Atlantic, a similar decrease in mackerel and herring was accompanied by an increase in the abundance of sandeel larvae (Sherman *et al.*, 1981). Fogarty *et al.* (1991) studied the interaction between sandeel, herring and mackerel, and found a significant negative relationship between an index of the abundance of the latter two species and sandeel recruitment over the time period 1970-86.

[19] The changes in mackerel, herring and sandeel stocks were not the only things that happened on Georges Bank. During the 1960s, the total fish biomass was more than halved as a result of increasing exploitation by distant water fleets (Fogarty and Murawski, 1998). After the establishment of the 200-mile limit in 1977, exploitation initially declined, but then increases in the domestic fleet led to a new increase in the exploitation of gadoids and flatfish, resulting in a reduction of their biomass to historically low levels. The reduction in the biomass of demersal target species was accompanied by an increase in small sharks and rays and, due to reductions in pelagic fishing effort, to an increase in the abundance of herring and mackerel in the late 1980s. Recently fishing has reduced the abundance of the smaller sharks and rays again.

[20] The increase in sharks and rays on Georges Bank in the 1970s and 1980s has been attributed to reduced competition caused by the decrease in the biomass of gadoids and flatfish with which they compete for food (Fogarty and Murawski, 1998). The reduced populations of demersal fish have recently exhibited high individual growth rates (Hunt, 1996) consistent with the hypothesis that competition for food is important in the system. The reductions in herring and mackerel biomass in the late 1960s and 1970s and the increase in sandeel abundance has been used to explain changes in the distribution of whales on the Georges Bank and in the Gulf of Maine (Kenney *et al.*, 1996)

Tropical shelves

[21] In the 1960s, intensive fisheries developed in the Gulf of Thailand (Pauly, 1988; Christensen, 1998). Overall catch rates declined from about 300 kg h^{-1} in 1961 to 54 kg h^{-1} in 1983 (Suvapepun, 1991). Declines were particularly dramatic for long-lived fish (e.g. rays and sawfish) as well as for several families of smaller fish, while squids increased in abundance. Shrimps initially declined but then increased somewhat again. Pauly (1985) found an inverse relationship between the mortality of small squid and the biomass of fish, and suggested that the increase in squid was caused by the removal of their predators. Harris and Poiner (1991) studied a similar system in the southeastern Gulf of Carpentaria, Australia, but found comparatively little change over time. Comparing the composition of the fish fauna before the start of the prawn fishery with surveys made 20 years later, the majority of the taxa examined showed no significant change in abundance. The modest levels of fishing compared to the Gulf of Thailand (Blaber *et al.*, 1990) may explain the different response.

[22] On the Saharan Bank, in West Africa, catches of cephalopods were low until the 1960s, when landings rapidly increased. Before the 1960s, the landings were mainly composed of demersal fish, and when the species composition changed towards cephalopods this was interpreted as a change in the ecosystem mediated by an overexploitation of sea breams (Sparidae) (e.g. Caddy and Rodhouse, 1998). However, a recent analysis of survey data shows that the changes in the relative species composition of the fauna were much less dramatic than the landings data would suggest (Balguerias *et al.*, 2000). Comparing survey data from 1942 with recent data, the most apparent change was a major decrease in the total catch rate in the surveys, by a factor of seven. This decrease was most severe for long-lived species of sharks and rays, but finfish and commercially important crustaceans such as lobsters and large crabs also declined in relative abundance, at the same time as other crustaceans and benthic cephalopods increased. The authors attribute the increase in benthic cephalopods to reductions in predator populations and increases in the food available to scavengers due to increased discarding.

[23] Sainsbury (1991) and Sainsbury *et al.* (1997) studied the changes in the fish fauna on the northwest shelf of Australia. A trawl fishery for demersal fish developed in the beginning of the 1970s, targeting mainly breams, lizardfish, emperors and snappers. Later a trap fishery for the two latter species evolved. Research surveys from 1960 onwards showed changes in species composition but little change in overall fish biomass. The abundance of emperors and snappers declined, while the biomass of lizardfish and breams increased. At the same time, the quantity of large epibenthos (mainly soft corals and sponges) declined, possibly due to fishing. To resolve the question of whether the changes in the fish fauna were due to changes in species interactions, to the removal of large epibenthos, or whether they could be explained by differences in the life history parameters of the four species, an experiment was designed in which a part of the area was closed to trawling. Later examination of data collected from the area suggested that the removal of soft corals and sponges by the fishery was the most likely explanation for the observed changes in species composition. Thus, in this case, the changes in the fish fauna seem to have been caused by habitat modification rather than by changes in predatory or competitive interactions between the species.

Upwelling systems

[24] Upwelling systems are subject to large, environmentally driven fluctuations. One of the most noticeable changes in such a system took place off Peru in 1972. The area along the Peruvian coast is highly productive due to wind-driven upwelling of nutrient rich water, and the production of pelagic fish in the area varies in response to the upwelling intensity. In years with weak winds and little upwelling, smaller catches are taken, and vice versa. The changes in the strength of the wind are influenced by the so-called El Niño – Southern Ocean oscillation (ENSO), driven by changes in atmospheric pressure systems. In 1972 and 1973, the upwelling intensity was particularly low and this had a major impact on the fishery of anchovies. In 1970, the fishery landed 13 million tonnes of anchoveta, but the landings fell to 2-3 million tonnes in subsequent years, and to 1 million tonnes in 1980. Following the decline of the anchoveta landings, sardine landings increased, but in 1995 anchovies recovered again. The reduction of the anchovy population had a large impact on species of seabirds such as the guanay cormorant, whose population declined due to starvation and reduced breeding. Figure 4 shows how the increase in the landings of anchoveta in the 1960s was accompanied by a reduction in the number of breeding guanay cormorants. Similar changes in seabird mortality and breeding success have been observed in other upwelling systems (Crawford and Dyer, 1995, Crawford and Jahncke, 1999).

[25] Shifts between anchovy- and sardine-dominated periods have been observed in many upwelling systems throughout the world (Schwartzlose *et al.,* 1999). The shifts seem to be triggered by the formation of one or a couple of extraordinary year-classes. This may happen while the other species is still abundant, and does therefore not necessarily represent a response to a reduction in the stock size of a competing species. Rather, a combination of environmental changes and fishing seem often to be involved. Excessive fishing may reduce the abundance of the dominating species to the point where a couple of low year-classes will lead to a collapse of the stock. Fishing may also concentrate on abundant year-classes and thus prevent the least abundant fish from becoming dominant. Records of scale deposits in anoxic sediments thus show that large population fluctuations have occurred in the Californian upwelling system over several millennia and long before any fishing started (Baumgartner *et al.,* 1992). Furthermore, many of the recent fluctuations exhibit a global synchrony, suggesting that climate may be the major driving force (Klyashtorin, 1997). However, in a review of the impact of ten major fisheries for small pelagic species, Beverton (1990) concluded that fishing was the main cause of the collapses observed in most, but not all cases, and the relative role of climate and fishing in the collapse of exploited stock of small pelagic species remains controversial (Cury *et al.,* 2000).

Deep-sea ecosystems

[26] Most of the fisheries exploiting continental slope and deep-sea resources have a relatively short history, and the indirect effects that these fisheries may cause are largely unknown. Deep-sea fish species are characterized by slow growth, extreme longevity, low fecundity and high age at first maturity, and any indirect effects of their removal are therefore likely to require considerable time before they may result in measurable change (Koslow *et al.,* 2000). Deep-sea fishing has, however, been shown to have a potentially severe impact on deep-sea corals and other benthos on the seamounts where many of the commercially exploited fish species congregate. The ability of the benthos to regenerate has not been investigated, but is most likely low. No data are available to demonstrate how the altered habitat will affect the remaining fauna.

Indices of fisheries generated changes in ecosystem structure and functioning.

[27] The general wish to develop precautionary management systems that take the ecosystem effects of fishing into account has generated a search for useful reference points for ecologically dependent species, as well as for overall trophic level balance (Christensen, 2000, Gislason *et al.*, 2000). In some instances, reference points for forage species have been developed that take the food requirements of their natural predators into account (e.g. Constable *et al.,* 2000; ICES 2001). The development of such reference points requires that strong trophic linkages can be identified and that biologically significant indicators can be monitored, such as the condition, diet composition, breeding success or abundance of the predator.

[28] Indicators that take overall trophic level balance into account have not yet been fully developed. A number of indices have been proposed, but their ability to reflect changes in trophic level balance awaits further investigation and reference points have not yet been identified. In the following, I will give a brief description of two of the proposed indicators, the slope of size spectra and the so-called Fishing-in-Balance (FIB) index.

[29] Size is an important determinant of trophic interactions in marine systems. Cod larvae will be feeding on plankton prior to settlement, juvenile cod on crustacea and other small invertebrates, while adult cod will eat larger invertebrates and increasingly more fish as they grow. It is therefore not unreasonable to assume that size by and large determines an individual’s trophic position in the food web. If this is so, then the shape of the overall size distribution should reflect how energy is transferred between trophic levels (e.g. Borgman, 1987; Thiebaux and Dickie, 1993). Pope and Knights (1982) compared the size composition of demersal fish caught by bottom trawl surveys in the North Sea and at the Faeroe Islands and found that a straight line fitted log numbers per size class versus size in both cases. Subsequent comparisons of size spectra from demersal fish communities from various parts of the world has confirmed that the log of the numbers per size group often is linearly related to the size of the fish and has suggested that the slope of the spectrum is related to fishing intensity (Pope *et al.,* 1987; Murawski and Idoine, 1992; Gobert, 1994; Bianchi *et al.*, 2000). Figure 5 shows how the slope of the size spectrum in the North Sea has changed over time. There are now relatively fewer large fish in the system than there were at the beginning of the time series. Similar reductions in the slope have been observed in a number of other systems (Bianchi *et al.,* 2000).

[30] Gislason and Rice (1998) modelled the North Sea size spectrum and found that the slope was inversely proportional to overall fishing mortality. However, the relationship was found to be sensitive to changes in species growth. Almost identical changes in slope were found for spectra simulated by single and multispecies models, suggesting that changes in predator prey relationships may be relatively unimportant compared to the other life history parameters of the included species. The finding that the slope of the size-spectrum is inversely proportional to fishing would make it suitable as an overall indicator of fishing impacts. However, as concluded by Bianchi *et al.* (2000) the usefulness of the size-spectrum slope for management purposes is currently limited, as there is insufficient empirical and theoretical background for the changes observed. It is also unclear how suitable reference points could be defined.

[31] The FIB index represents another attempt to capture the effect of fishing on the energy transfer in the food web (Pauly *et al.*, 2000). The FIB index attempts to capture the effect of predator removals. Biological production increases by roughly a factor of ten moving one trophic level down in the food web. If fishing reduces the mean trophic level by one, we would assume that this would generate a ten-fold increase in landings, provided the fishery was able to harvest the surplus production. The FIB index of a given year, *y*, is calculated relative to the FIB index in the first year, 1, of a time-series of catch data from the equation:

$$\mathrm{FIB} = \log\left[\left(\mathrm{Catch}_y \times \mathrm{TE}^{\mathrm{TL}_y\text{-}1}\right)/\left(\mathrm{Catch}_1 \times \mathrm{TE}^{\mathrm{TL}_1\text{-}1}\right)\right]$$

where TL is the average trophic level and TE is the mean energy-transfer efficiency between trophic levels (Christensen, 2000). The FIB index will stay constant if a decrease in the average trophic level is matched by a sufficiently large increase in the catch.

[32] Christensen (2000) applied the FIB index to the Gulf of Thailand and the North Atlantic. For the latter area, the index increased as the fishery expanded over the period from 1950 to 1976 and then decreased from 1976 onwards. For the Gulf of Thailand, the index initially rose, but then remained at a constant level for the remaining period (Figure 6). This would indicate that the fishery in the Gulf of Thailand is in balance as the catches increased in the expected way even though the average trophic level of the catch declined from approximately 3.4 to 3.2. In the North Sea, the FIB index shows an overall increase up to 1970, before it levels off (Figure 7), while the global FIB index increases up to 1987 before it stabilizes (Figure 8).

[33] It is still too early to judge the utility of the FIB index as a measure of trophic balance. It tries to capture the extent to which fishing disrupts the flow of energy from the lower trophic levels. The index can be easily quantified from landing statistics, and trophic levels from published ECOPATH models, but just as for the size-spectrum slope, it is not known exactly when a reduction in the index is a cause for alarm. Assume, for instance, that the fishing effort in the North Sea is halved, resulting in a 50% reduction in the catch of all species the following year. In this case, the average trophic level of the catch remains constant, but since the catches are halved the FIB index will decline in the short term and not increase until either the catch or the average trophic level increase again.

A brief summary of the changes observed

[34] Fishing may affect ecosystem structure and function through at least four mechanisms. Firstly, direct removal of species with different life histories may lead to shifts in the relative abundance of species within the community, independent of any change in species interactions. Secondly, the changes in the relative abundance of target and non-target species may lead to indirect effects mediated by changes in predator-prey relationships or competition. Thirdly, gear in contact with the seabed may modify the habitat by removing stones and boulders or by damaging corals and other fauna or flora that provide a structural habitat, and this may influence the composition of the fauna. Finally, discarding of fish and offal may increase populations of scavenging species. All of the four processes probably work in combination, and all result in shifts in the relative abundance of the various species in the community.

[35] It is well documented that fishing can lead to shifts in community structure and composition by removing fish with different life histories. Fishing imposes mortality on target and by-catch species, and life-history theory predicts that populations of large, slow-growing, late-maturing species should decline more in response to fishing than small, early-maturing species (Kirkwood *et al.*, 1994). Comparing the relative decline of large and small species within closely related groups, Jennings *et al.* (1999a, b) thus found a significant greater decline in the abundance of the larger species, both in reef fishes in Fiji and in demersal fishes in the northern North Sea. Many species of sharks and rays are large, grow slowly and mature at a high age, and the virtual extirpation of some of these species from large regions (Stevens *et al.*, 2000) provides a good

example of the importance of life history characteristics for the ability to withstand fisheries-generated mortality.

[36] Reductions in populations of forage fish have been reported to affect the growth, reproductive rate, and population size of their natural predators. For instance the condition and growth of cod in the Barents Sea and around Iceland changed in response to changes in the abundance of capelin (Mehl and Sunnanå, 1991; Yaragina and Marshall, 2000; Stefánsson *et al.*, 1998), and cod growth in the Baltic seems to be related to the abundance of sprat (Gislason, 1999). There have also been well documented cases where natural or fisheries-induced reductions in forage fish abundance have led to collapses of seabird populations. The most prominent examples come from upwelling areas, where changes in pelagic fish stocks can have a large impact on the seabird populations feeding upon them (Crawford and Dyer, 1995; Crawford and Jahncke, 1999). There are also examples from other areas, such as the starvation of seabirds in colonies along the Norwegian coast following the fisheries-induced collapse of the Atlanto-Scandian herring stock (Anker-Nilssen *et al.*, 1997). For mammals, the reductions in the growth of Steller sea lions (NCR, 1996) and the lack of food that resulted in a mass migration of harp seals along the coast of Norway in 1987 (Livingston and Tjelmeland, 2000) may be linked to fishing.

[37] Predator removal has been suggested as leading to increases in prey populations. In a range of ecosystems, predation has been estimated to remove between 2 and 35 times more of the total fish production than fishing (Bax, 1998). It would therefore be surprising if prey populations did not respond when fishing reduced the abundance of their predators. However, prey-releases following predator removal does not appear to be quite as common as intuition would suggest. In the coastal zone, sea urchin populations on coral reefs and in kelp beds have responded to changes in predator abundance, but reductions in the abundance of fish-eating fish species on coral reefs have not lead to increases in the abundance of their fish prey (Roberts, 1995; Jennings and Kaiser, 1998). Comparisons of the fish fauna inside and outside areal closures in coastal, tropical and subtropical areas also suggest that indirect effects are of minor importance (Mosquera *et al.*, 2000). Systems found in deeper waters are not as easily manipulated and the lack of controlled experiments makes most of the evidence from these areas circumstantial. The increases in populations of forage fish such as the sprat population in the Baltic (Rudstam *et al.* 1994), sandeel on Georges Bank (Fogarty *et al.*, 1991), and capelin in the North West Atlantic (Carscadden *et al.*, 2001) have been attributed to fisheries-generated reductions in predator populations. However, environmental changes may be involved as well.

[38] Competition has less often been suggested as a likely explanation for changes in species abundance. There have been dramatic shifts in species composition in the fisheries for small pelagics, where one species apparently replaced another, but a closer look at the available time series data show that the subordinate species often started to increase before the dominant began to decrease. In many cases the shifts are correlated over large distances, suggesting that change in global climate is involved (Schwartzlose *et al.*, 1999). Perhaps the best example of competition comes from Georges Bank, where fishing greatly reduced the biomass of demersal fish and this in turn led to an increase in small sharks and rays. However, as Fogarty and Murawski (1998) comments, it is unknown whether resources such as food and space were in fact limiting for the sharks and rays prior to the change. In their review of the ecosystem effects of fishing, Jennings and Kaiser (1998) concluded that little evidence exists to suggest that fishing has resulted in compensatory replacements of one species by another.

[39] The experimental studies of areal closures on the North West Shelf of Australia by Sainsbury (1991) and Sainsbury *et al.* (1997) demonstrate that habitat modification can be important. The removal of soft corals and sponges by the fishery was the most likely explanation for the changes observed. Similar results emerge from studies of fish assemblages on coral reefs. In deeper waters, it has generally been difficult to link changes in fish assemblage structure to

fisheries-generated habitat changes. However, a recent study links low survival of juvenile cod to reductions in habitat complexity caused by mobile fishing gear (Lindholm *et al.,* 2001).

[40] A large proportion of the discards from fishing vessels is eaten by seabirds. For some of the species involved this seems to have resulted in population increases, with subsequent changes in the species composition of the seabird community (Tasker *et al.,* 2000). The fate of the fraction of the discards that sinks through the water column is uncertain, but studies suggest that mid-water scavengers, such as cetaceans and sharks, may benefit. The proportion that ends on the seabed adds to the benthos, together with fish that have been damaged or killed by the gear but escaped before it was brought on deck (Jennings and Kaiser, 1998). This source of food is eaten by a number of scavenging invertebrates and fish. While the effects of discarding on seabird population are reasonably well understood, the long-term effects on mid-water and demersal scavengers are unknown, as are the consequences of the changes in the interactions with their natural prey.

[41] Most of the evidence for fisheries impacts on ecosystem structure comes from systems where biota important for the structure of the habitat has been affected either directly or indirectly (e.g. coral reefs, soft corals and sponges) or where strong trophic linkages occur, such as in the so-called “wasp-waist” systems, where the major part of the energy has to pass through one or a few species positioned at an intermediate level in the food web (e.g. capelin and herring in the Barents Sea; sardines and anchovies in upwelling systems). This is not to say that food web effects can be safely neglected elsewhere. The availability of data and scientific effort differs from one system to another and this could bias the conclusion. Coastal ecosystems are much more accessible for direct observation and experimentation than systems in deeper water. Species richness increases as one moves from boreal and temperate systems towards the tropics, at the same time as the availability of data and scientific effort decrease. The common use of regressions to relate ecosystem change to fishing and the existence of diffuse effects in complex systems (Yodzis, 2000) probably means that the likelihood of identifying a relationship decreases as the complexity of the systems increases, at the same time as the number of possible explanatory variables grow. However, the relative scarcity of reported effects from the more complex systems may also reflect a real difference in stability. Theoretical studies have shown that increasing diversity will increase food web stability provided the interactions between the species are weak (McCann 2000) and this could very well be one of the underlying overall themes.

ACKNOWLEDGEMENTS

[42] Thanks to Villy Christensen for providing figures on changes in the FIB index for the Gulf of Thailand, the North Sea and for Global Marine Fisheries landings, as well as to Tom Fenchel, Louize Hill and Morten Vinther for providing useful comments and suggestions on draft version of the paper.

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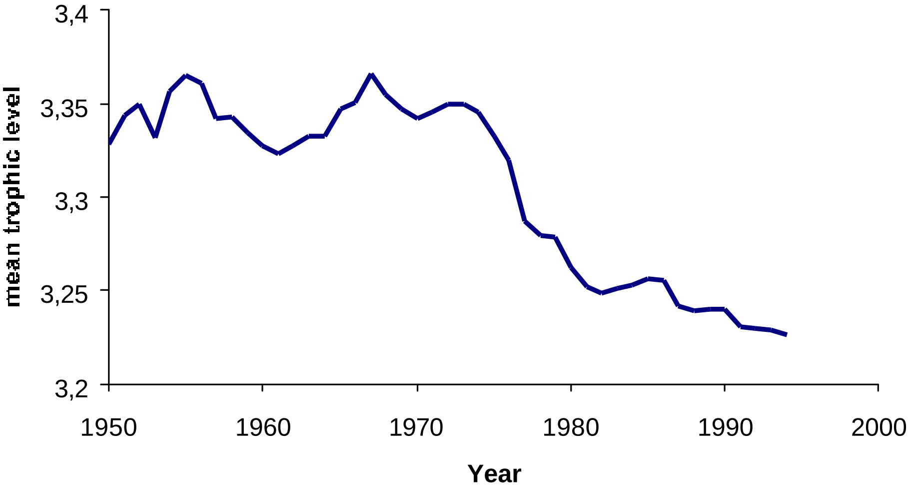

Figure 1. Mean trophic level of global landings (from Pauly *et al.* 1998)

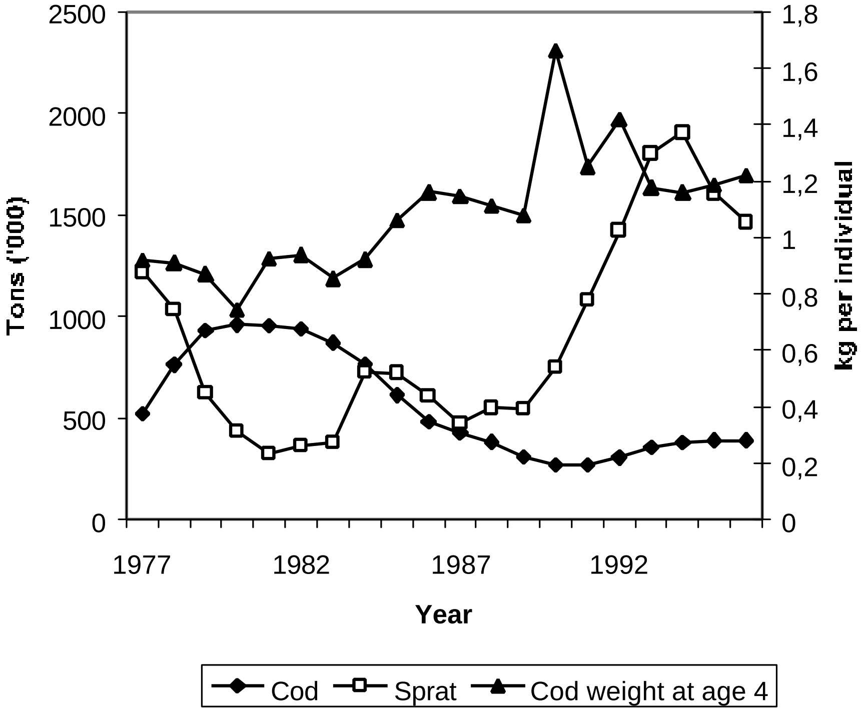

Figure 2. Changes in Spawning Stock Biomass of cod and sprat in the Baltic together with cod weight at age 4 (modified from Gislason 1999)

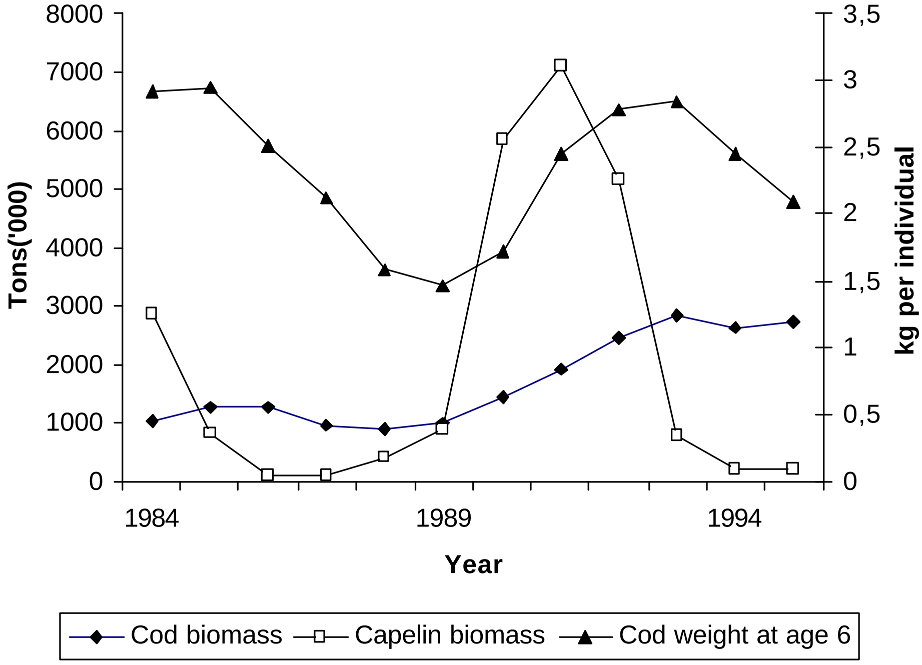

Figure 3. Changes in average biomass of cod and biomass of capelin in the Barents Sea together with cod weight at age 6 (data from Bogstad and Mehl(1997))

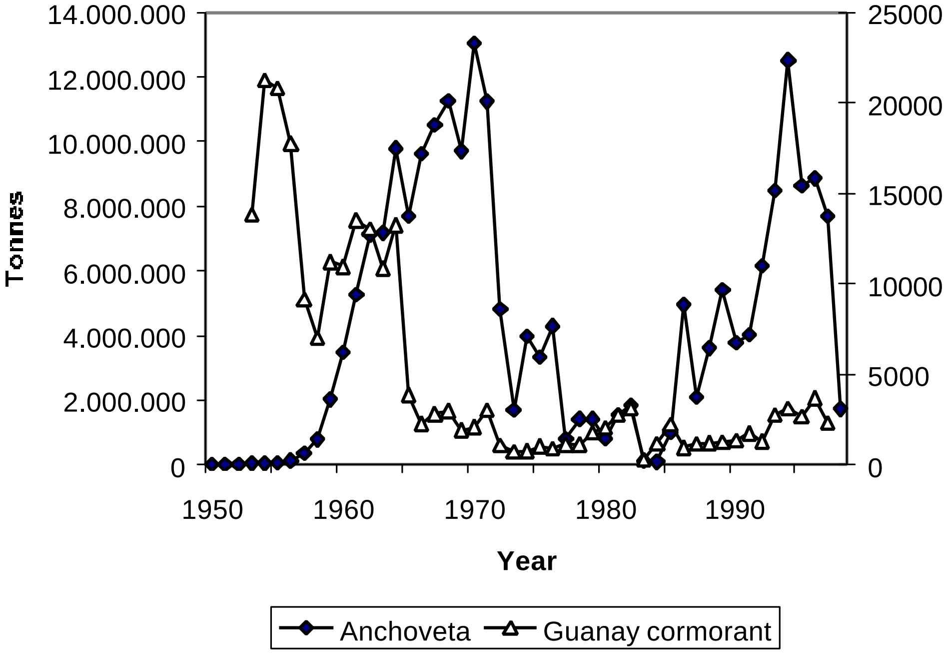

Figure 4. Landings of anchoveta and sardines in Peru and Chile and population size of Guanay cormorants (data from FAO landings statistics and Crawford and Jahncke(1999))

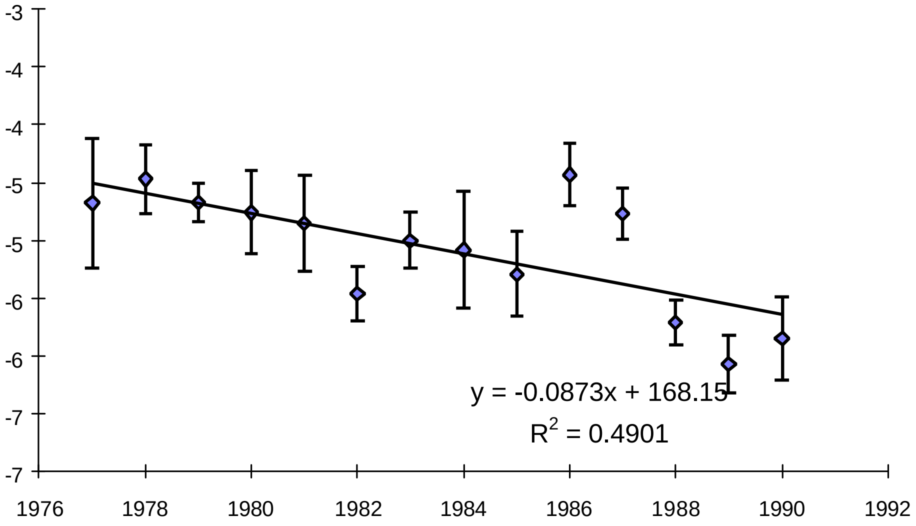

Figure 5. Changes in the slope of the size spectrum of North Sea fish as caught during the International Bottom Trawl Survey (ICES 1996)

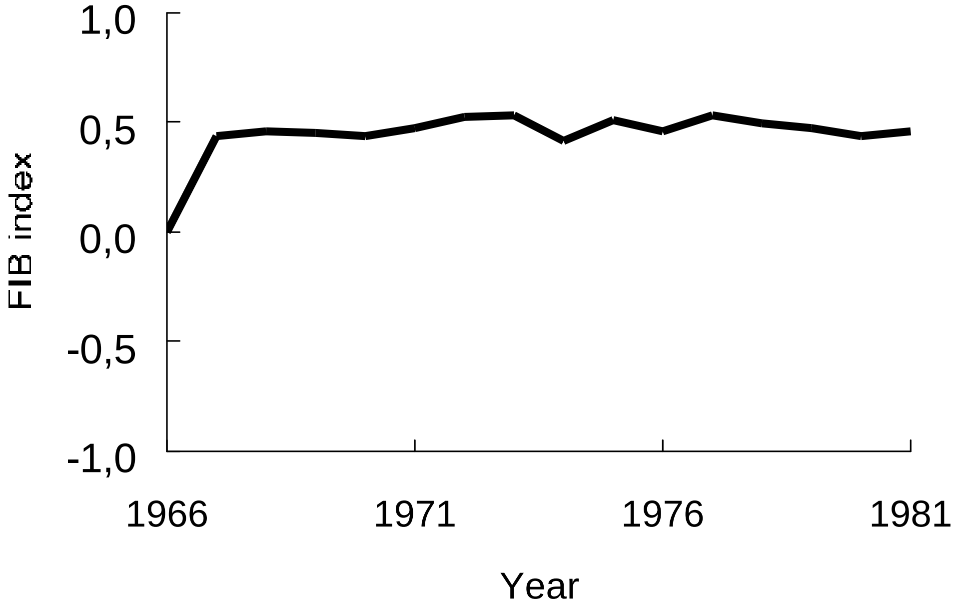

Figure 6. Changes in the FIB index of the Gulf of Thailand landings (from Christensen, 2000)

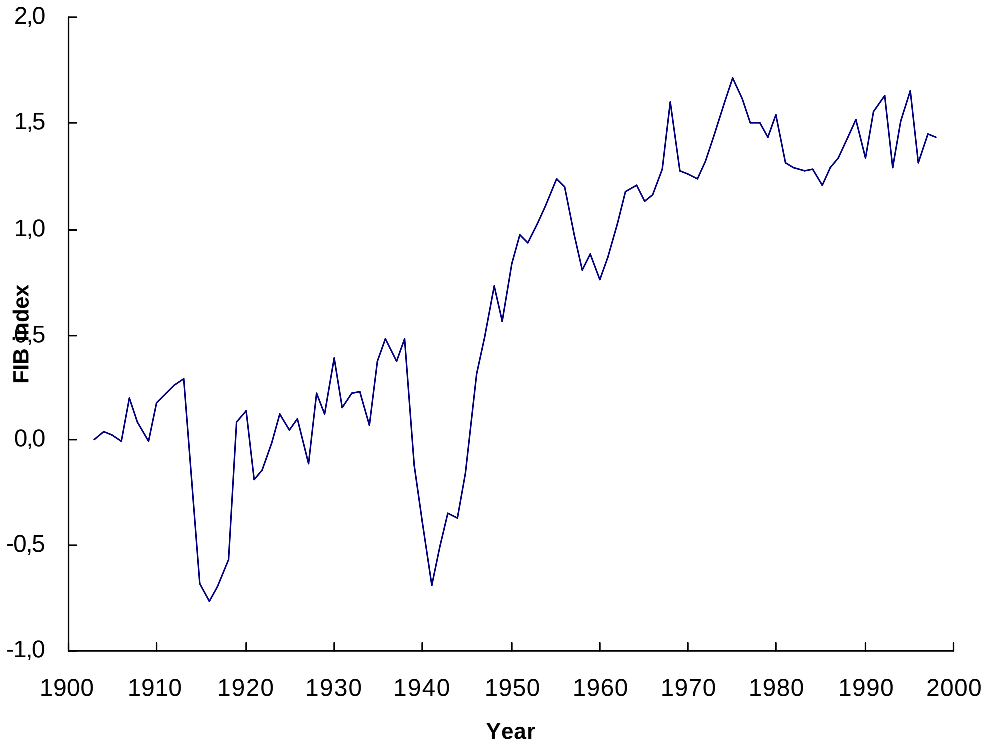

Figure 7. Changes in the FIB index of the North Sea landings (data kindly supplied by Villy Christensen)

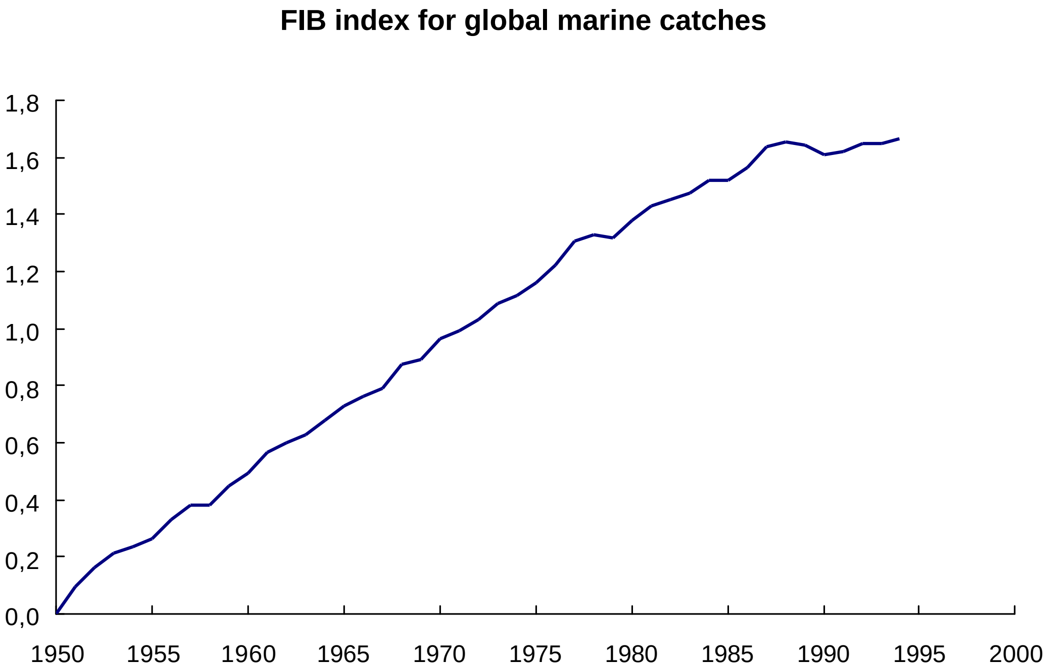

Figure 8. Changes in the FIB index of global marine landings (data kindly supplied by Villy Christensen)