Managing fisheries involving predator and prey species

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Abstract

Several management strategies for ecosystems with biological interaction are discussed, including predator removal, predator–prey coexistence, prey exploitation, overexploitation, and introduction of sanctuaries. Some case studies related to ecosystem management are briefly presented; these describe Lakes Victoria and Tanganyika, discarding from shrimp trawl fisheries and the development in the North Sea that led to introduction of multispecies analysis. The concept of 'fishing down the food web' is discussed and the average trophic levels at which the fisheries operate in different ecosystem types are estimated based on quantified trophic flow models. On a global level, while on average fisheries operate around two trophic levels above the primary producers, still one third of the catch of the 70 major fish species caught in the world is of piscivorous fish. Using exploitation-predation rate indices for different ecosystem types, the amount of finfish

consumed globally by finfish is roughly estimated to be three times the catches of finfish. Finally some implications for the management of ecosystems are drawn up. It makes little difference if short-term prognoses are based on single-species or multispecies considerations. Multispecies models may, however, give the better long-term advice, and adaptive management may facilitate the move towards such long-term goals.

Introduction

Biological interaction between fish species was largely ignored in the pioneering decades when fisheries science developed into a quantitative discipline. More recently – at least since the mid 1970s – a continued discussion has focused on how best to manage fisheries resources taking, where necessary, biological interaction into account. As one example, Pope (1979) developed Schaefer's surplus-production model to account explicitly for biological and technological interactions, where the biological interactions were considered in context of predator–prey or competitive relationships. Based on Pope's (1979) study it can be concluded that if the fish species in an ecosystem are linked mainly through predator–prey relationships, the overall maximum sustainable yield (MSY) for the system will be higher than if the species are mainly competing with each other. This illustrates the importance of considering predator–prey interactions in fisheries management: proper management incorporating biological interactions may lead to increased yield.

Management of ecosystems with biological interaction

Empirical evidence points to ecosystems being conservative units. For heavily exploited systems, we often see that species abundances and compositions of the catches are highly variable, yet the total system biomasses and catches do not vary much (Ursin, 1982). Often it seems that a (smaller, faster-growing) species will take over the niche made vacant from another (larger, slower-growing) species (review: Daan, 1980). Yet it is difficult to show that such replacement is actually caused by either competition or predation (Shelton, 1992).

We may expect fish populations to influence each other, but does this actually show up when examining variation in population abundances? The evidence is not conclusive. Sissenwine *et al.* (1982) examined 724 combinations (with time lags) of population units of the Georges Bank and southern New England area without finding any valid evidence of population interactions; yet they did make a positive finding: strong year classes of fish predators and prey species did not co-occur.

In contrast, Fogarty *et al.* (1991) found for the same area that recruitment of sand lance (*Ammodytes* spp., Ammodytidae) was negatively correlated with abundance of its two main predators, herring (*Clupea harengus*, Clupeidae) and mackerel (*Scomber scombrus*, Scombridae). Also Henderson *et al.* (1973) found for the simpler, pelagic ecosystem of Lake Tanganyika that 80% of the variance in clupeid abundance was due to the predatory *Lates* spp. (Centropomidae), while fishing effort and clupeid abundance showed no significant correlation.

On the same topic, Punt and Hilborn (1994), in a comparison of fishery models with and without cannibalism, concluded that one cannot assume beforehand that inclusion

of multispecies interactions in assessment and management procedures will necessarily provide for better fisheries regulation.

At present there are no clear guidelines for how biological interaction should influence management; there are, however, many examples of how management has progressed with or without consideration of biological interactions. In the following I will give an overview of a number of such management strategies ranging from predator removal to introduction of sanctuaries.

PREDATOR REMOVAL

As a fishery develops in an unexploited area, the initial target species are often the larger, higher-priced species, i.e. the top predators. Likewise, in offshore ocean areas, the only economically viable strategy for exploring the vast expanses has so far been fishing for the apex predators. This initial exploitation pattern may well be called the 'tuna strategy' following Pauly (1979). If well managed, the strategy can result in a sustained biomass of top predators around half of their maximal level, and in total catches maintained at the maximal sustainable level, MSY.

A second form for predator removal is as well known, and much more debated, the 'whale strategy' of Pauly (1979). Here the top predators are fished so heavily that their biomass and production decline to close to zero, resulting in an increase of their prey's biomass to a maximum level. Fisheries interests in such cases have often included a targeted exploitation of the increasingly abundant prey. In the case of the Antarctic system this concerns krill, *Euphausia superba*, which is now exploited at a level around 300 000 tonnes·year^{-1}.

A third type of management strategy involving predator removal exists where both predator and prey stocks are exploited, and catches perhaps are diminishing. Fisheries biologists worldwide adhere in such cases to their traditional advice: 'reduce fishing mortalities', which translated to managers reads: 'reduce fishing'. What needs to be reduced is, however, the total mortality, a large fraction of which may be due to predation. Therefore, the feasibility of reducing predation and thus gaining more for the fisheries has often been considered.

Such a situation can be illustrated from Munro's (1983) studies of the Jamaican trap fisheries (Fig. 1). Here a comparison of five localities showed an inverse relationship between fishing intensity and predator biomass. Munro (1983) also reports that the
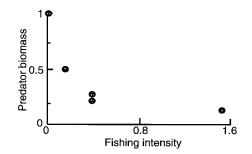

Fig. 1. Relative biomass of predatory fishes as a function of relative fishing intensity in five different areas of the Jamaican trap fisheries (based on Munro, 1983).

recruitment of prey fish species seemed to be better in the more intensively fished areas, indicating that the reduced predator biomass might actually lead to more prey fish for the fisheries. This may seem obvious, but it has rarely been demonstrated.

To illustrate aspects of the discussion that has taken place on the potential of the predator removal strategy, three case studies will briefly be presented. Two of these concern the African Great Lakes, where drastic improvements of catches have often been suggested as possible through exploitation of the lower trophic levels (see contributions in Pitcher and Hart, 1995). The third case deals with discards from trawl fisheries and is included to show the complexity of the discard issue when biological interaction is to be considered.

Lake Victoria

The possibility for increasing catches through predator removal was considered by Marten (1979), who wrote: "Lake Victoria's artisanal fishery has an overfishing problem. A possible solution is suggested by records showing that fish catches are best where predator populations have been reduced by fishing. It may be possible to remedy overfishing by increasing fishing effort, provided that additional effort is directed toward predators."

The predators discussed by Marten (1979) were catfish; the prey fishes for which increased catches were hoped were tilapia and haplochromines. We can study more closely what happened to the ecosystem of Lake Victoria around the time and after Marten made his suggestion, using two trophic models of the shallow and intensively exploited Kenyan sector of Lake Victoria, representing the time periods 1971–1972 and 1985–1986, respectively. The models were presented by Moreau *et al.* (1993b) and some of their results are summarized in Table 1.

Between the two study periods, the catches increased by a factor of five due to the proliferation of Nile perch, *Lates niloticus*. The Nile perch were introduced in the 1960s but only a couple of decades later were they caught in sizable quantities. The high catches were, as suggested by Marten (1979), linked with increased fishing effort, and with a fishery targeted on predators. This did not, however, lead to reduced predation, nor were the increased catches composed of prey fish. Instead the increased catches are linked with much higher trophic transfer efficiencies on the upper trophic

Table 1. Biomasses, catches and loss to predation (all in tonnes·km^{-2}·year^{-1}) for four species groups, and for all fishes of the Kenyan sector of the Lake Victoria ecosystem in 1971–1972 and 1985–1986 (based on data from Moreau *et al.*, 1993b)

Species group	Biomass		Catches		Predation loss	
	1971–1972	1985–1986	1971–1972	1985–1986	1971–1972	1985–1986
Nile perch	0.0	17.3	0.0	10.0	0.0	5.3
Catfish	2.8	1.7	0.8	0.2	1.3	1.2
Tilapia	2.5	13.0	0.7	2.0	1.7	9.3
Haplochromines	8.4	0.6	1.1	0.0	15.8	1.5
All fish	27.0	43.4	3.3	16.5	33.3	30.8

levels (Table 2). This is indicative of how the fish resources of Lake Victoria are now much more utilized for human consumption (Moreau *et al.*, 1993b).

The situation as it evolved was very different from that suggested by Marten (1979), and we can only speculate whether additional increases may be gained by increasing the fishing pressure on the predators even more. We may equally speculate whether the drastic changes in the Lake Victoria ecosystem, with the reported depauperation of haplochromine diversity (Achieng, 1990), were due solely to the impact of Nile perch or whether commercial fisheries for haplochromines accentuated the process. For the offshore haplochromines, it is thus reported that bottom trawling from 1973 resulted in a serious decline in haplochromine biomass (Witte and Goudswaard, 1985), while Nile perch from 1983 added to the removal so that the fishery stopped in 1986 when catches were close to nil (Wanink *et al.*, 1988).

Lake Tanganyika

Lake Tanganyika is an old, deep, African lake with a highly productive pelagic zone of some 31 000 km². In its lightly exploited state the lake showed remarkably high biomasses of predatory fish relative to prey fish (Coulter, 1981). Typically, purse seining in areas with no or low fishing pressure would yield catches with 50–70% by weight of predatory fish. Therefore Coulter (1981) hypothesized that it would be possible to increase the overall yield from the lake considerably through applying a high fishing pressure on the predatory fish species.

In an attempt to quantify the potentially harvestable production of small pelagics in Lake Tanganyika, Coulter (1981) came to an estimate of 1.1 million tonnes·year^{-1} (or 35 tonnes·km^{-2}·year^{-1}) for the lake, using what he considered to be a conservative version of Gulland's (1971) formula for quantification of potential harvest. This was based primarily on the assumption that the excessive predation pressure on the clupeoids (*Limnothrissa miodon* and *Stolothrissa tanganicae*) could be diminished through a high purse-seine fishing pressure which primarily would influence the longer-lived fish species, notably the predatory Nile perches (*Lates* spp.) in the lake.

The development has not progressed as suggested by Coulter (1981). For the Burundi sector of the lake, i.e. the same area as studied by Coulter, Moreau *et al.* (1993c) presented catch rates which were half of those from the mid 1970s to the early 1980s, while fishing rates increased (Table 3). The explanation of this is that the predation mortalities which Coulter (1981) assumed would be reduced drastically following intensified fishing, increased instead of decreased (Table 4), resulting in a reduction in yield.

Table 2. Trophic transfer efficiencies (%) for the Lake Victoria ecosystem before and after the proliferation of Nile perch. Transfer efficiencies are computed as the percentage of the flow entering a trophic level that is subsequently transferred to the next trophic level or harvested. Estimated using ECOPATH from data given by Moreau *et al.* (1993b)

	Trophic level				
	II	III	IV	V	VI
1971–1972	16	12	7	5	5
1985–1986	16	19	11	11	11

Table 3. Catches (tonnes·km^{-2}·year^{-1}) from the Burundi sector of Lake Tanganyika (from Moreau *et al.*, 1993c, based on data from various sources)

Species/group	Catch (tonnes·km^{-2}·year^{-1})	
	1974–1976	1980–1983
Large predators	0.6	0.05
Small predators	3.5	1.8
Limnothrissa sp.	1.4	0.8
Stolothrissa sp.	6.5	3.1
Total	12.0	5.8

Table 4. Fishing (F) and predation mortalities ($M2$) (both year^{-1}) for small pelagics in the Burundi sector of Lake Tanganyika in the mid 1970s and early 1980s (calculated from data in Moreau *et al.*, 1993c)

Species/group	F		$M2$	
	1974–1976	1980–1983	1974–1976	1980–1983
Limnothrissa sp.	0.3	0.5	2.6	3.3
Stolothrissa sp.	0.5	0.7	4.2	4.5

Shrimp fisheries

Shrimp fisheries are a major source of income in many developing countries. A major problem associated with these fisheries has been that large quantities of fish are taken as bycatch, and subsequently the vast majority is discarded due to limited possibilities for holding onboard and limited market demand. Alverson *et al.* (1994) estimated these discards at 9.5 million tonnes annually on a global level, corresponding to more than 5 times the shrimp landings.

The ecosystem impacts of the high discard rates from the shrimp fisheries are unknown. Estimates from Kuwait (Pauly and Palomares, 1987) indicate that fish consume about three times as much shrimp (in weight) as is landed, even with the current high discard rates of fish. One might then speculate whether reduction of the fish bycatch level would actually be counterproductive as more surviving fish would lead to increased predation. Adding to the problem is that there is evidence from at least one tropical area of an impact of fish predation on penaeid shrimp recruitment (Pauly, 1984).

Discards can potentially increase shrimp production if the shrimp feed on the discards, as discussed by Cushing (1984). Cushing noted that the shrimp stocks in the Gulf of Mexico had been exploited without recruitment failure for decades, and raised the question whether discards provide enough food for the shrimps to counter potential recruitment overfishing.

Whereas the interpretation of the studies above may be to exercise caution before introducing selective trawls to reduce discarding of finfish, the study of Sheridan *et al.* (1984) suggested that predation by fish on shrimps may be of less importance, as only

a few fish species seem to take penaeid shrimp in notable proportions of their diets. Based on two modelling approaches, Sheridan *et al.* (1984) also found that a reduction of discards through selective trawls seemed to have only minimal influence on shrimp abundance. Their modelling suggested that the increased abundances of predatory fish would lead to increased stocks of dolphins, which subsequently would reduce the predation pressure on the shrimps by feeding on the predatory fish. Such a long-term, indirect modelling prediction may or may not hold true.

Other studies also indicate that discards may be of minor importance as food for shrimps. Hill and Wassenberg (1990) found that sharks, dolphins and birds were the most important scavengers of discards from shrimp trawl fisheries off northern Australia, whereas scavenging by invertebrates, including shrimps, was negligible.

In conclusion, we do not have sufficient information to tell whether selective shrimp trawls aimed at reducing discarding of finfish would subsequently have detrimental impact on the shrimp stocks. To explore the problem, more studies of the trophic dynamics of shrimp ecosystems are needed.

PREDATOR AND PREY COEXISTENCE – MULTISPECIES MANAGEMENT

Removal of predators, as discussed above, has been done successfully in lakes, even if an occasional by-product of predator removal has been large populations of growth-limited prey species of little interest for human exploitation. However, in more complex systems it may not be a realistic measure, and less radical, but from a scientific point of view more difficult, measures may be of interest. Focus here is on management of systems where predator and prey species coexist and both are harvested through targeted fisheries, which is best discussed based on the area where multispecies modelling has progressed furthest, the North Sea.

The North Sea experience

In the 1970s, the industrialized fisheries in the northern temperate North Sea faced severe problems of overfishing. It was clear that the biological advice needed improvement, and that new methodologies were necessary to achieve this. The methodologies used by fisheries biologists at the time assumed that fish populations could be managed independently. Working groups of the International Council for Exploration of the Sea (ICES) in Copenhagen, Denmark, gave advice for each of the commercially important fish species in the North Atlantic based on the assumption that management interventions for one species in an area would not have noticeable influence on other species in the area. For lightly exploited stocks this often holds true, but in overexploited areas the methods risk failure, and it appears now that such failures were committed.

The advice from different working groups – of predator and prey species alike – to the managers and fishers would practically always be to reduce fishing effort to a fraction now, and they could foresee great increases in catches; more and bigger fish in a few years time when the stocks have rebuilt. The advice was used by the managers to set quotas, which nearly always ended up being higher than recommended by the biologists, while the actual catches were even higher as economic constraints do not allow fishers to wait a few years. The higher catches were in turn often taken as an explanation (or excuse) for why the stocks did not improve as they should have.

A problem faced was that if the stocks and average sizes of predatory fish increase,

their consumption of prey fish will increase as well. In addition, many fish change diet as they grow, larger fish often taking prey fish as an increasing proportion of their diet. A reduced fishing pressure on predators may therefore result in less prey fish. They are not unaffected as predicted from single-species management.

An early attempt to study the effects of biological interaction, e.g. of changing the exploitation pattern so as to increase the fishing pressure on the predator species and ease predation on harvestable prey species, was conducted by Andersen and Ursin (1977) in their North Sea simulation model. Their theoretical analysis gave speculative directions for how to double the catches from the North Sea. This illustrated how to set management objectives incorporating multispecies interactions: increased catches may be obtained by fishing intensively on the (larger) predatory species while the (smaller) prey species along with non-piscivore species are allowed to grow before harvesting. The increased catches from Andersen and Ursin's study did not come without a price: the increases were measured in weight, and because the harvest of predatory species was of smaller individuals, the value of landings would probably not double.

Andersen and Ursin's (1977) study was timely. In the 1960s and 1970s the large stocks of herring and mackerel in the North Sea were heavily fished, and both experienced a collapse. In 1978 this led to a ban of the herring fisheries in the North Sea, but despite the ban a Danish fishery for sprat (or rather juvenile herring) for industrial reduction continued.

At the time, the Herring Assessment Working Group of ICES used a natural mortality of 0.2 year^{-1} for all ages of herring to account for all non-fishery mortality (mainly predation) for calculation of stock sizes. When comparing the catches with year-class strength estimates using the (low) natural mortality rate, it seemed that the Danish industrial fishery for juvenile herring totally eradicated the recruitment in the years following the ban. This naturally led to an uproar in which Andersen and Ursin were caught in the middle. Their study pointed to the importance of species interaction for management of ecosystems, and to natural mortalities being a function of body size. Using the higher estimates of natural mortalities for juvenile herring that they estimated from their model (6.0, 1.1, 0.32, 0.18 and 0.12 year^{-1} for age groups 0, 1, 2, 3 and 4+, respectively) would lead to eight times higher population estimates of 0-groups. This again would change radically the predicted impact of the industrialized fisheries: the vast majority of the juveniles would be eaten by predatory fish if they were not caught.

Andersen and Ursin's pioneering ecological work led to a focus in ICES on incorporation of multispecies consideration in the biological assessment (Daan and Sissenwine, 1991). Yet, their North Sea model was not used for management: it was a complex research tool with many guessed parameters, and their conclusions were therefore too uncertain.

To obtain more data on biological interaction, ICES declared 1981 the Year of the Stomach. Research vessels from most North Sea fishing nations participated in a major, coordinated operation where some 45 000 stomachs were sampled and analysed in detail. Concurrently an ICES Multispecies Working Group was established to develop an analytical approach for estimating the importance of fish species interaction. Work in this group has, with a tremendous effort, led to development through ICES of well-founded tools for multispecies analysis (Sparre, 1991), along with probably the best database on biological interaction between harvested species anywhere in the world. The results from the ICES multispecies work have led to a profound change in our

perception of the role of predation in the marine ecosystem, but not yet to any change in the management paradigm. The reasons for this are numerous, and may best be illustrated by looking at the likely consequences of changes in mesh size in the North Sea roundfish fisheries.

The simulations of the ICES Multispecies Working Group (ICES, 1989) showed that the single-species models, as expected, predict increases for all roundfishes as mesh sizes were increased, while the other species were unaffected. In contrast, the multispecies analyses showed overall decreasing catch levels from increasing the mesh size. The catches of most gadoids decreased, only saithe (*Pollachius virens*, on which predation is very low) was virtually unaffected. The decreases were explained by increased predation rates from higher populations of the large predators. The ultimate prey fish species, sandeel and sprat, were – as in the single-species models – nearly unaffected; they do get more large predators, but in return fewer small predators.

PREY EXPLOITATION

Prey exploitation can lead to overfishing on a scale where all stocks are extinguished from an economic point of view. This has often been the result of large-scale industrialized fisheries operating with marginal profit, landing for reduction purposes. Empirically it seems that ecosystems react to such removal of abundant stocks by other, often shorter-lived species, becoming more abundant. A good example is the intensive mackerel and herring fisheries in the 1960s and 1970s in the North Sea which, once the mackerel and herring stocks were severely reduced, were followed by large increases in the fisheries for smaller prey species. The development here led Pauly (1979) to call this form for management the 'North Sea strategy'.

Decline in abundance of prey species may affect not just the fisheries but also the predators. For instance, in the north-western North Sea/Shetland area, increased sandeel populations following the decline of herring and mackerel led to the historically highest abundances of those bird species which preyed on sandeels. The industrialized fisheries for sandeels which developed in Shetland resulted in a shortage of sandeels and large-scale breeding failures of the predatory bird species (Bailey *et al.*, 1991), a development corresponding to the 'Lilliput strategy' of Pauly (1979).

The fisheries may also influence top predators indirectly through food web interactions. Trites *et al.* (in press) in a recent analysis described this using the term 'food web competition'. They analysed the food webs of the fisheries and marine mammals of the Pacific, and calculated for each of the seven FAO statistical areas in the Pacific how much of the primary production was required to sustain the fishery catches and the consumption of the marine mammals. Their results indicate that as fishery catches increase, the proportion of the primary production appropriated by the marine mammals diminishes as their population levels are lower in fished than in unfished areas. This may be a result of the fisheries outcompeting the marine mammals.

REMOVE EVERYTHING – OVEREXPLOITATION

A by now classic analysis of how a marine ecosystem 'develops' from an unexploited state to being overexploited was presented by Pauly (1979) for the Gulf of Thailand ecosystem where trawl fisheries through the 1960s rapidly depleted the resources. Here, the catch rates of high-grade fish rapidly declined with an order of magnitude, while

those of small trash fish were roughly constant, indicating major changes in the community composition as the fishery progressed. The Gulf of Thailand scenario is typical for tropical trawl fisheries, where intensive exploitation usually leads to sustained, but lower than optimal, catches of small organisms.

Another type of overexploitation scenario should be discussed. The 'hit and run' or 'pulse' fishing strategy is a probably rather rare form where a sudden burst of fishing intensity rapidly depletes the resources. Pulse fishing is often associated with distant-water fleets constantly on the move. However, it has also been practised for years by the now banned, 'muro-ami' fleets in the Philippines and South China Sea area, in which boats carrying 200–400 young boys move from reef to reef: the boys surround a reef area while swimming, and using scare lines with rocks as weights they drive all fish towards a funnel-shaped drive-in net.

An example of the efficiency and devastating effect of the muro-ami fishing technique comes from Sumilon Island in the Central Philippines. Here fish stocks and yields had been building up over some years due to the introduction of fish sanctuaries and abolition of destructive fishing methods. A period with intensive muro-ami fishing along with reintroduction of other destructive fishing methods such as blasting, resulted in initial high catches, but subsequent catch rates were significantly lower than those prior to the muro-ami burst (Alcala, 1988).

THE GARDEN OF EDEN

A final form for ecosystem management needs to be discussed: marine parks, or the 'Garden of Eden strategy' (Pauly, 1979). Marine parks are areas where fishing has been banned, or where at least destructive fisheries are prohibited. They may then serve as refuges for biological diversity and as sources for surplus production for neighbouring systems.

Experience on how protection may influence fish populations has been gained in the Philippines over several decades. Some of the lessons learned are that the benefits from increased yield from a sanctuary are worth the effort of protecting it – the protection from fishing can lead to very high densities and biomasses of fish of importance for fisheries; that a reserve can enhance fisheries yield in areas adjacent to it; and that reserves can act to minimize the risk of fishery collapse by protecting a critical level of spawning stock biomass (Russ and Alcala, 1994). Of much importance may also be that the fish in a sanctuary will tend to grow bigger, enhancing their reproductive potential and reducing the risk of recruitment overfishing. A number of the management options discussed above include aspects of a fundamental issue in multispecies management of ecosystem resources: fishing down the predator stocks to increase yield of prey species and overall yield. This process will be described next.

Fishing down the food web

In unfished areas we can expect ecosystems to be in some sort of balance, often with relatively high abundances of predatory fish. Initially, fisheries may target the larger, predatory, and often higher-priced species. Gradually the fishing pressure will make the larger species more scarce, and fishing will move towards the smaller species. As this develops we may or may not experience increasing catches overall, but typically the catch per effort will diminish, making us perceive the development as a fishery crisis.

As discussed earlier, it has often been assumed that we can increase catches substantially by targeting the development briefly outlined above: by fishing down the food web. We expect from Slobodkin's (1980) studies that the trophic transfer efficiencies by trophic level are around 10%, and indeed more recent studies have shown this to be quite reasonable (Christensen and Pauly, 1993a; Pauly and Christensen, 1995).

With this background we may expect potential catches to increase if we fish out the predators and fish on their prey instead. If the prey is one trophic level below the target fish species, might we be able to increase the catches by a factor of 10? Or would it actually be more as the prey grow bigger in a situation without predation? Or would it be less as there would not be food enough for the prey species? We do not know the answers to these questions, nor is it likely that they can be answered in general. Part of the predator/prey picture can, however, be presented.

Based on Pauly and Christensen's (1995) study of primary productivity and global fisheries, the trophic levels at which fisheries operate in different resource system types can be quantified (Fig. 2). The results show an inverse correlation between the amount of catch taken and the trophic level of the catches; the higher the catch, the lower its trophic levels.

As a data source for further comparisons I have extracted information from 33 quantified trophic models of interactions in exploited, aquatic ecosystems (Table 5). All of the models are published and all are constructed using the ECOPATH software system (Christensen and Pauly, 1992). Such models have a number of common features, most notably that they all are constructed to ensure mass-balance. Thus, they are physiologically realistic models that incorporate our best knowledge of the trophic interactions in the ecosystems concerned, especially for the higher trophic levels where human interest is the strongest. For a very brief summary of most of the models see Christensen (1995c), and Christensen and Pauly (1993b), in which many of the models are published.
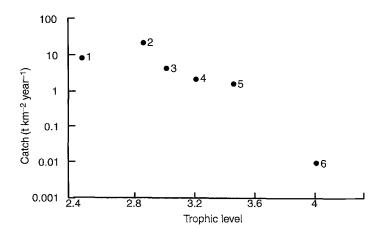
Fig. 2. Average annual catch of finfish (log scale) vs. average trophic level of the catch for six different resource system types globally (based on information in Pauly and Christensen, 1995). The six systems are: (1) coastal, (2) upwelling, (3) freshwater, (4) tropical shelves, (5) non-tropical shelves and (6) oceanic.

Table 5. Overview of the trophic models of aquatic ecosystems used for comparison of exploitation–predation rate indices. The systems are separated into African lakes, coastal and shelf systems, and upwelling-dominated systems. Some of the models are used in a form slightly modified from the original publications in order to facilitate comparison (details: Christensen, 1995c)

No.	System	Year(s)	Source
1	Lake Turkana	1973	Kolding (1993)
2	Lake Turkana	1987	Kolding (1993)
3	Lake Chad	1970–1972	Palomares *et al.* (1993)
4	Lake Kariba	1980s	Machena *et al.* (1993)
5	Lake Victoria	1971–1972	Moreau *et al.* (1993b)
6	Lake Victoria	1985–1986	Moreau *et al.* (1993b)
7	Lake Tanganyika	1974–1976	Moreau *et al.* (1993c)
8	Lake Tanganyika	1980–1983	Moreau *et al.* (1993c)
9	Lake George	1970s	Moreau *et al.* (1993a)
10	Celestun lagoon		Chávez *et al.* (1993)
11	Yucatan shelf, Mexico		Arreguín-Sánchez *et al.* (1993)
12	N. Gulf of Mexico shelf		Browder (1993)
13	Maputo Bay, Mozambique		Paula E Silva *et al.* (1993)
14	Lingayen Gulf, Philippines		Guarin (1991), Pauly and Christensen (1993)
15	Bolina reef flat, Philippines		Aliño *et al.* (1993)
16	Gulf of Thailand, 0–10 m		Pauly and Christensen (1993)
17	Brunei Darussalem EEZ		Silvestre *et al.* (1993)
18	Vietnam coast, 10–50 m		Pauly and Christensen (1993)
19	Kuala Terengganu EEZ, Malaysia		Christensen (1991)
20	Gulf of Thailand, 10–50 m		Pauly and Christensen (1993)
21	South China Sea, 50–200 m		Pauly and Christensen (1993)
22	Schlei Fjord, Germany		Nauen (1984), Christensen and Pauly (1992)
23	North Sea	1981	Christensen (1995a)
24	W. Greenland shrimp ground	1991–1992	Pedersen (1994)
25	Peru upwelling	1950s	Jarre *et al.* (1991)
26	Peru upwelling	1960s	Jarre-Teichmann and Christensen (in press)
27	Peru upwelling	1970s	Jarre-Teichmann and Christensen (in press)
28	Namibia upwelling	1971–1977	Jarre-Teichmann and Christensen (in press)
29	Namibia upwelling	1978–1983	Jarre-Teichmann and Christensen (in press)
30	Northwest Africa upwelling	1970–1977	Jarre-Teichmann and Christensen (in press)
31	California upwelling	1965–1972	Jarre-Teichmann and Christensen (in press)
32	California upwelling	1977–1985	Jarre-Teichmann and Christensen (in press)
33	NE Venezuela shelf		Mendoza (1993)

In a manner corresponding to that represented in Fig. 2 we also find a negative relationship, on an ecosystem basis, between the trophic level on which the fishery operates and the overall catch level of finfish (Fig. 3). We cannot, however, produce any general rule for what changes in catches to expect from fishing down the food web, because differences in productivity between resource system types are ignored in Figs 2 and 3. Primary productivity is the single most important factor for potential catches, and productivity will not be changed by fishing down the food web. Still, the finding
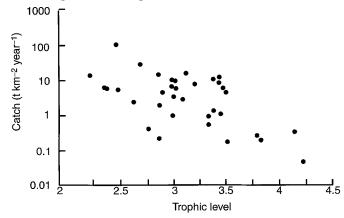
Fig. 3. Average annual catch of finfish (log scale) vs. average trophic level of the catch based on 36 models of aquatic ecosystems. Thirty-three of these are listed in Table 5, while the additional three represent the open ocean part of the South China Sea (Pauly and Christensen, 1993), Lake Ontario (Halfon and Schito, 1993) and Lake Kinneret (Walline *et al.*, 1993).

that high catches are associated with fishing at low trophic levels – and generally in systems with high primary productivity – is valid.
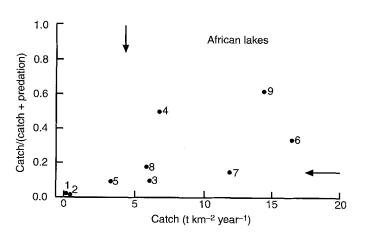
CATCHES AND PREDATION PRESSURE

The African lakes case studies discussed above show diverging results. In Lake Victoria the catches (and fishing pressure) due to the Nile perch increased to a very high level in spite of the increased predation pressure exerted by the Nile perch in the lake. In contrast, the catches diminished in Lake Tanganyika as fishing pressure increased along with the predation pressure. In a search for general patterns one might hypothesize on the relationship between catches and predation pressure.

For comparison of predation pressure over time, and even more importantly between systems, I will use an exploitation–predation rate index equal to the total catch of finfish relative to the total 'explained' mortality, estimated as the summed catch and predation of all finfish in a system. The 'explained' mortality is used as a proxy for the total mortality ignoring the usually small mortalities caused by diseases, starvation etc.

The trophic models included here (Table 5) are grouped in three types of resource systems: African lakes; coastal and shelf systems; and systems dominated by upwelling. Expressing the finfish exploitation rate index as a function of total catches of finfish in the three system types produces the results shown in Figs 4–6.

As is obvious from Fig. 4, the exploitation–predation index for the African lakes increases with the catches. What is more interesting is that even where exploitation is at its highest, predation still outweighs catches. Only for three of the models do the catches reach more than 25% of the predation; these are (4) Lake Kariba, (6) Lake Victoria 1985–86, and (9) Lake George. Of these, Lake Kariba is an artificial lake, where the catches are totally dominated by an introduced small clupeid, for which the predation rate is very low. For Lake Victoria, the high catch rate is due to the dominant Nile perch on which predation is low, while the Lake George system is dominated by

Fig. 4. Finfish exploitation–predation rate index as a function of total catches of finfish (tonnes·km^{-2}·year^{-1}) in nine trophic models of African Great Lakes, numbered as in Table 5. The horizontal arrow indicates the median exploitation rate index, while the vertical arrow indicates the average catch rate for the world's freshwater ecosystems (based on Pauly and Christensen, 1995).
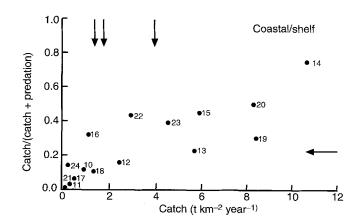

Fig. 5. Finfish exploitation–predation rate index as a function of total catches of finfish (tonnes·km^{-2}·year^{-1}) in 15 trophic models of coastal and shelf ecosystems, numbered as in Table 5. The horizontal arrow indicates the median exploitation rate index, while the three vertical arrows from left to right indicate the average catch rate for the world's non-tropical shelves, tropical shelves, and coastal ecosystems, respectively (based on Pauly and Christensen, 1995).

high biomasses and catches of herbivorous tilapia; thus, predation rates are low in this system as well.

By rough extrapolation, the average catch of finfish in freshwater systems globally amounts to some 3.8 tonnes·km^{-2}·year^{-1} (Pauly and Christensen, 1995), and based on Fig. 4 we can expect that predation perhaps outweighs catches by a factor of 4, leading to a predation of some 30 million tonnes·year^{-1}.
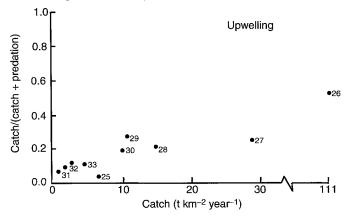
Fig. 6. Finfish exploitation–predation rate index as a function of total catches of finfish (tonnes·km^{-2}·year^{-1}) in nine trophic models of systems characterized by upwelling processes, numbered as in Table 5.

Based on 15 models of coastal and shelf systems the pattern in Fig. 5 emerges. Here the exploitation–predation rate index seems to level off asymptotically for catches larger than some 2 tonnes·km^{-2}·year^{-1}. The level reached is higher than for the African lakes (and the predation pressure thus lower), with indices between 0.3 and 0.5, i.e. the catches range between half as much, and as much as the predation losses.

There is recorded only one system for which the catches are much higher than the predation, (14) Lingayen Gulf, a very intensively fished soft-bottom gulf in north-western Philippines. Here overfishing 'down the food web' results in high catch rates of very small fish, from most points of view a not very desirable situation. Yet this may be the direction increasing fishing pressure will take in many areas in the future.

Globally, tropical and non-tropical shelves have average catch rates of finfish of 1.5 to 1.9 tonnes·km^{-2}·year^{-1}, respectively (Pauly and Christensen, 1995). From Fig. 5, the predation rates for such systems may be about twice as high as the catches. Extrapolated to the world shelves, this points to predation on finfish of the order of 32 and 56 million tonnes for tropical and non-tropical shelves, respectively. In a similar manner, we obtain for coastal systems that an average finfish catch level of 3.9 tonnes·km^{-2}·year^{-1} may be associated with a predation level three times as high, i.e. globally of the order of 48 million tonnes·year^{-1}.

For the remaining type of resource system, the upwelling systems, the results are given in Fig. 6. Here, too, predation clearly outweighs catches; for the four systems with catch rates of less than 10 tonnes·km^{-2}·year^{-1}, predation is nearly an order of magnitude higher than catches. For systems with catch rates between 10 and 30 tonnes·km^{-2}·year^{-1}, predation is about three times as high as the catches, and only for the Peru system in the 1960s where catches soared to more than 100 tonnes·km^{-2}·year^{-1} did catches approximately balance the predation. For upwelling systems, on a global scale, the average catch of finfish amounts to 22 tonnes·km^{-2}·year^{-1} (Pauly and Christensen, 1995). Thus, on the global scale, predation may be perhaps three times as high, which would amount to around 50 million tonnes·year^{-1}.

From the very rough estimates of predation levels discussed in the text above, the results in Table 6 emerge. Globally we may have that predation 'losses' outweigh catches by a factor of three or so. This does not, however, mean that we can increase catches by such a factor. One cannot avoid predation in natural ecosystems, even if, with proper tools and knowledge, we may be able to manage systems so as to consider the role of predation. In addition, the extrapolation is very uncertain and the implicit assumptions underlying it may not hold, e.g. that the models are representative of the world's average ecosystems. To give one example, I have excluded systems where no catches are taken. Therefore Table 6 only gives an indication of the order of size of the predation losses of finfish to other finfish.

Overholtz *et al.* (1991) studied the impact of predators on the pelagic fish ecosystem of the north-western USA, and found that predator consumption was about twice as high as the catches, with predatory fishes, mainly spiny dogfish (*Squalus acanthias*, Squalidae), accounting for most of the predation.

Bax (1991), in a comparative study in six marine ecosystems, found similar ratios as here between fish loss to predatory fish and to the fisheries for the North Sea, and the Barents Sea. For Georges Bank, the Eastern Bering Sea and the Balsfjord in Norway, however, the predation losses outweighed catches by 7–9 times, while this ratio reached 35 for the southern Benguela Current. This indicates large differences between the Overholtz *et al.* (1991) study of the north-western Atlantic and Bax's study of the Georges Bank, and also between Jarre-Teichmann and Christensen's (in press) study of the northern Benguela Current – whose results were similar to those reported here – and Bax's of the southern Benguela, calling for some caution in interpretation of the results.

The discussion above relates to the famous Gulland (1971) equation where the potential catch of a stock is estimated as half the natural mortality times the original biomass of the unexploited stock. Subsequent analysis has shown that this equation will generally overestimate the sustainable catch (Kirkwood *et al.*, 1994), and this is also the conclusion of the present analysis. Predation by far outweighs potential yield.

WHO ARE THE PREDATORS, AND WHO THE PREY?

The extrapolation in Table 6 above indicates that losses of finfish due to predation from other finfish may be of the order of three times the present catches. We may expand on this by looking at the main contributors to the world's catches to get further indications of the role of predation (Table 7).

Table 6. Catches of finfish in 1991 by resource system types (FAO, 1993) and tentative estimates of the global estimates of predation loss of finfish. Oceanic systems are not included here. Units are million tonnes·year^{-1}

Resource system type	Catch of finfish	Finfish eaten by other finfish
Upwelling	17	50
Tropical shelves	16	48
Non-tropical shelves	28	56
Coastal	8	30
Freshwater	8	30
Total	77	214

Table 7. Catches (10³ tonnes) in 1991 of the world's top 70 species (FAO, 1993). Size options are based on asymptotic maximum length, L_∞ for finfish, where large is $L_\infty \geqslant 90$ cm, medium is 30 cm $\leqslant L_\infty < 90$ cm, and small includes fish with $L_\infty < 30$ cm and invertebrates. Food type includes pisc. for piscivores, inv. for invertebrate feeders, and herb. for herbivores and detritivores; species are roughly allocated based on where at least 50% of their food is taken from (judged mainly from ECOPATH models and information in FishBase; Froese and Pauly, 1994)

Common name	Scientific name	Catch	Size			Food type		
			Small	Medium	Large	Pisc.	Inv.	Herb.
Alaska pollack	*Theragra chalcogramma* (Gadidae)	4893			X	X	X	
South American pilchard	*Sardinops sagax* (Clupeidae)	4190		X			X	X
Anchoveta	*Engraulis ringens* (Engraulidae)	4017	X				X	
Chilean jack mackerel	*Trachurus murphyi* (Carangidae)	3853		X		X		
Japanese pilchard	*Sardinops melanostictus* (Clupeidae)	3711	X				X	
Skipjack tuna	*Katsuwonus pelamis* (Scombridae)	1557			X	X		
Silver carp	*Hypophthalmichthys molitrix* (Cyprinidae)	1396		X				X
Atlantic herring	*Clupea harengus* (Clupeidae)	1383	X				X	
European pilchard	*Sardinia pilchardus* (Clupeidae)	1378	X				X	
Atlantic cod	*Gadus morhua* (Gadidae)	1339			X	X		
Common carp	*Cyprinus carpio* (Cyprinidae)	1271		X			X	
Capelin	*Mallotus villosus* (Osmeridae)	1252	X				X	
Chub mackerel	*Scomber japonicus* (Scombridae)	1179	X				X	
Grass carp	*Ctenopharyngodon idella* (Cyprinidae)	1066		X				X
Yellowfin tuna	*Thunnus albacares* (Scombridae)	1012			X	X		
Largehead hairtail	*Trichiurus lepturus* (Trichiuridae)	806			X	X		
Pacific cupped oyster	*Crassostrea gigas*	775	X					X
Bighead carp	*Hypophthalmichthys nobilis* (Cyprinidae)	701		X			X	
Atlantic mackerel	*Scomber scombrus* (Scombridae)	681		X			X	
Araucanian herring	*Strangomera bentincki* (Clupeidae)	584	X				X	
Gulf menhaden	*Brevoortia patronus* (Clupeidae)	551	X					X
Japanese scallop	*Pecten yessoensis*	530	X					X
Argentine hake	*Merluccius hubbsi* (Gadidae)	521		X			X	
Japanese anchovy	*Engraulis japonicus* (Engraulidae)	501	X					X
Blue mussel	*Mytilus edulis*	492	X					X
California pilchard	*Sardinops caeruleus* (Clupeidae)	467	X				X	

Table 7. (*cont.*)

Common name	Scientific name	Catch	Size			Food type		
			Small	Medium	Large	Pisc.	Inv.	Herb.
Blue whiting	*Micromesistius poutassou* (Gadidae)	446		×			×	
Pink salmon	*Oncorhynchus gorbuscha* (Salmonidae)	438			×		×	
Cape horse mackerel	*Trachurus capensis* (Carangidae)	432		×			×	
Saithe	*Pollachius virens* (Gadidae)	429			×	×		
Pacific cod	*Gadus macrocephalus* (Gadidae)	420			×	×		
Milkfish	*Chanos chanos* (Chanidae)	418		×				×
Atlantic horse mackerel	*Trachurus trachurus* (Carangidae)	411		×		×		
Pacific saury	*Cololabis saira* (Scomberesocidae)	402		×			×	
Atlantic menhaden	*Brevoortia tyrannus* (Clupeidae)	398		×			×	
Round sardinella	*Sardinella aurita* (Clupeidae)	387	×				×	
Japanese flying squid	*Todarodes pacificus*	384	×				×	
Blue grenadier	*Macruronus novaezealandiae* (Gadidae)	378		×		×		
European anchovy	*Engraulis encrasicolus* (Engraulidae)	373	×				×	
Nile perch	*Lates niloticus* (Centropomidae)	358			×	×		
Indian oil sardine	*Sardinella longiceps* (Clupeidae)	349	×					×
Norway pout	*Trisopterus esmarki* (Gadidae)	303		×			×	
Japanese clam	*Venerupis japonica*	288						×
European sprat	*Sprattus sprattus* (Clupeidae)	274	×				×	
Chum salmon	*Oncorhynchus keta* (Salmonidae)	267			×		×	
Nile tilapia	*Oreochromis niloticus* (Cichlidae)	251	×					×
Japanese Spanish mackerel	*Scomberomorus niphonius* (Scombridae)	249			×	×		
Japanese jack mackerel	*Trachurus japonicus* (Carangidae)	245		×				
Azov tyulka	*Clupeonella cultriventris* (Clupeidae)	240	×				×	
Bigeye tuna	*Thunnus obesus* (Scombridae)	238			×	×		
Indian mackerel	*Rastrelliger kanagurta* (Scombridae)	236	×			×		
Akiami paste shrimp	*Acetes japonicus*	235	×				×	
Antarctic krill	*Euphausia superba*	233	×				×	
Northern prawn	*Pandalus borealis*	231	×				×	
Southern blue whiting	*Micromesistius australis* (Gadidae)	228		×			×	

Common name	Species		1	2	3	4	5	6
Atlantic salmon	*Salmo salar* (Salmonidae)	228			×	×		
Fleshy prawn	*Penaeus chinensis*	227	×	×				
Rainbow trout	*Oncorhynchus mykiss* (Salmonidae)	227				×	×	
Crucian carp	*Carassius carassius* (Cyprinidae)	221	×				×	
Pacific herring	*Clupea pallasi* (Clupeidae)	215	×				×	
Giant tiger prawn	*Penaeus monodon*	213						×
Sea scallop	*Placopecten magellanicus*	211	×					×
Toli shad	*Tenualosa toli* (Clupeidae)	203		×			×	
Haddock	*Melanogrammus aeglefinus* (Gadidae)	189		×			×	
Ocean quahog	*Arctica islandica*	186	×					
European plaice	*Pleuronectes plastessa* (Pleuronectidae)	183		×			×	×
Atka mackerel	*Pleurogrammus azonus* (Hexagrammidae)	182			×	×		
Channel catfish	*Ictalurus punctatus* (Ictaluridae)	177			×	×		
Patagonian grenadier	*Macruronus magellanicus* (Gadidae)	174			×	×		
Gazami crab	*Portunus trituberculatus*	172	×				×	

From the table the following picture emerges: the catches of the world's 70 major species (contributing more than half of the total world catches) are about evenly distributed between large, medium, and small groups (Table 8). Because one-quarter of the catches are of large (and piscivorous) groups, global-level fishing is quite high in the food chain. This agrees with Pauly and Christensen (1995), who found that the average catch globally was at a trophic level approximately two trophic levels above the primary producers.

Examination of the main food types of the species caught shows that one-third are piscivores and half predominantly eat invertebrates, while herbivory and detritivory are rare.

The conclusion based on Table 8 is that globally the fisheries are taking large, piscivorous fish to quite an extent. Fisheries in general thus have not moved far down the food web, or at least they have not reached the bottom. Whether or not we want or expect them to do so is another matter, which cannot be given a fair evaluation in this context.

Guidelines for management incorporating biological interaction

The analyses above point to biological interaction between fish resources being a factor for consideration in fisheries management. Larkin (1979), in a review of predator–prey relationships in fishes, gave some advice to managers which still holds:

- In most natural situations, most species of fish are both predators and prey having both multiple prey and predators. Do not expect big changes for the predator that loses a few prey species.
- Do not expect long-term benefits to the prey from predator control.
- Depressed stocks can in some cases be enhanced by providing refuge from predation.
- Most introductions of predators are unsuccessful, but successful introductions may have far-reaching consequences for the ecosystem.
- Because natural predators tend to stabilize ecosystems, the selective removal of predators may be particularly destabilizing.
- To avoid perturbations, harvest should be much less selective than hitherto.

Table 8. A summary of the 1991 catches (10^6 tonnes) of the world's 70 most caught species aggregated by size and main feeding type. Distribution after size is: large are fish with $L_\infty \geqslant 90$ cm, medium are fish with 30 cm $\leqslant L_\infty \leqslant 90$ cm, and small are fish with $L_\infty < 30$ cm and all invertebrates

Size	Main food (10^6 tonnes)			Total (%)
	Fish	Invertebrates	Plants and detritus	
Large	12	0.7	0	24
Medium	4.9	9.9	3.4	34
Small	1.5	17	3.2	41
Total (%)	35	52	13	100

Larkin thus mainly advocates a cautionary approach to management, which indeed is very reasonable in view of the numerous examples where human interventions have had profound impacts on ecosystems. We cannot, however, stop the trend towards increasing intervention, and must instead strive to get the best possible out of e.g. introductions and selective fisheries, while experiencing as much caution and care for the ecosystem as possible. Improved knowledge of predator–prey interactions and of how these influence management of multispecies is important in this context; we still know far too little to do proper ecosystem management.

Another set of cautionary management advice comes from the May *et al.* (1979) treatise of management of multispecies fisheries:

- or top predators the MSY concept will often remain useful. The stocks should be kept at a level where they provide the greatest natural increment.
- Prey populations should not be depleted so that their populations or those of the predators are significantly reduced.
- For monitoring multispecies ecosystems, the longest time scales, i.e. most often those of the top predators, should be used.
- To ensure sustainable yields, harvesting levels should be set conservatively, allowing for safety factors to guard against accidental overexploitation following e.g. environmental variation.

What May *et al.* (1979) advocate resembles the Garden of Eden discussed above: near-pristine levels of both predators, and prey. This may be a natural consequence of the main topic they discuss: management of Antarctic resources where low exploitation rates are a possibility. However, for areas with high population densities, the Garden of Eden cannot be made the prevalent option. Guidelines are needed for how management in more exploited areas should proceed to ensure high, sustainable yields.

INTRODUCING NEW MANAGEMENT SCHEMES

Some lessons for how to move towards a better management can be gained from the North Sea experience. Here results from multispecies management analysis have been available for nearly a decade, and it is generally accepted by fisheries biologists that for management of complex, exploited ecosystems, single-species models do not suffice. At the trophic levels from which most catches are obtained they do not produce credible results.

The reactions of managers to the radical change in advice that may be the result of multispecies management have expectedly been slow. Drastic changes in management strategies are not easy to cope with. This was a clear conclusion presented by Gulland (1991) when discussing the conditions under which multispecies models would lead to better fisheries management:

It should be clear to scientists that there is a lot more to the management of fisheries resources than the scientific advice itself. New advice is most likely to be used if:

- it implies changes in current management practice that are straightforward and preferably minor;

- the science involved is transparent to a non-specialist such that the inclusion of new information clearly suggests changes in the advice on management of the resource;
- the new results are scientifically uncontroversial, i.e. the provision of the new advice will not be accompanied by substantial debate over the science itself;
- suggested new measures will reduce or at least not increase conflicts between different interest groups;
- there will be no clear losers that cannot easily be justified and dealt with.

Basically, the message is to go slowly. This is to a large degree due to the previous decades when rules of regulations were painstakingly incorporated. As expressed by Brugge and Holden (1991):

> Management measures based on single-species models are criticized because it is recognized that they do not correspond with reality: fish species do interact. Species-interaction models respond to this criticism and they are, therefore, more convincing than single-species models. However, what they gain in credibility on this point they more than lose on others. As with all models, the results obtained depend upon the assumptions made, the quality of the available data, and the complexity of the models, in terms of number of species and the interactions between those species. . .

> From the manager's point of view, there would be considerable difficulty in getting the fishing industry to accept that the results from these models were sufficiently convincing to form a sound basis for management.

> One of the major problems that these models present for fisheries managers is that the results which they predict are, in some cases, contrary to the perceived wisdom based on more than half a century of single-species models.

The main divergences between single-species and multispecies models occur in the long-term forecasts. The short-term advice from the two types of models is not very different. As the main management interest is focused on the short-term advice, it is of less importance what type of model is used. For the long-term scenario, the decision on how to manage the ecosystem calls for strategic thinking new to biologists and managers alike (Pauly, 1994). Combine this with the problem of a paradigm shift (Hilborn and Walters, 1992), and the obvious safe reaction is 'let's wait and see; meanwhile, keep up the good work'.

From the North Sea experience it is not enough to come up with the best possible management models; it must also be possible to implement them. When changes are to be made they should, as discussed above, be gradual. Drastic steps should be avoided. To some extent this makes the task easier for those drawing up the management options: the important question is not the ultimate position but simply what direction should be taken. As an example we may, by manipulating the exploitation patterns in multispecies models, come up with predictions for the directions in which fishing effort for the different gears and fleets operating in a system should move so as to increase yield through lowered predation levels. Generalized models for this use are only starting to emerge (Christensen, 1995b); however, as discussed by Christensen (1996), an important feature is that they can be made simpler than the multispecies models applied so far.

If we can give such directions for how to change fishing effort, they can be used in

the context of adaptive management. Adaptive management is a management form with a feedback loop where the management is constantly changing direction as more experience is gained. It includes two key aspects: a monitoring system to follow how catch rates and stocks develop over time, and an effective response system which should make it possible to change exploitation patterns as quickly and as often as necessary to optimize bio-economical variables (Walters, 1986; Hilborn and Sibert, 1988).

The monitoring system must cover catches and effort over an appropriate time frame for all important gears in an area. Further, as pointed out by Hilborn and Sibert (1988), the monitoring must prioritize the harvesting and processing sectors equally, because economics play as important a role for fisheries management as does biology.

The response system is the most problematic part of the adaptive management scheme. It is very difficult for managers to implement catch reductions and strategies for doing so. This must be an integral part of the management, although beyond the scope of this contribution. The purpose of introducing adaptive management considerations here is mainly to point out how the improved biological advice we may obtain can actually be used in practice.

Acknowledgements

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