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## Apparent changes in the trophic composition of world marine harvests: the perspective from the FAO capture database

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### Abstract

Almost 50 yr of global multispecies harvests are represented in the FAO capture production database, and offer a broad perspective on events that underlie the major observed changes in global marine harvests. The likely relevance of top-down and bottom-up trophic interactions, versus the impacts of changes in fishing technology and markets on the trophic level of landings, are discussed on a regional basis. Despite the low resolution of this global data set, several common features emerge. Rapid increases in fleet size and technological advance, and imperfect fisheries management measures, are probably responsible for declines in peak multispecies production in many areas since the 1970s, and internal evidence suggests that peak production is not far away in the remainder. Staggered dates of peak landings in different world areas seem to reflect the spread of industrial fishing fleets from 'core areas' to the rest of the world's oceans, which largely took place from the 1960s to 1990s. A general move to higher exploitation of piscivores in global landings is implied in some areas. The hypothesis that top-down removal of predators is affecting lower trophic production is however only one explanation for declining mean trophic levels, and is more likely to emerge from local food web studies. In some regions an increased proportion of short-lived invertebrates in harvests later in the time series supports a move downwards in trophic level targeting. In the North Atlantic and some other areas, fishing down marine food webs may be a likely cause of the increase in landings of shelf planktivores. A shift from depleted apical resources to species lower in the food web may have been made on economic grounds however, independent of possible effects of a release of predatory pressure. Sharp increases in planktivores later in the time series show up in the Eastern Central Atlantic and in the Southeast Pacific and do not appear to be primarily related to depletion of predators. They seem to reflect intermittent strength of upwelling systems, and hence bottom-up effects on food web production, together with changes in harvest technology. For some areas, piscivore landings increased later in the

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time series than those of planktivores. In the Mediterranean, this seems mainly a bottom-up response to increased marine productivity associated with land run-off and consequent improvements in predatory foraging. In some tropical areas, later increases in piscivorous landings mainly result from expansion of distant water tuna fleets, and are probably unrelated to exploitation of forage fishes. The technological revolution of the 1950s and 1960s involved rapid application of synthetic fibres to improved gear. This led to large-scale mid-water trawling and purse seining by industrial fleets and has especially increased vulnerability of small pelagic stocks over the last few decades. This appears mainly responsible for the apparent decline in mean trophic level of harvests in areas with large stocks of these resources. From an analysis of variances of the sample data set, 'Punctuated equilibrium', involving actual changes in ecosystems, rather than just continuous change in the relative harvest rates of species in a given ecosystem, is suggested as an important phenomenon, reflecting both ecological change and changing exploitation strategies. © 2000 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

The last half-century since the Second World War has seen an unprecedented expansion in fishing by industrial fleets from 'core' areas in the North Atlantic and North Pacific, to areas that were unexploited or underexploited in the 1950s. Evidence has accumulated [1–4] that many world areas have now passed their period of peak harvests with a subsequent decline in world marine landings now being evident. Most analyses to date has been based on trends in overall production, but Pauly et al. [5] examined the FAO capture production database in terms of the trophic levels of the catch. This approach was followed up by the present authors in a report on marine ecosystem trends to be included into the World Resources Institute publication 'Pilot Assessment of Global Ecosystems' [6]. In this last cited report we took into account the comments of Caddy et al. [7] on the Pauly et al. [5] paper, which pointed to the difficulties of completely breaking down the above FAO database to trophic categories, and assigning specific causes to observed trends. The former difficulty stems from annual reporting of some FAO member countries that incompletely assigns catches to species categories. Inevitably, there are problems in completely dissecting all catches down to trophic levels which dictates the sample approach followed here.

We address this problem in the present paper and in the report to WRI mentioned above, by choosing a set of species in each of 4 trophic categories for each area studied, and using them as indicator species. The present report analyses further the data subset used for the WRI report. Taken together, the two reports avoid the assumption that there are necessarily trophic linkages between the indicator species at different trophic levels chosen from each regional data set, but that such changes might be taken as indicators of relevance to the marine ecosystems involved. This approach seems appropriate, given the large size of FAO Fishing Areas which incorporate a number of distinct sub-regional ecosystems. Some species selected may be geographically distant from the area of capture of others in adjacent trophic

categories. Thus, we are looking at the outputs from each statistical area without necessarily assuming a causal linkage at the trophic level between the type species selected. Statistics expressed by FAO area may also combine landings from more than one stock of some species. This analysis should therefore be viewed as a 'coarse scale' overview of the way that ecosystem exploitation over the last half-century has proceeded, both from a trophic perspective, but remembering this to be a period of unprecedented development of fishing technology and fleet capacity. Our conclusions suggest that although the net result of fisheries development may be a reduction of the mean trophic level of the catch in some areas, the gross dynamics of fisheries at the regional and global scale, in many cases can often be explained by considerations other than trophic cascading.

This analysis follows the behaviour of a number of well-documented indicator species in each category and area, though several simple indices are derived and found to be useful for tracking changes. One index based on the multispecies variance of the sample species set seems to measure the (in)stability of multispecies fishery harvests, and perhaps by implication, of the underlying ecosystems they come from. Another looks specifically at the relationship between recorded landings of piscivores and zooplanktivores. While the changes we document may not all be perceived at the local level, we feel they deserve to be investigated in more detail by smaller scale ecosystem studies.

Pauly et al. [5] concluded that a decline in mean trophic level was evident in the FAO data set, and was caused by 'fishing down marine food webs', that is, removing top predators first, thus releasing predatory pressure on lower trophic levels. It was implied that this release in 'top-down' predatory pressure on smaller forage fish that form the food of top predators, might then lead to a subsequent expansion of their biomass, and hence of harvests. Such a mechanism would presumably show up as a progressive decline in the piscivore/zooplanktivore ratio from initially high values if the fisheries concerned focused on top predators early on, but these were later depleted as commercial targets.

As noted by Caddy et al. [7] such a decline in mean trophic level of overall harvests could in some cases be a 'bottom-up' effect due to an increase in nutrients to naturally nutrient-limited marine production systems, even if all levels of the food web are being exploited at a constant rate. An increase in forage fish abundance, in turn, might even lead to subsequent increases in fish predator biomass and harvests. In terms of our piscivore/zooplanktivore index, we might then see a high value of the ratio before small pelagic fisheries began, and a decline as forage fish landings increased. This might in theory, be followed by a reversal if predatory fish populations expanded in response to more abundant food (as per the Lotka–Volterra predator–prey cycles described for coupled terrestrial predator–prey populations, [8]).

An alternative to both the above two mechanisms over the short to medium term, at least in interpreting the FAO data set, is that apparent changes in trophic composition of catches could be due to changes in market demand, capture technology, or to changes in environmental conditions. All of these mechanisms could have changed species dominance and/or relative market preference and

availability/commercial attractiveness to industrial fisheries, especially over the last 30 yr of the data set. Technological improvements, such as the commercial onset of purse seining with power blocks (invented in 1953) or midwater trawling (developed in the 1950s [9]) dramatically increased the vulnerability, especially of small pelagic resources, and rendered distant water exploitation more profitable. This, rather than a release of predator pressure, could be largely responsible for the higher proportion of small pelagic fish in global multispecies harvests in recent decades.

## 2. Methods

Recognising the above problems in dissecting the whole multispecies catch as represented in the FAO database, the approach adopted in the WRI report and in the present study was to select 5 species over the period 1950–97 for each of 4 trophic level categories (piscivores, zooplanktivores, zoobenthivores and herbivores/detritivores). These indicator species were used as rough indices of ecosystem change, even though for the reasons mentioned, it would be presumptuous without further data to extrapolate directly the conclusions of this global study to local events affecting any one stock of the indicator species chosen.

The capture production of the twenty species selected in each FAO Fishing Area were analysed in three different ways:

(a) The observed trends in summed annual harvests of the 4 trophic categories over the 1950–97 period were followed for the five species selected in each category:

(b) The piscivore/zooplanktivore (PS/ZP) ratio as represented by the ratio of landings of our index species for these 2 categories for a given year is provided. This ratio was seen in the WRI report as a rough but useful way of monitoring ecosystem change. We suggest that declines in this index can either be a result of 'fishing down marine food webs', be an indication of increased biological productivity or nutrient availability [1,10] particularly valid for semi-enclosed seas, or result from market preference or technological change. Considering only biological interactions, a consistent increase in the PS/ZP ratio of landings would seem to imply either an increase in forage fish abundance due to predatory release or environmental change, or a decrease in piscivore abundance (supposing that demand for piscivores has declined, which seems unlikely). If we were considering purely biological/food web types of explanations, an increase in the PS/ZP ratio in the FAO data set, supports both bottom-up (e.g. eutrophication) and top down (predator depletion) types of mechanism, assuming landings reflect real changes in relative abundance. Obviously, a definitive decision on the predominant mechanism (more than one of which may be in operation) will require in-depth local study.

(c) A study of the sum of squared deviations (SSD) in catch composition of our 20 indicator species provides some interesting indications, both of stable exploitation patterns and of abrupt changes in these that may provide warnings of approaching ecosystem instability or the onset of unsustainable exploitation patterns.

Data on capture production are reported to FAO by Member Countries as collected by the national institution in charge of fishery statistics or, where data are

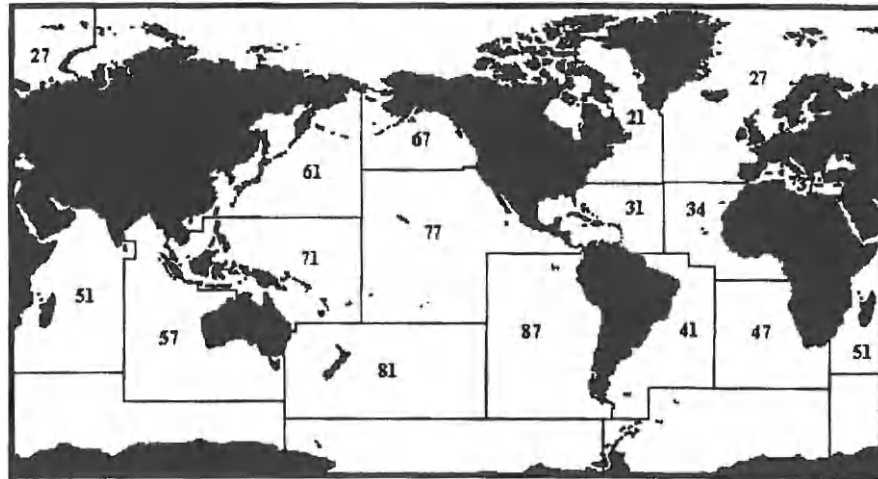


Fig. 1. FAO Fishing Areas for statistical purposes.

lacking or are considered unreliable, the best alternative sources of information are utilised [11]. The data represent nominal catches, or live weight equivalent of the landings, and exclude discarded species which in some fisheries can be a major source of mortality [12]. In many cases, the identification and separation of landings by species is very difficult or impossible and landings are reported at higher taxonomic level than species (i.e. genus, family, order, etc.). Given that species belonging to the same genus can sometimes present differences in their feeding habits, only items reported at the species level have been considered for this study.

Capture data for 15 FAO Fishing Areas (exclusively Arctic and Antarctic areas were not considered) shown in Fig. 1, were extracted from the FAO Fishery Statistics Database.<sup>2</sup>

### 2.1. Characteristics of the database

The data set consists of recorded nominal catches, and not biomasses: as such care must be taken in extrapolating from a catch trend to a trend in biomass in the sea. Nonetheless, it is reasonable to suppose that except for some semi-enclosed seas where an increase in landings may reflect eutrophically enhanced biomasses [13], or where changes in upwelling-driven systems led to biomass changes, that in most areas, large increases in harvests reflect increased fishing pressure on the stocks. No independent measure of fishing pressure exists in the FAO database, and hence we will largely be commenting on landing trends in the context of the evolutionary

<sup>2</sup>Downloadable, with the FISHSTAT PLUS software, at the Web page <http://www.fao.org/waicent/facinfo/fishery/statist/fisoft/fishplus.htm>

fishery model proposed by Caddy [14] and Grainger and Garcia [4] which seems supported by a longer historical perspective on fishery landing changes.

Only 65.9% of the total capture production reported to FAO for 1996 was at the species level, with a striking difference between temperate areas, where in some areas this percentage is about 90%, and tropical areas where it is often lower than 40% (Table 1). In addition to improved reporting procedures in developed (mainly temperate zone) countries, the higher biodiversity of multispecies catches, and poorly documented tropical artisanal fisheries where many species contribute small amounts to total catches, contribute to this difference.

As a result, a significant proportion of catches cannot be attributed to a trophic category, and as noted, this analysis only deals with a sample of the more important species in each region that can be classified trophically, selected by objective criteria. Considering the entire 1950–97 period, the species selected in this study and classified by trophic category represent 62.3% of total global capture production (see Table 2). For reasons mentioned above, high percentages occur in temperate areas and low percentages in tropical areas.

## 2.2. *Species selection and statistical processing*

Given the large number of individual time series in the FAO database, selecting representative species from a large but incomplete database presents some difficulties, and the approach adopted is described below.

The summed capture production of each species over the entire 1950–97 period was calculated for each FAO Fishing Area separately and then sorted in decreasing order. Starting with the species for which the largest weight of regional multinational landings was recorded, successive species were assigned to one of four trophic categories (see below), until a total of 5 species had accumulated in each category. Subsequently, this list was revised where the procedure resulted in one group of species (e.g. tunas, salmons) completely dominating a trophic category. Other species in the same category having a different role in regional ecosystems were chosen, and substituted for one or more of the 'dominant' group. This procedure for choosing key species has a degree of arbitrariness but seems inevitable, given the large proportion of landings which cannot be assigned to a trophic category because reported to FAO at a level higher than species.

FAO catch and landing fishery statistics have traditionally included both capture and aquaculture production, but work is well under way to disaggregate them into two separate components. This has so far been completed, working backwards through the database, since 1984. Hence, data for years 1950–83 in this analysis will still include aquaculture production but for marine waters this was not important in those years except for a very limited number of species, and a low tonnage of production. Species for which there are no catch data after 1983 because they are now in the aquaculture database, or that show a steep decrease between 1983 and 1984 due to most of their production being assigned to aquaculture, were not selected. In some areas it has been difficult to reach five species in the herbivore

**Table 1**  
 Capture production reported at the species and higher taxonomic levels in 1996

Fishing Area	Taxonomic level	1996	
		mt	%
21 Northwest Atlantic	Species	1,847,140	90.9
	Higher than species	183,950	9.1
	Total	2,031,090	
27 Northeast Atlantic	Species	9,590,025	86.8
	Higher than species	1,459,985	13.2
	Total	11,050,010	
31 W. Central Atlantic	Species	1,133,491	66.5
	Higher than species	570,634	33.5
	Total	1,704,125	
34 E. Central Atlantic	Species	2,331,281	69.3
	Higher than species	1,033,891	30.7
	Total	3,365,172	
37 Mediterranean and Black Sea	Species	1,089,278	72.8
	Higher than species	406,465	27.2
	Total	1,495,743	
41 Southwest Atlantic	Species	1,763,486	71.3
	Higher than species	710,585	28.7
	Total	2,474,071	
47 Southeast Atlantic	Species	675,383	65.5
	Higher than species	356,333	34.5
	Total	1,031,716	
51 Western Indian O.	Species	1,435,342	35.6
	Higher than species	2,595,461	64.4
	Total	4,030,803	
57 Eastern Indian O.	Species	778,275	20.2
	Higher than species	3,079,448	79.8
	Total	3,857,723	
61 Northwest Pacific	Species	13,463,510	53.9
	Higher than species	11,502,781	46.1
	Total	24,966,291	
67 Northeast Pacific	Species	2,587,233	89.8
	Higher than species	293,297	10.2
	Total	2,880,530	
71 W. Central Pacific	Species	2,391,393	27.1
	Higher than species	6,447,125	72.9
	Total	8,838,518	

(continued on next page)

Table 1 (continued)

Fishing Area	Taxonomic level	1996	
		mt	%
77 E. Central Pacific	Species	1,071,896	68.3
	Higher than species	496,780	31.7
	Total	1,568,676	
81 Southwest Pacific	Species	433,472	67.9
	Higher than species	205,334	32.1
	Total	638,806	
87 Southeast Pacific	Species	16,746,398	98.3
	Higher than species	281,713	1.7
	Total	17,028,111	
All areas	Species	57,337,603	65.9
	Higher than species	29,623,782	34.1
	Total	86,961,385	

Table 2

Tonnages and percentages of the 20 selected species as a proportion of total capture production accumulated over the 1950–97 period

FAO fishing area	20 species capture production (mt) in the 1950–97 period	Total capture production (mt) in the 1950–97 period	Percentage
21 Northwest Atlantic	122,729,721	149,328,826	82.2
27 Northeast Atlantic	342,851,517	461,836,182	74.2
31 W. Central Atlantic	47,963,353	69,521,132	69.0
34 E. Central Atlantic	54,941,599	105,773,283	51.9
37 Mediterranean Black Sea	38,909,220	60,262,641	64.6
41 Southwest Atlantic	33,976,868	53,310,916	63.7
47 Southeast Atlantic	74,795,458	89,897,667	83.2
51 Western Indian Ocean	27,780,940	93,634,530	29.7
57 Eastern Indian Ocean	9,095,752	79,496,211	11.4
61 Northwest Pacific	365,227,503	734,234,098	49.7
67 Northeast Pacific	76,703,027	94,922,858	80.8
71 W. Central Pacific	43,689,218	208,409,229	21.0
77 E. Central Pacific	31,560,985	48,348,305	65.3
81 Southwest Pacific	9,957,677	17,015,676	58.5
87 Southeast Pacific	176,125,251	390,939,573	96.2
<b>Total</b>	<b>1,656,308,089</b>	<b>2,656,931,127</b>	<b>62.3</b>



category and in fact in this category there are 12 species which have less than a total of 5000 mt in the 1950–97 period (i.e. about 100 mt per year).

### 2.3. Trophic categories

Four trophic level categories have been identified for the purpose of this study. They are listed in the Table 3 with their main food items.

The food items, and the corresponding trophic categories, mostly coincide with those listed in FishBase (Box 21 in Froese and Pauly [15]), the finfish database prepared by ICLARM with the support of FAO and the European Commission. Species in the top category were referred to as piscivores (instead of the more correct but less known term nektivores) and includes species also recorded as feeding on pelagic squids. Zooplanktivores comprise species feeding on those small animals transported passively by currents and waves gathered under the name 'plankton'. The major food items of zoobenthivores in FishBase are invertebrates living on the sea bottom, but those predominantly invertebrate feeders that also include (mentioned below) a proportion of bottom-dwelling fish in their diet have also been classified as zoobenthivores. The herbivore category includes species feeding on phytoplankton and plants but also those described as detritus feeders. In all cases we recognise that these are artificial categorisations, as dietary lability is the rule rather than the exception for most finfish species.

### 2.4. Classification criteria

Marine organisms change their feeding habits during the life cycle and in many species, the size of prey changes markedly with age. Most marine species are to a degree opportunistic feeders, and switch between food items depending on seasonal availability, so any trophic classification is to a significant degree arbitrary, depending as it does on availability of prey [16]. In several widely distributed species, geographical differences in food items have been also observed (see below). Furthermore, stomach contents usually contain a wide spectrum of organisms. The approach adopted in ECOPATH (Boxes 18 and 20 in Froese and Pauly [15]) was to calculate a fractional trophic level of prey species based on weighting of species of known trophic level in stomach contents, then add a value of 1 to get the trophic level of the predator. The simplified approach we have adopted here is to use these

Table 3  
The four trophic categories

Trophic category	Food items
Piscivores	Finfish, pelagic cephalopods
Zooplanktivores	Zooplankton, early stages of fish, jellyfish
Zoobenthivores	Benthic organisms
Herbivores/detritivores	Plants, phytoplankton, detritus, suspended organics

fractional trophic levels of predators where available, supplemented by other information from the literature on species diet, to classify the species into the four trophic level categories adopted in this study.

The criteria followed were: (a) the life stage considered is that at which the species is exploited (i.e. usually the adults). Hence trophic levels of larvae, post-larvae and juveniles have been ignored; (b) species showing seasonal variations in diet have been classified on a case-by-case basis, according to the available literature; (c) when geographical differences in the food items of a species have been found in the literature, it has been classified according to the data collected in the fishing area where the species has been selected; (d) when stomach contents revealed a broad or omnivorous food spectrum, the predominant food items in number and weight were used to assign the species to one of four trophic level categories as described above.

Seventy percent of the fish species were classified using the information contained in FishBase [17] and the current literature, and in three cases (see below) the trophic category assigned in FishBase was changed. Trophic values calculated by the ECOPATH model and through diet composition analysis are also available in FishBase for 96 and 53 of the selected fish species, respectively. For those fish species for which trophic data are not assigned in FishBase, and for all non-fish species, assignment to a trophic category was based on scientific articles located through the Aquatic Sciences and Fisheries Abstracts (ASFA). We also consulted the FAO Species Catalogues which cover major marine resource groups.

### 2.5. Controversial cases

According to FishBase, Alaska pollock (*Theragra calcogramma*) mainly feeds on zoobenthos but has been classified as piscivore in the Northeast Pacific area [18,19] and as a zooplanktivore in the Northwest Pacific area [20–22]. Similarly, the snoek (*Thyrsites atun*), which is a zooplanktivore in FishBase, has been classified as such in the Southwest Pacific [23,24] but as a piscivore in the Southeast Atlantic [25–27]. The kelee shad (*Hilsa kelee*) was classified in FishBase as a zooplanktivore on the basis of Babu Rao [28] quoted in Whitehead et al. [29]. Given that this species has numerous and fine gill rakers [30], which are an adaptation to small planktonic organisms, and its very low ECOPATH value (2.1), the kelee shad has been classified as a herbivore.

In the Northeast Pacific area, there were difficulties in classifying salmon species belonging to the genus *Oncorhynchus*, because in their marine life stage they are feeding on a range of zooplankton and fishes. According to the different percentages of fish and/or zooplankton in their diets reported in the literature [31–35] the coho salmon was classified as a piscivore, and the pink and sockeye salmon as zooplanktivores.

The chub mackerel, a cosmopolitan species abundant in many regions, is an opportunistic and non-selective feeder [36]. Geographical differences have been found on its food items but it has been classified as zooplanktivore in all fishing areas in consideration of the low value it has scored in ECOPATH (3.3) and by diet composition (3.1) [17]. The genus *Trachurus* (horse mackerels) is also widely distributed and comprises several species by region. Out of 7 selected species

belonging to this genus, 3 have been classified as piscivore (*T. declivis* in Southwest Pacific, *T. mediterraneus* in the Mediterranean and Black Sea area and *T. trachurus* in Northeast Atlantic) while the other 4 have been considered as zooplanktivores (*T. capensis* and *T. trecae* in Northeast Atlantic, *T. murphyi* in Southeast Pacific and *T. symmetricus* in Eastern Central Pacific).

As noted earlier, the zoobenthivore category should include only species feeding on benthic invertebrates but it has been applied also to those species which have a strict benthic behaviour and a mixed fish-invertebrates diet (i.e. Pacific halibut, *Lutjanus* and *Genypterus* species). Commercial species in the herbivorous category are mostly bivalves in temperate areas and fishes in tropical areas.

We are sure that there are many other species where this or any other categorisation will only be approximate and be incorrect in particular seasons, and will vary according to areas, seasons and sizes of predator/prey, but this is a defect of any such broad classificatory approach.

#### 2.6. A simple multispecies index (SSD) of variability derived from the capture production of the indicator species

The mean annual capture productions for the 1950–97 period were calculated separately for each of the 20 indicator species (*s*) as  $\bar{C}_s$ . A simple multispecies index was then calculated for each statistical area and year (*t*) in the time series as the sum of the squared deviations (SSD), defined by

$$SSD_t = \sum_{s=1}^{20} [\bar{C}_s - C_{s,t}]^2$$

This index appears to provide a rough measure of drastic changes in the multispecies harvest from year to year for the 20 species harvested in the FAO area, and shows wide departures from long-term stability where there have been a major changes in target species or in overall exploitation strategy.

### 3. Results

#### 3.1. Changes in catch trends by trophic categories and their possible reasons

This section discusses long-term changes in breakdown of capture production by trophic category notably between piscivores and zooplanktivores. Such changes can occur for four reasons:

- (1) 'fishing down marine food webs';
- (2) bottom up effects due to increased/decreased nutrification;
- (3) due to new technology, or changes in commercial interest and market-driven exploitation patterns;
- (4) long-term environmental or ecological change.

It is perhaps easier to deal with the third category first, and note that although trawling technology has improved with time, most shelf demersal resources have been available to exploitation since the 1960s. From a market perspective there has been an upward elasticity in prices with time for these resources; a feature shared with other 'seafood' delicacies such as most shellfish. A decline in landings is therefore unlikely to represent a loss of commercial interest. It is more likely to represent fleet strategies away from targeting the depleted resource to those which were formerly less favoured but is now more available or desired, due to new fishing or processing techniques and/or changing consumer tastes. The first species may still be exploited incidentally in the new fishery (e.g. groundfish, often juveniles, may still be under pressure in a fishery now aimed at shrimp or cephalopods over the same grounds). This provides an argument for considering declines of high-priced, long-lived species in regional harvests as a good, or at least precautionary, indication of likely overexploitation. Examples here are cod in the North Atlantic where landings fell from about 4 million tons in 1968 to 1.1 million tons in 1993. Independently we know from the scientific literature that most stocks of this species are overfished or even seriously depleted [37,38].

The contrary does not necessarily hold however: Northwest Atlantic American lobster stocks have long been considered overexploited, but harvests have risen since 1974 [39]. This may represent some as yet unexplained ecological change (e.g. [40]) such as covered by point (4) above, but certainly given the high fishing mortality rates calculated for *Homarus americanus*, a rise in landings cannot be regarded as an indication of underexploitation. Similarly the long-term rise in fish landings per shelf area in the Mediterranean does not necessarily imply underexploitation in the 1960s and 1970s, if we take into account the evidence for nutrient run-off to a formerly oligotrophic sea [10,41].

Another relevant example for the discussion of point (3) is the Southern bluefin tuna. Landings from the Eastern Indian Ocean are now a fraction of their former size due to heavy exploitation [42], but this is not recorded to have led to increased landings of small pelagics within its ecological range. The increase in landings of yellowfin tuna and skipjack noted later in the time series for the Indian Ocean and Western Central Pacific does not necessarily imply increases in abundance of these stocks due to increased forage fish abundance, or to any environmental or anthropogenic cause. Rather, tunas are more readily available to harvest now, thanks to technological improvements introduced in the late 1950s by more efficient distant water fleets, as well as the development over the last few decades of an efficient global market in seafood products. Ecologically, these changes in landings of offshore piscivores then, have probably little to do with changes in abundance of inshore shelf stocks predominantly fished by inshore artisanal fleets in the same FAO statistical area. Numerous other examples could be given of fisheries whose development was initiated by a technical innovation, and/or an unsatisfied demand for a product. A recent example is the spectacular increase since the 1980s in harvests of deep-water species such as orange roughy and Patagonian toothfish.

As noted above, the relatively late onset of large scale pelagic fisheries reflects more the invention of the purse seine power block and the mid-water trawl than any

increase in abundance of these stocks due to a predatory release caused by top predator depletion. Similarly, the decline in small pelagic landings/harvest after 1990 off West Africa, can be at least partly ascribed to a change in targeting by eastern European distant water fleets towards higher priced products. This followed the end of subsidised fleets formerly focussed mainly on small pelagics under centrally planned economies [4], and does not necessarily imply a decline in stock size of small pelagic fish. This in fact seems to be one of the rare examples that contradicts the usual rule, that a decline in landings usually reflects a scarcity of resources rather than a decline in fishing effort or demand. One other factor that can affect profitability of distant water fisheries can be noted but is not pursued here, namely changes in global oil prices, which have been relatively low over the last decade; thus encouraging distant water fishing especially for small pelagics.

With respect to the first two hypotheses above, as noted, they both have similar effects. Fishing down top predators leads to their decline and potentially allows their prey species to expand in biomass (assuming alternative predators do not emerge). They then form an attraction for further exploitation and hence potentially for increased landings of zooplanktivores lower down the food web. A similar result can occur if the food available to plankton feeding fish increases due to a rise in primary productivity. For reasons explained in Caddy [13], Caddy et al. [1] and de Leiva et al. [10] eutrophication, as for large lake ecosystems [43], eventually renders benthic habitats less suitable for demersal predatory species, especially in semi-enclosed seas. This is mainly due to reduced oxygen levels in bottom waters, either seasonally or permanently. Thus the decline of Black Sea demersal resources [44,45] and of the Baltic stock of cod [46] are at least in part due to a decline in the environmental conditions needed to support healthy stocks of demersal benthivores and piscivores. The decline in landings of large demersal fish and parallel increase in small pelagics due to nutrient run-off into semi-enclosed marine areas [10], both could contribute to the high pelagic/demersal ratio in landings from semi-enclosed seas.

Based on the same causes, the increase in biomass of Baltic fish stocks noted by Thurow [47] in the second half of this century, and the increase of Mediterranean fishery production per shelf area in the 1970s and 1980s [41], are probably due in part to increased nutrient run-off. Hence bottom-up production increases, and not just due to increased exploitation. In both cases the stocks had been considered to be fully, or close to fully exploited, over the last several decades.

One question to note here is that the catch trends for individual fisheries rarely show stability. Fluctuations can be driven by a variety of mechanisms such as environmental oscillations, Lotka–Volterra type of predator–prey oscillations [8], or even linked to economic cycles which can lead to a rate of fleet construction and renewal which is not typically stable in time, especially for industrial fleets. Fleet construction tends to occur as ‘pulses’ when favourable conditions for credit, new resources and new technology make fleet renewal economically attractive [48]. We are dealing here however with combined data from regional fisheries for several species in each trophic category. Therefore, it is perhaps not surprising that such oscillations are less evident in the FAO data set than those documented by Caddy and Gulland [49] and Spencer and Collie [50] for unit resources.

What is evident from the FAO data set however, are long-term trends in the PS/ZP ratio. Which of mechanisms (1)–(4) listed above are these in response to? An analysis of trends in the piscivore/zooplanktivore ratio was made for the 1974–97 period that is the second half of the available time series and starts "...when the major expansion of distant water fishing ceased..." [4]. This revealed that at least 9 of the 15 statistical areas seem to show a long-term linear trend ( $R^2 > 0.17$ ) in the ratio, either upwards or downwards in time (Table 4). Negative slope values imply declines in piscivore relative to zooplanktivore harvests, and vice versa. Examples of positive and negative slopes were found in both tropical and temperate areas.

A brief summary of key events for individual areas is provided below. For each FAO Fishing Area, Figs. 2–5 show total landings, sum of squared deviations (SSD), PS/ZP ratio, and a list of the 20 indicator species selected.

### 3.2. A broad-brush analysis by FAO Fishing Area

#### 3.2.1. Northwest Atlantic (Area 21)

Capture production peaked in 1968 and 1969 at about 4.5 million tons, coinciding with peaks for cod landings in 1968 of 1.8 million tons by distant water and local fleets, and of herring in 1969 (almost one million tons). These years were also characterised by peaks in the SSD index which reacted to the 'imbalance' of these species compared with the long-term species composition of landings from Area 21. By 1970, presumably in reaction to cod depletion, more species such as Atlantic mackerel and silver hake were taken, and the species composition returned rapidly to the long-term average. In 1990, the SSD started to rise again in correspondence this time with the collapse of landings of cod and some other groundfish, and an increase in landings of invertebrates such as blue crab, ocean quahog, lobster and Northern

Table 4  
Parameters of the linear regression of the PS/ZP ratio in each FAO Fishing Area for the 1974–97 period

Fishing area	Slope	Intercept	$R^2$
21	-0.0344	1.3784	0.3061
27	-0.0060	0.5805	0.1767
31	-0.0008	0.3838	0.0014
34	-0.0061	0.3564	0.3280
37	0.0051	0.1258	0.3359
41	0.1590	1.0882	0.6225
47	0.0022	0.4071	0.0153
51	0.0401	4.1074	0.0239
57	-0.0310	2.2473	0.2371
61	0.0063	0.1042	0.3273
67	-0.0465	5.0068	0.0575
71	0.0806	2.0922	0.8474
77	0.0063	0.6198	0.0341
81	0.1653	1.5174	0.4470
87	-0.0005	0.0431	0.0405

prawn. Were these rises in part due to reduced predatory pressure, or simply to diversion of fishing effort from depleted groundfish stocks?

In terms of behaviour of the PS/ZP index, the 'fishing down marine food webs' hypothesis seems a reasonable one, since piscivores (notably cod) are known to have declined since the early 1970s, and zooplanktivore landings were highest between 1968 and 1976. At the same time, this switch over of target species could have occurred due to decisions on fleet strategy in light of declining demersal resources, without any increase in pelagic resource abundance. The trend to target lower trophic levels seems to be supported by increased harvests of benthivores such as shrimp, crabs and lobsters which might reasonably be expected to increase in response to reduced predation. Again however, this switch over by coastal state fleets in the 1980s and 1990s, could simply be due to the lack of economic alternatives following scarcity of bottom fish.

### 3.2.2. *Northeast Atlantic (Area 27)*

During the 1970s, there were declines in biomass of planktivorous herring and Atlantic mackerel, and increases in biomass of gadoids, the so called 'gadoid dome' [51], which maintained rather constant high landings/harvests of groundfish during the 1970–85 period. The first peak in our SSD index in 1964–66 was due to herring catches being double the long-term average, and harvests of capelin and blue whiting were below average for the whole time series in those years.

In contrast to the concept of 'fishing down marine food webs', Jones [52] ascribed the subsequent increase in catches of gadoids (corresponding in Fig. 2 to the 1975–77 peak in landings, and 1977 peak in SSD) as in part due to more food being made available to adult demersal predators. This was seen as caused by the collapse of populations of once-dominant pelagic fish stocks: herring and mackerel. The 1975–77 peak harvests owed a lot to high landings of saithe, whiting, capelin and sprat in those years. Continued high landings in 1979–80 were dominated by a zooplanktivore, blue whiting. Since 1990, a general rise in harvests of zooplanktivores has been observed.

From the downward trend in the PS/ZP ratio, the concept of 'fishing down marine food webs' seems a candidate mechanism for explaining multispecies catch trends, although it is unlikely that the FAO database could provide unambiguous proof of this. Bottom-up mechanisms cannot be excluded as an explanation for events in coastal waters and the Waddensea however, where Boddeke and Hagel [53] suggest that changing nutrient run-off to the North Sea from rivers may have been a key factor in near-shore ecosystem change. Natural environmental variability could have also played a key role in relation to fluctuations of forage fish low in the food chain. Thus, strong year classes in the highly productive Northern regions of this statistical area have been linked to warming phases of the climate, acting either through faster larval development or transportation, and/or increased food availability in warmer years [54].

Increased predation on cod eggs and larvae by increases in herring and sprat [55] resulting from increased planktonic production, is another possible cause of cod declines. Given high biomasses and feeding rates of planktivores, this kind of 'reverse

trophic flow' where prey become predators on eggs and larvae of piscivores, must be fairly common, but is not easily incorporated into top-down models such as ECOPATH [56].

Industrial scale fisheries for forage fish can have the reverse effect in leading to food shortages for top predators, to conventional 'top-down' harvest effects. Although sand eels are important planktivores and make up a significant part of the catch from area 27 in later years, they are classified as *Ammodytes* spp in the FAO data base, and hence were not eligible for selection at the species level. Nonetheless, the effects of intensive fisheries for this species in the North Sea adjacent to sea bird breeding colonies has been a subject of concern as another possible bottom-up effect on predator populations [57].

### 3.2.3. *Western Central Atlantic (Area 31)*

The Caribbean Sea and Gulf of Mexico comprise a wide range of ecosystems from muddy bottom areas in the Gulf of Mexico and southern Caribbean, to coralline islands and oceanic fisheries. As such, expecting to see trophic linkages in the FAO database would be optimistic, though overexploitation and depletion of top predators, grouper and snapper, and swordfish in the pelagic biome, seems indicated, and should have affected local food webs. For example, top predators in the Caribbean demersal fishery such as the red grouper have been seriously depleted by overfishing [58]. From experimentation using the ECOPATH model with different levels of grouper biomass, it is not surprising that in a steady-state model alternative predators such as red snappers and sharks would increase as groupers declined in biomass [59].

The steady rise to peak regional harvests (and peak values for the SSQ index) in 1984 was made up of a wide range of species, but was dominated by an offshore piscivore, yellowfin tuna, and by herbivores, largely from the Gulf of Mexico (Gulf menhaden, American cupped oyster and calico scallops). Fishery production in the Gulf of Mexico is affected by river run-off (especially from the Mississippi), and high levels of nutrients have led to large hypoxic areas in the Gulf in recent years [60]. Although it seems likely that river sources of nutrients were in part responsible for high production of herbivores/detritivores in Gulf of Mexico landings early in the time series, the extent to which excessive nutrient run-off as opposed to overexploitation, contributed to the overall harvest decline after 1984 is not clear. It may even have led to increased production in surrounding areas.

In general, independent evidence [61] suggests that fishery resources of island shelves and reef ecosystems have been heavily overexploited, and that top predators such as groupers and snappers are generally depleted, as may be pelagic predators such as swordfish and bluefin tuna [62]. At the same time, the PS/ZP ratio shows no clear downward trend, though temporal fluctuations, possibly due to changing upwelling strength are important, especially for small pelagic production in the Southwest Caribbean. In fact, Venezuelan sardinella landings have been related to both fishing effort and an index of annual upwelling strength [63].



### 3.2.4. Eastern Central Atlantic (Area 34)

The early rise in total landings here from 1950 to 1977 was dominated by small pelagics: sardine and sardinella. An early trawl fishery by distant water fleets depleted demersal predatory fish, in particular sparids. This is believed to have reduced predatory control on octopus stocks [64] harvests of which peaked in 1975. Since the 1970s, a wider variety of species contributed to the multispecies catch, including pelagics (sardines, chub mackerel and piscivorous skipjack and yellowfin tunas), but also deep water species (e.g. largehead hairtail). No clear evidence of other trophically driven changes seem to emerge: upwelling regimes of variable strength seem to be the main bottom-up driving influence. Increases in sardine harvests along the Moroccan coast between the 1950s and mid-1970s have in fact been related to the long-term increase in upwelling intensity [65]. Changing upwelling strength was probably largely responsible for the low landings/harvest of small pelagics in 1993–94 from this statistical area, but also for their strong subsequent recovery. Overall, the PS/ZP ratio for the sample species shows no obvious long-term trend.

### 3.2.5. Mediterranean and Black Seas (Area 37)

Here, the steady rise in total harvests from 1970 to the peak in 1988 is mainly due to increased harvests of piscivores (Mediterranean horse mackerel and whiting) and of all zooplanktivores (sardine, anchovy, sprat and chub mackerel). In the same period the PS/ZP ratio increased steadily, peaking in 1990 coincident with the collapse of anchovy stocks in the Black Sea [66]. This shows up in the decline of the PS/ZP ratio and was largely due to the mass proliferation of the ctenophore *Mnemiopsis leidyi*, introduced into the Black Sea in shipping ballast water. This species preys voraciously on zooplankton and fish eggs and larvae [45].

The increase in landings per unit shelf area for northern sub-areas of the Mediterranean basin documented by Caddy et al. [1] in the 1970s and 1980s, is difficult to explain as a result of increased rates of exploitation alone. The Mediterranean, with its narrow shelves had already been considered fully exploited in the 1970s. The continued rise in landings seems in part due to an increase in biological production. The contribution of nutrients from land run-off has been proposed as major factor here [10,13]. The peak landings of piscivores (e.g. swordfish and hake) later in the time series than for zooplanktivores, appears consistent with such an overall bottom-up response to the earlier increase in abundance of forage fish. Recently, the high proportion of landings of the Eastern Atlantic/Mediterranean stock of bluefin tuna coming from the Mediterranean (whose stock size is reported by ICCAT to have seriously declined over the study period), suggests that this migratory species now finds improved foraging within the Mediterranean part of its range.

### 3.2.6. Southwest Atlantic (Area 41)

The picture here is of a steady rise in overall landings, with an early peak in 1967 due to Argentine hake, and a later one in 1987, due mainly to Argentine shortfin squid. Whether the presumed trophic linkage between these two species is responsible for this delay in peak production, or whether the later timing of squid

exploitation is due to political events around the Falklands/Malvinas Islands, cannot be decided from the data set alone. Since the main forage species in the region, the anchovy, is not heavily exploited, it is also difficult to point to a fishery-induced trophic linkage between this species and harvests of its main predators, hake and squid, despite the relatively simple food web that applies here. It will be interesting to see what ecological effects result from the current overexploitation of Argentinian hake on the other shelf resources [2]. In this context, the sharp rises in the SSD index at the end of the time series suggests significant changes in ecosystems may be occurring in recent years. If these parallel those shown during the period of peak landings in areas where landings have since declined, we may take this as a warning that production here is also approaching a peak.

Caddy et al. [1] noted that peak landings per shelf area of shelf resources in southern hemisphere fisheries were significantly lower than from similar climatic zones in the Northern hemisphere. They hypothesized that relatively lower nutrient run-off and less enclosed and sheltered shelf areas could lead to a greater loss of larvae and nutrients from more open Southern hemisphere shelf waters.

### 3.2.7. Southeast Atlantic (Area 47)

Landings rose rapidly from the 1950s to the 1960s, largely due to the South African pilchard fishery, and this shows up as early low values for the PS/ZP ratio. A fishery mainly targeting hake species, predominantly by distant water fleets, showed later peak landings in the 1970s until this fishery depleted the resources. This was documented by the ICSEAF Fishery Commission that formerly exercised (minimal) control over resource exploitation in the region. With the assumption of fisheries management responsibilities by the Government of Namibia after the country's independence in 1990, a period of stock rebuilding was initiated with restrained harvesting of demersal resources [67]. Later peaks in landings occurred in 1968–69, 1972–73, 1978 and more recently, in 1987, which seem to mainly reflect peak harvests of different zooplanktivore species (respectively, the South African pilchard, Cape horse mackerel and South African anchovy). The exception was the 1972–73 peak that was mainly due to harvests of *Merluccius* spp. For the small pelagic planktivores, intermittent upwelling regimes are probably the dominant influence on biological and fishery production here. Recruitment of small pelagics (e.g. the South African anchovy) seems largely determined by meteorological conditions: strong south easterly winds lead to cool conditions and offshore loss of eggs and larvae [68]. Presumably however, the risk of overfishing is highest when recruitment is reduced due to a temporarily unfavourable environment.

After rebuilding by restrictive management by Namibia since independence, recent declines in hake [69] seem be associated in part with low oxygen bottom water and excessive levels of upwelling production [70], and are not obviously due to overfishing.

### 3.2.8. Western Indian Ocean (Area 51)

A steady rise in fishery production throughout the time series, without any apparent peak in production so far, reflects combined harvests from several distinct

ecosystems. Thus, the 1993 peak for piscivores corresponds to high landings of yellowfin tuna mainly by distant fishing fleets that operated offshore in the area, and is unlikely to be related to the subsequent peak landings of zooplanktivores that occurred in 1996. These were dominated by landings of Indian mackerel, a neritic species mainly caught around the Indian subcontinent. For this statistical area, Tsarin [71] showed that albacore and bigeye tunas, as well as some abundant oceanic squids, depend to a significant extent on the mesopelagic myctophid resources of the deep scattering layer. These resources which exist as high biomasses in most world oceans, are not yet being exploited at present, and this would seem to provide some degree of stability to food webs supporting top oceanic predators. The PS/ZP ratio here does not show any overall trend, but the SSD index suggests progressive departure from ecological equilibrium towards the end of the time period.

### 3.2.9. Eastern Indian Ocean (Area 57)

Recent highs in total landings in 1996–97 reflect peak landings of herbivores, mainly shads and Indian oil sardine in the Bay of Bengal. Landings of the most important piscivore species, the Southern bluefin tuna from the southern part of the area, peaked earlier, in 1961 and its stock is now depleted. This shows up as a downward trend in the PS/ZP index. It seems unlikely however that these two events are linked trophically, though such top-down effects on local shelf ecosystems are not excluded. The steep upwards trend in the SSD index at the end of the record suggests that ecological change is going on, and that peak landings for the area may be approaching.

### 3.2.10. Northwest Pacific (Area 61)

A steady rise in overall harvests peaked in 1986–89, and largely coincided with peak landings of Alaska pollock and Japanese pilchard, both classified as zooplanktivores in this area. This rise confounds trends in smaller landings of a wide range of species from an area where marine fisheries have always been high in importance. The hundredfold increase of Japanese pilchard landings between 1972 and the peak year of 1988, was probably environmentally driven [72]. Despite high exploitation rates, this mechanism may also apply for other fluctuating resources in the region such as *Todarodes pacificus* [73]. Currently, the environment seems to have shifted back to an unfavourable regime, since Japanese pilchard landings are now back to early 1970s levels, while an increase of Japanese anchovy landings was noted in the 1990s. In the Yellow Sea [74], exploitation of piscivores and benthivores was followed by peaks in landings of zooplanktivores. Similar observations were made for the Seto Inland Sea [75]. Whether these sequential changes reflect the effects of removal of predatory pressure from top predators, simply reflects sequential depletion, or are also due to increased nutrient run-off favouring planktivores, is impossible to say from the FAO data set. Decreases in landings of Alaska pollock have been recently followed by increased landings of largehead hairtail, Japanese Spanish mackerel, yellow croaker and Japanese flying squid. With the exception of the last-mentioned valuable species, this may in part reflect how commercial interest is transferred from a high value species to less valuable ones when the former target

species has been depleted, though environmental fluctuations are not excluded here also.

The linkage between wide historical fluctuations in landings which is typical of many fish stocks [49,76] in some areas seems largely driven by environmental variations. Thus, in the Pacific as a whole, highly variable pelagic fish landings (e.g. Peruvian, Japanese and Californian sardines, Chilean Jack mackerel and others) appear to occur in synchrony, and can be linked to atmospheric circulation and other geophysically determined indices [77] in a manner that seems to support bottom-up type of mechanisms.

### 3.2.11. *Northeast Pacific (Area 67)*

The fisheries for Alaska pollock (here classified as a piscivore, see 2.5) and the three species of salmon selected (one mainly a piscivore; the other two mainly zooplanktivores), dominate the evolution of landings in this region. Alaska pollock was the subject of high discarding [12] until the development of the surimi process led to it became highly sought after. Harvests first peaked in 1972, and reached their maximum in 1987, together with those of Pacific hake. There seems evidence that these peaks are in some sense environmentally linked [78,79], as perhaps are the peaks in 1993 and 1995 for sockeye and pink salmon respectively. Overall, peaks in the trajectory of the SSD index (Fig. 4) seem consistent with the decadal-scale cycle of production reported for this area [80,81]. Although fisheries have been largely responsible for depletion of some key resources such as king crabs [82] the underlying non-equilibrium production cycle, with its major ups and downs of key resources, seems to support the idea of environmentally-driven cycles of primary production dominating for this area.

More conventional bottom-up food web interactions can be mediated by shortage of forage fish for apical predators. Thus, intensive fishing has led to declining shrimp resources, and with declines in capelin resources, has affected seal and Northern Sea lion populations in the Gulf of Alaska [83]. At the same time, regular shrimp surveys [84] show that changes in dominant species in the demersal community are a useful index of regime shifts also linked to changing temperatures. The jump in the PS/ZP index in the 1960s perhaps mainly reflects declines in Pacific herring stocks, and a switch to dominance of fisheries landings by Alaska pollock, a species which was formerly often discarded, but revalued upwards by the surimi industry.

### 3.2.12. *Western Central Pacific (Area 71)*

Rising landing trends in recent years are fairly typical of most tropical areas, and for Area 71 show a steep rise in landings following a late onset of industrial fisheries, with a total multispecies harvest which peaked in 1994–97. A marked peak in the multispecies SSD index occurred in 1991, and corresponds to maximum harvests of skipjack and Bali sardinella. These peak landings of an offshore piscivore, skipjack, seems unlikely to be trophically tied to a simultaneous peak of the zooplanktivorous Bali sardinella whose landings are reported only by Indonesia. The early peak harvests of other zooplankton feeders, such as short mackerel in 1969 and rainbow

sardine in 1977, are also difficult to relate to the continuous increase of landings of pelagic piscivores. In all cases this is more likely to be a response to the late rise in fishing effort and global adoption of more efficient fishing technologies for tunas and tuna-like species.

#### 3.2.13. *Eastern Central Pacific (Area 77)*

The first peak in multispecies harvests for this region in 1981 coincide with high landings of skipjack tuna and Californian anchovy: the former associated with the onset of large-scale purse seining, the latter largely as an early expansion of a local canning industry, and both coincide with a peak in the SSD index. The rise and subsequent collapse of Pacific anchoveta whose landings peaked in 1985, and of the Californian pilchard (peaked in 1989), and the collapse of the anchovy fishery in 1990–94, may all in part have been fishery-induced. However, evidence such as the alternation of fish scales of pelagic resources in cores of bottom sediments prior to exploitation [85], suggests that environmentally driven production cycles have always been the norm here in an area of intermittent upwelling. The expansion of a formerly regional tuna fishery through the 1970s and 1980s to distant water fishing grounds, accompanied by increased diversification and efficiency of gears and vessels, rather than any biological change, seems responsible for the peaks in landings of bigeye and yellowfin tunas in 1986 and 1988, respectively.

#### 3.2.14. *Southwest Pacific (Area 81)*

The steady rise in multispecies yield over 4 decades to a peak in 1991–92 follows the evolution of a fishery initially dominated by distant water fleets (mainly Japan, former USSR and Taiwan, Province of China) and was largely driven by increased availability to capture, and changing market demand. Early peak landings of mainly offshore resources such as albacore and Southern bluefin tuna in 1965–69 seem unlikely to be trophically linked to later peak harvests of planktivorous species. These started to be significant in 1970, notably snoek (which peaked in 1977) and Southern blue whiting (in 1992). The later peak harvest of deep-water long-lived species in the 1990s, such as orange roughy and blue grenadier, were presumably driven by developing techniques for deep water trawling, and by the opening up of markets for these new products.

#### 3.2.15. *Southeast Pacific (Area 87)*

This area is the classical example of upwelling-driven fisheries [86], where some of the world's largest fisheries in terms of biomass harvested are of zooplanktivores, responding by major fluctuations in biomass and species range to changes in primary productivity associated with upwelling nutrients. Thus, peak landings of anchoveta of 13 million tons in 1970 did not recur until 1994, after which the landings sharply declined to the very low level of 1998, influenced by a strong El Niño phenomenon in 1997–98 [87]. Although the influence of heavy fishing, mainly for reduction to fishmeal, cannot be discounted as contributing to collapse of pelagic stocks, the overall timing of production cycles seems to be driven by bottom-up peaks in

primary production. Order of magnitude abundance changes of the South American pilchard (*Sardinops sagax*) seem in fact to be largely determined by upwelling, which also influences the balance between sardine and anchovy populations [88]. The series of peaks in the SSD index seem to illustrate the 'punctuated' non-equilibrium nature of the main fisheries here.

It is interesting to note that zooplanktivores formed a small proportion of landings in the first years of the time series (1950–55), which were dominated by South Pacific hake and Eastern Pacific bonito; both piscivores. Landings of South Pacific hake were again dominant and peaked in 1978, but there seems no likelihood that the subsequent decline of these piscivore stocks was responsible for subsequent increases in anchoveta biomass. As evidence of ecosystem switching in the period between the two anchoveta peaks, a second zooplanktivore, South American pilchard was temporarily dominant with landings peaking in 1984–85.

The subsequent discovery and offshore expansion beyond 200 mile jurisdiction of fisheries for Chilean jack mackerel were led initially by distant water fleets prior to the 1995 peak harvest. A subsequent peak in landings of Patagonian grenadier in 1996 diagnoses expansion of bottom fisheries into deeper water, a tendency seen in other FAO areas late in the time series. Although there was early fishing down of top predators such as hake in this area, trophic linkages between harvested species through the food web do not seem to be the most convincing explanation for subsequent changes in pelagic fish abundance. These seem firmly linked to El Niño-Southern Oscillation (ENSO) large-scale meteorological cycles [89].

Figs. 2–5 illustrate the evolution of peak catches in each of the statistical areas considered. These show clearly the early peak exploitation in the 1960s and 1970s of the Northwest, Northeast, Eastern Central, and Southeast Atlantic; the last two predominantly by distant water fleets, and the later rise in exploitation of the very large North Pacific grounds in the 1980s. More recently, exploitation of areas such as the Southwest Atlantic, the Indian Ocean and Western Central and Southwest Pacific have also peaked. There are reasons to believe [1,4] that we are not far off a peak in catches for the remaining marine areas also, if it has not already occurred. What this implies about the overall state of full exploitation or even overexploitation of world stocks has been commented on by various authors [1,4,5].

### 3.3. A diversity of observations on ecosystem productivity?

Interpretation of trends by trophic categories does not follow one simple rule when viewed from the FAO database aggregated over large marine areas. As we have said, one or other mechanism may predominate at local scales and in particular ecosystems.

One useful perspective emerges when we categorise FAO Fishing Areas into three main types:

- (A) Temperate areas (Areas 21, 27, 37, 41, 61, 67, and 81),
- (B) Tropical areas (Areas 31, 51, 57 and 71),
- (C) Upwellings areas (Areas 34, 47, 77 and 87).

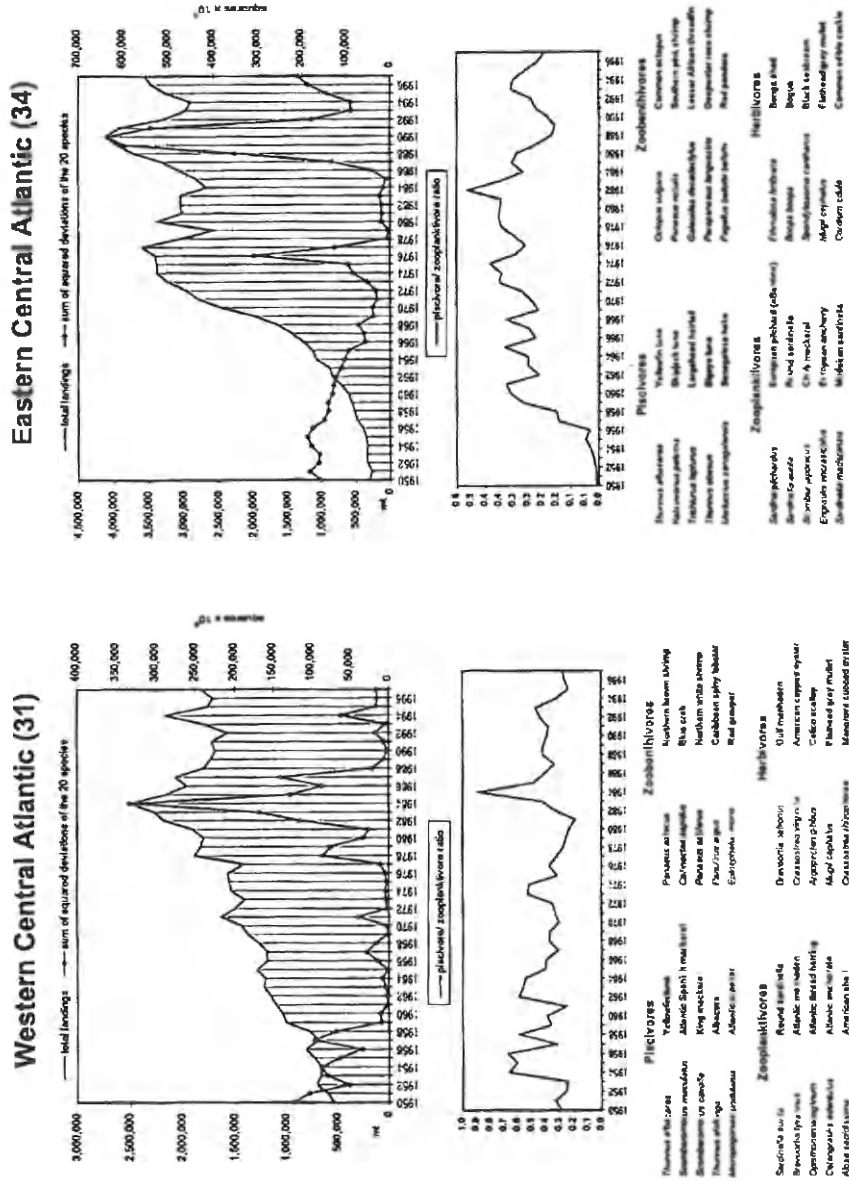


Fig. 2 (continued)

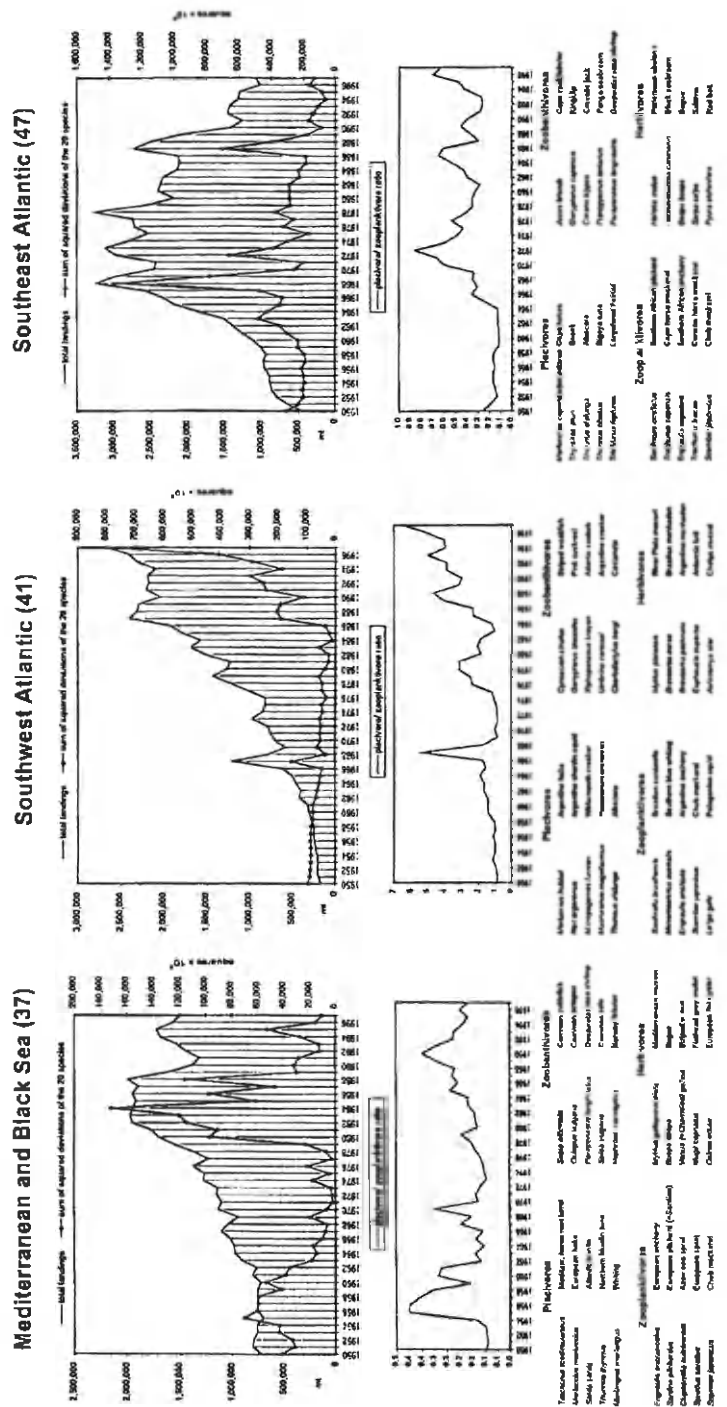


Fig. 3. Total landings and SSD index, PS/ZP ratio, and species selected for the 37, 41 and 47 FAO Fishing Areas.



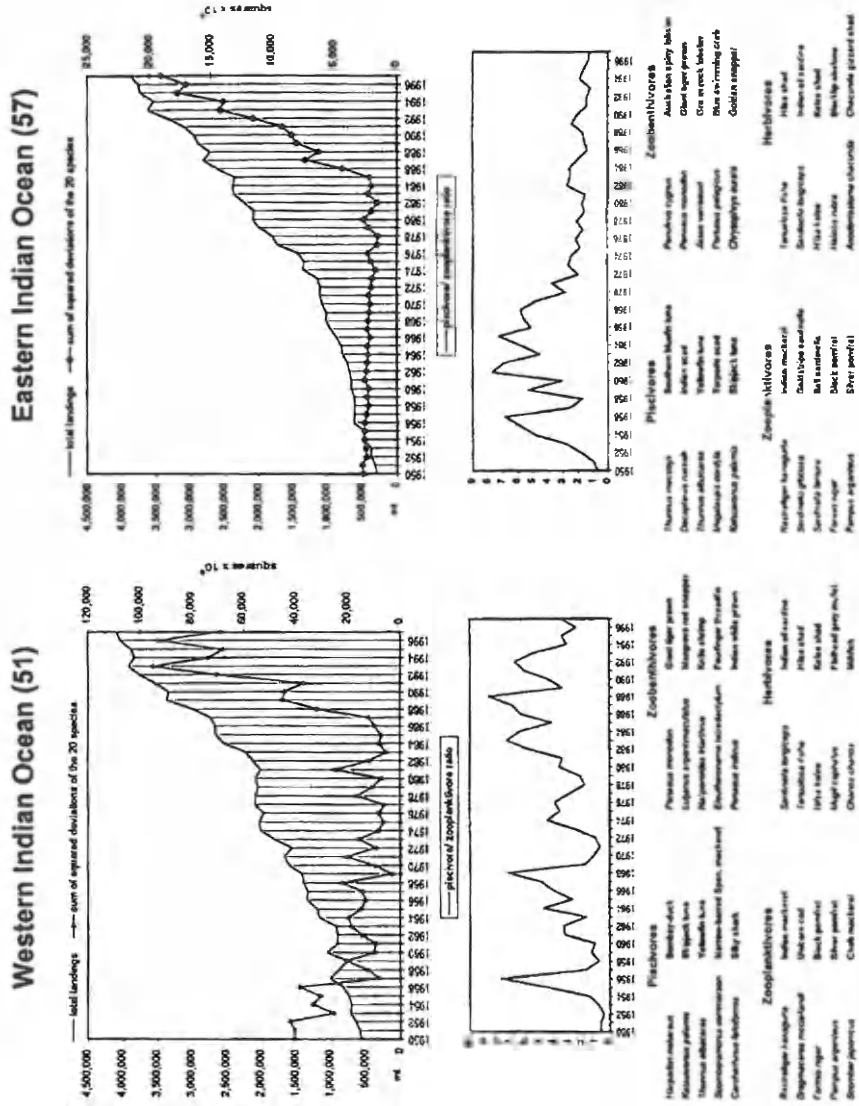
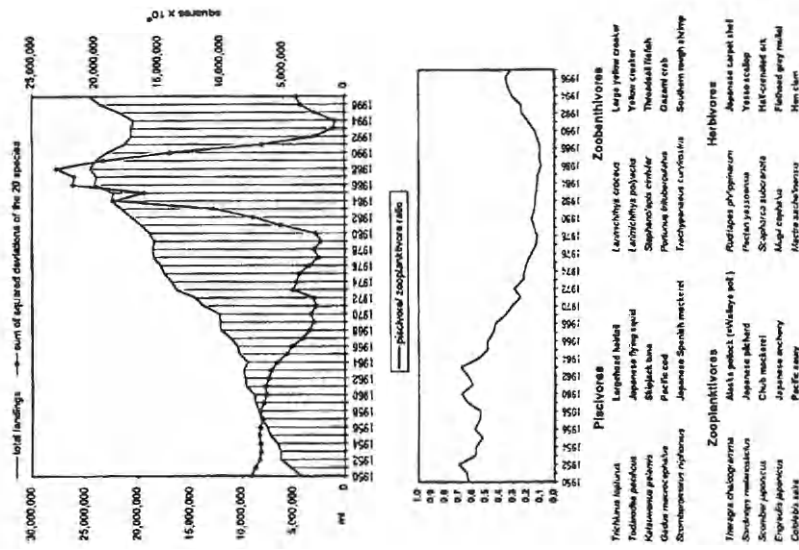


Fig. 4. Total landings and SSD index, PS/ZP ratio, and species selected for the 51, 57, 61 and 67 FAO Fishing Areas.

### Northwest Pacific (61)



### Northwest Pacific (67)

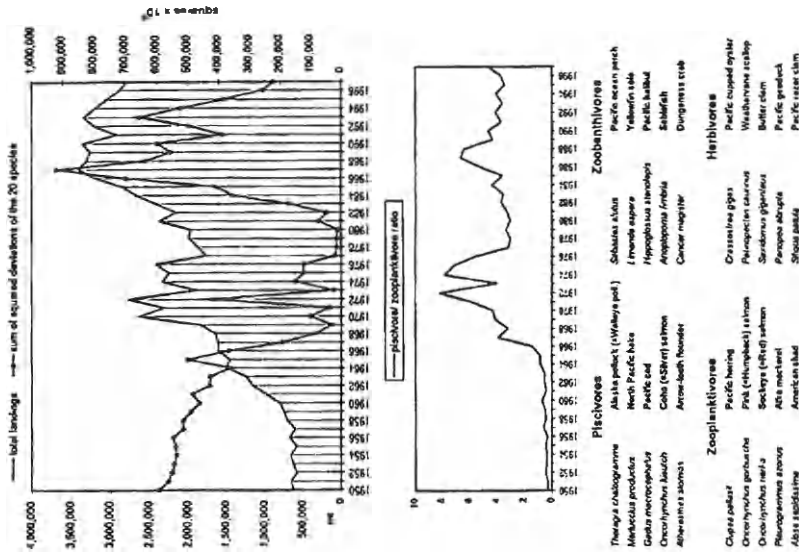


Fig. 4 (continued)

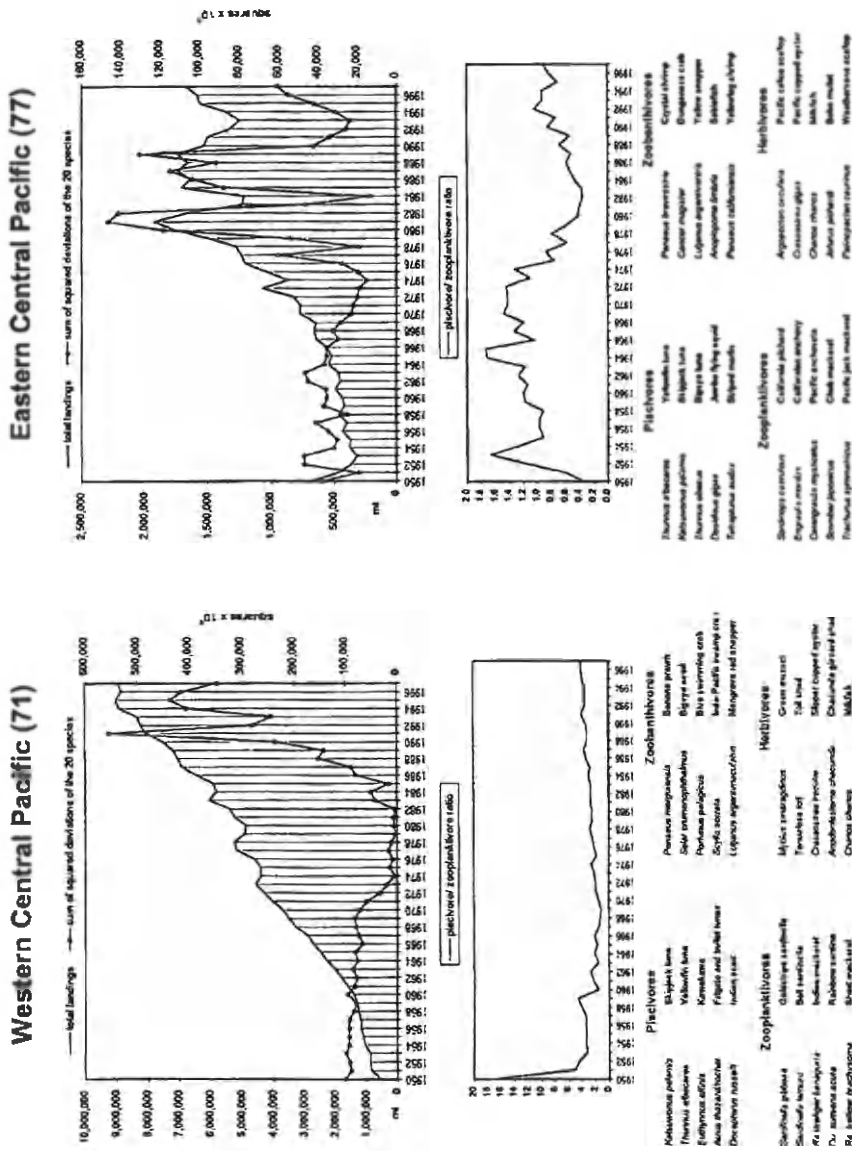


Fig. 5. Total landings and SSD index, PS/ZP ratio, and species selected for the 71, 77, 81 and 87 FAO Fishing Areas.

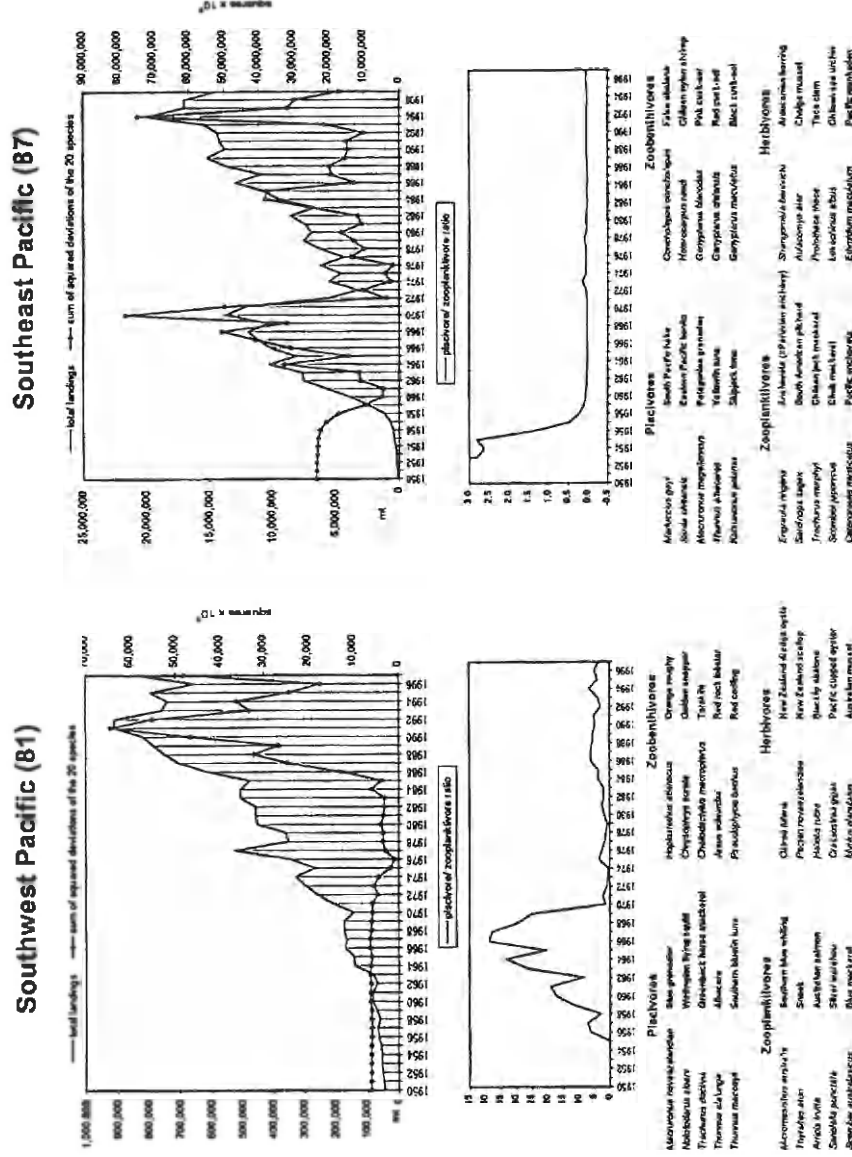


Fig 5 (continued)

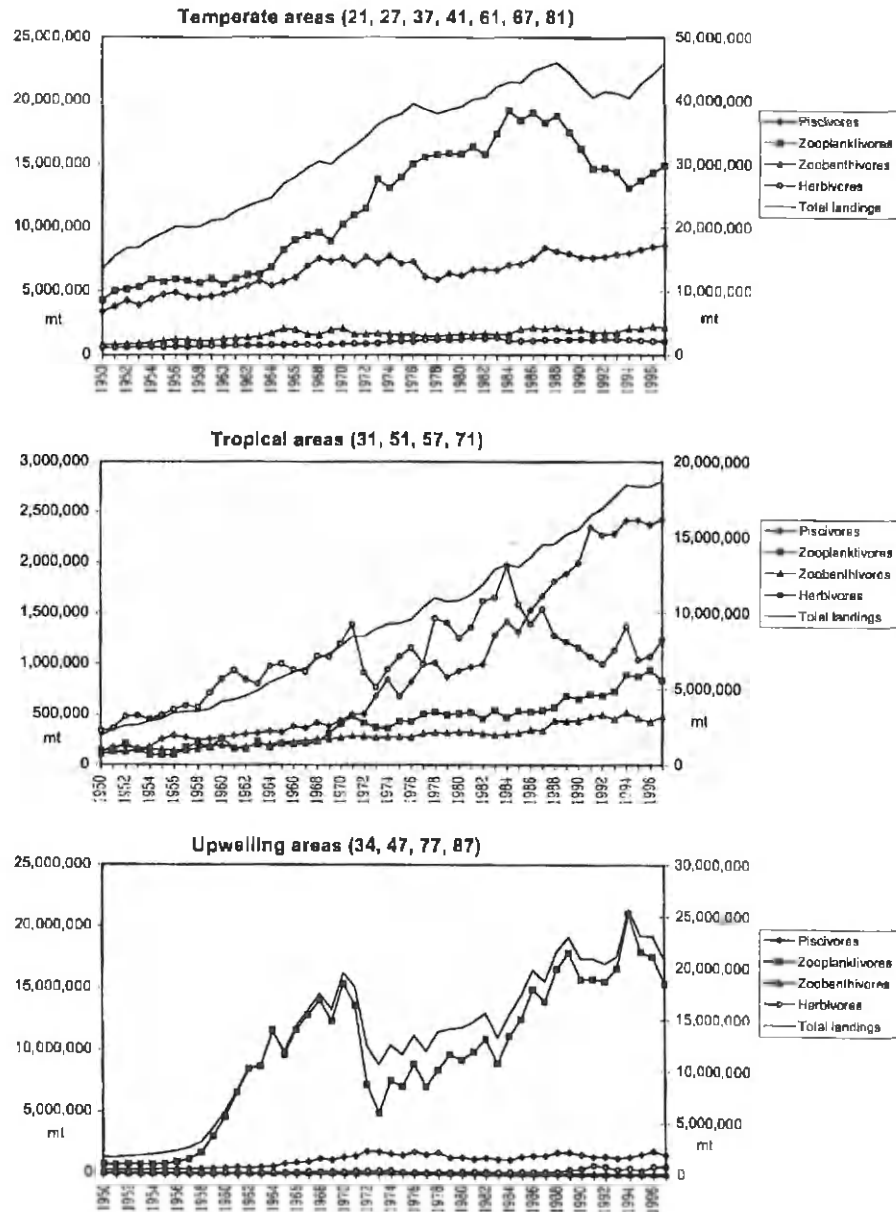


Fig. 6. Total landings (secondary axis) and totals of the four trophic categories (primary axis) in temperate, tropical and upwelling areas.

Below are briefly discussed the landing trends (Fig. 6) of each of the four trophic categories and the total landings (scale on secondary axis) for the three typologies mentioned above:

(A) In temperate areas, there has been a generally positive increase in landings of piscivores during the whole time series, but at a rate of increase lower than for the total catch. In recent years the decrease in landings has been largely due to a decrease in zooplanktivores.

(B) In tropical areas outside major upwelling zones (many of these are stratified areas of relatively low fishery productivity; Caddy et al. [1]), declines in herbivore harvests are largely due to the marked decrease of Gulf menhaden landings in Western Central Atlantic after the 1984 peak. The most notable increase since the 1970s was of piscivore landings throughout the whole time series which was principally associated with offshore tuna fishery development.

(C) For areas subject to major upwelling events [90] total landings show strong fluctuations, which reflect very labile zooplanktivore landings with piscivores making up a small and relatively constant share of the fishery production and probably not having much influence on total productivity.

The conclusion seems to be that although top down effects are not excluded at a local scale, the evidence, judging from the coarse-grained FAO data alone, for a release of predatory pressure on zooplanktivores leading to expanded biomasses, is ambiguous at a high scale of aggregation, even for temperate areas. In tropical areas, increasing oceanic production, especially from tuna like species and oceanic squids, appears to have been predominantly technologically driven in recent decades.

#### **4. Discussion**

As noted by Christensen [91], quantified trophic flow models such as ECOPATH II [56] can be very useful in examining steady-state situations. They lead to important conclusions such that the amount of finfish consumed globally by other finfish is likely to be roughly three times the global catch of these organisms. Using these models to explain real changes in the FAO database will require additional information, indices and hypotheses however. We suggest that the multispecies SSD index and the PS/ZP indices are rough measures of ecosystem change which are not hypothesis-specific. We may even presume that when major shifts in exploitation patterns occur leading to changes in species dominance, these can lead to partial substitutions of one species assemblage by another. Such changes are typically accompanied by an abrupt increase in landings of one component and the decline of others, so that the composition of landings in that year differs sharply from the average composition of landings for the entire 1950-97 period. Hence, this shows up as a sharp peak or trough in our multispecies SSD index. Conversely, if the ratio of landed weights of our indicator species remain more or less constant, a steady index is (a less certain) indication that the ecosystem may not yet have undergone a dramatic change.

Figs. 2–5 illustrate the evolution of peak landings in each FAO Fishing Area. They show clearly the early exploitation in the 1960s and 1970s of the Northwest, Northeast, Eastern Central, and Southeast Atlantic, the last two predominantly by distant water fleets, and the somewhat later rise in exploitation of the very large North Pacific grounds in the 1980s. More recently, exploitation of areas such as the Southwest Atlantic, the Indian Ocean and the Western Central and Southwest Pacific, has peaked. There are reasons to believe [1,4] that we are not far off a peak in landings for the remaining areas also, if this has not already occurred. What this implies about the overall state of full exploitation or even overexploitation of world stocks has been commented on by various authors [1,4,5]. Interestingly enough, in many of the tropical areas where landings are highest in the last few years of record, we see our multispecies variance index rising sharply over the last few years of record. This may be a precautionary index of an approaching peak in overall catches, and the rather chaotic ecological situation this seems to be associated with: landings of certain species rising sharply, while others decline from recent averages.

This analysis has inevitably been tentative, and it would be over-ambitious to specify which mechanisms have been dominant in realising ecosystem change. This is especially true since as noted by Caddy [92], the time span of global landings we have discussed (1950–97) was a period when a number of anthropogenic influences were increasing almost monotonically. World populations and hence demand and prices paid for fish have been growing, as have fleet sizes, their fishing power and mobility, and the development of global trade in fish. The impact of land run-off, especially of nutrients into aquatic systems, and consequent stresses on coastal aquatic ecosystems have also increased synchronously over the same time period. This makes any attempt at a definitive statement as to 'prime causes' presumptuous. We believe it is useful however to draw some tentative conclusions as to the key factors that seem to be operating in different global areas and for different resources, since the policies that need to be developed in this millenium will need to take such likely changes into account.

According to Christensen [91], predation usually outweighs harvests as a source of mortality in marine ecosystems. Globally, fisheries are exerting heavy pressure on large piscivorous fish, and this shows up in the FAO database, not only in terms of increases in landings of these species, but probably in subsequent increased landings of short-lived species such as squids [64]. This may apply also to shrimps and other short-lived demersal or shelf-associated species. As Christensen notes [91], herbivory and detritivory among commercially exploited fish species is comparatively rare (though not so for many commercial invertebrates which are beginning to occupy a larger proportion of harvests, particularly in heavily exploited areas). We may find it more difficult, however, to find clear evidence from the landings database alone for an increase in productivity of these lower trophic levels in response to a release in predator pressure. This is especially true for small pelagic resources, since they are also highly susceptible to bottom up influences and the changing productivity of oceanic waters, especially in the upwelling areas whose productivity dominates world landings.

The case has been made for the likely applicability of top-down effects, commonly referred to as 'fishing down marine food webs' [5]. As noted, such effects are predicted by theory, and should show up most clearly in stable, well-studied shelf ecosystems, both in the tropics and in temperate regions. This mechanism would seem to imply not only a switch to harvesting a target species lower in the food web, but also that this is a response to an increase in abundance of the latter as a result of reduced predation. Obviously this is an inevitable consequence of trophic models [56] especially if they assume constant productivity. Distinguishing such a switch from a simple change in target species as a result of depletion of the top predators would be difficult from the present type of analysis. Bottom-up trophic interactions also seem to be particularly influential for semi-enclosed seas, and independent analyses seem to point to these [1,13] as important. For areas subject to intermittent upwelling strength, changes in pelagic biomass and composition [93] are likely to be of at least an order of magnitude in some cases, and hence most probably would obscure evidence for likely smaller changes in lower trophic level production due to top-down mechanisms.

All of these biologically mechanisms are valid and predicted by theory, but fisheries are also closely associated with technical change and with the recent spectacular growth of global markets for sea products over the last few decades. The impacts of the dramatic changes in fishing technology and markets over the last 30 yr are, we believe, the most apparent influences that show up on the large geographical scale of the FAO database. Changes in the valuation of some high and low trophic components have also occurred over the time series [94], which we have not explicitly considered here, but could be very important. Unfortunately, we rarely have information on target species taken in multispecies harvests. However, the large stocks of small pelagics distant from home ports of developed countries were previously relatively untouched by traditional techniques. They became suddenly vulnerable to heavy exploitation due to improved fishing technologies introduced in a widespread fashion, mainly after the late 1960s. Because their landed weights swamp landings of other species (especially top predators) in the FAO landings data base, this inevitably reduces the mean trophic level of global landings. It seems unlikely however that small pelagic fish in upwelling areas which contribute largely to landings of these resources are primarily controlled in size by predator populations. It has even been suggested [95] that these systems are 'wasp-waisted' [93], implying perhaps that the large but variable biomass of small pelagics has an effect principally on its predators, but perhaps also on its prey the zooplankton. This latter will presumably reflect the quantity of nutrients entering surface waters and remaining in the stock area as phytoplankton/detritus, and zooplankton.

With respect to large oceanic predators, the technological revolution has promoted emergence of oceanic predator control as a potential mechanism relatively late in the time series for many tropical areas, since the wide diffusion of distant water tuna fisheries was probably most evident from the late 1970s to early 1990s. We are unable to predict at this time what effect the growing harvest of ocean predators is having or will have on oceanic ecosystems. As suggested by Caddy and Rodhouse [64], the increased landings of cephalopods may not be entirely a function



of new products and markets opening up for these species, though trophic interactions between cephalopods and piscivorous fish are potentially easier to document for shelf ecosystems. Here, top-down release of predatory pressure on cephalopods seems a reasonable hypothesis stemming from earlier depletion of large demersal predators such as for example, gadoids, serranids and sparids. Showing similar effects on oceanic food webs as a result of tuna exploitation, on myctophid or oceanic squid populations, will probably prove difficult from existing data sets.

Member States of FAO have in fact reacted with concern to depletion of some 'charismatic' top predators, (e.g. sharks and sea birds) by developing guidelines to protect endangered populations [96]. Christensen [91] notes that in most situations, predators and prey have multiple preys and predators, respectively. Thus although the removal of all predators is likely to be particularly destabilising, predator control is not necessarily going to be as easy to verify in nature as in a steady-state model such as ECOPATH. This is especially true, since in nature, wide fluctuations in environmentally driven inputs at the bottom of the food web make it difficult to quantify top-down impacts of predator depletion. This is not to deny the reality of species interactions, but as noted by Brugge and Holden [97], convincing fishery managers of the often counter-intuitive results of ecosystem modelling as a basis for action, has so far often proved difficult in a period of rapid technological change and growing fishing capacity.

A move towards lower percentages of piscivores in shelf fisheries in some regions, and to increased proportions of short-lived invertebrates in others, seems supported: in this latter case, perhaps also reflecting the move to shellfish mariculture techniques. In the North Atlantic, top-down effects due to fishing down of food webs seem a likely cause of declining piscivore/zooplanktivore ratios, though 'punctuated equilibrium' involving actual changes between ecosystems, rather than just continuous change in a single ecosystem, seems supported.

The effects of nutrient run-off are evident in areas of formerly low productivity such as the Mediterranean. Like top-down predator depletion, this also show up as a reduction in the PS/ZP ratio [10] but in this case, is probably mainly due to increased planktivore production. This bottom-up effect can also be detected from remote sensing of water colour in semi-enclosed seas [98].

In the Mediterranean, the time sequence of events suggests that recent increases in landings of bluefin tuna, swordfish and hake could be resulting from earlier increases in forage fish abundance attracting local concentrations of migratory fish, or increasing production of local predators, rather than vice versa. The possibility that this is an example of Lotka-Volterra predator-prey linked cyclic production [8] cannot be discounted at this stage.

Zheng [99] showed that globally, the recruitment of forage fish can be highly variable (from 1:12,000 between years of minimal and maximal recruitment). 'Boom and bust' type fisheries tend to follow these peak recruitment years. In these circumstances, although predator populations may respond to increased prey abundance, it seems unlikely that multiyear class predators could respond as quickly to such increases in abundance so as to completely control the forage fish population, and presumably predator-prey cycles could result.

There is a tendency on the part of fishery biologists to forget that the application of new technology to industrial fisheries has developed at the same rate or even faster than technological innovation in other industries. Fishing power of fleets and their range of action and versatility have increased dramatically, and this is nowhere more evident than for small pelagic fishes. The conversion from sail to engine power and associated hydraulic systems began before the first World War, so that the use of large otter trawls and seines occurred fairly early on. Since the Second World War however [3] fisheries applications stemming from the invention of synthetic fibres in the 1950s made possible development of industrial fleets purse seining with the power block, and the use of large mid-water trawls for pelagics in the 1960s and 1970s. Gill and trammel netting, key low-energy fishing methods are now widespread, especially in developing countries, and modern long lining techniques also depend on synthetic fibres.

The increase in landings of small pelagic fish shown in the FAO record in the 1960s seems to reflect these technological changes, though there is no doubt that predator depletion and environmental change have played a part. In fact we may question what effect such intensive fisheries for forage fish are having on the possibility of recovery of stocks of predatory fish. For some top predators such as cod, but also marine mammals, part of the allowable quota is now routinely set aside for them in some areas of the North Pacific and North Atlantic. As noted, unrestricted harvests of capelin or other forage fish such as sand eels, may limit the potential recovery of populations of apical predators, whose needs should be taken into account in setting quotas.

The staggered timing of peak landings throughout the world has also reflected the growth and spread of industrial fisheries technology world wide [1,4]. Starting early on in the North Atlantic and Pacific and Southeast Atlantic, peak production levels have been reached later in developing country areas such as the Indian Ocean, distant from developed country markets. The evidence here is that the sequence of exploitation largely reflects differential availability and changing demand for resources. Inshore and shallow shelf resources in some case have been partly protected by traditional rights systems and local marketing, but have been drastically changed by the growth of heavy industrial fishing pressure as in the Gulf of Thailand [100]. Later developments such as large-scale fisheries for small pelagics, tunas and deeper water species such as orange roughy and mesopelagic fish, reflect as much as anything, developing markets and technologies, whose ecological implications are relatively unknown at this point in time.

The slower application of technology to control and surveillance [101], and delays in arriving at agreements for setting harvest targets for shared, straddling and highly migratory species, are mainly responsible for peak productivity being exceeded in many areas. Few attempts have been made to date to reverse excessive fishing pressure, and in light of the growing demand for fish globally, optimism on this possibility seems hard to sustain.

Technological improvements in fleet design and harvesting techniques have been also responsible for the late initiation of tuna fisheries in some developing tropical countries, and for the recent development of deep water fisheries whose landings are now beginning to show up in the FAO database.

One overriding perspective that emerges from this broad-brush review is that now most fisheries are at or beyond the level of exploitation that optimizes the multispecies yield from an area, ecosystem management is required in the context of environmental change. This fact is likely to play a major role in determining the economic performance of a regional fishery. Although new technologies will have to be applied more carefully than in the past to 'tune' productivity from local food webs, we may expect that further progress will depend on better application of technology to control and surveillance. This will only be possible if conceptual breakthroughs in efficient dispute resolution allow agreed sharing of resources to be realised.

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