# Observed Patterns in Multispecies Fisheries 

J.A. Gulland and S. Garcia<br>Dept. of Fisheries, FAO<br>Rome, Italy


#### Abstract

Virtually all fisheries exploit more than one species of fish, but the range of species exploited and the ability and willingness of fishermen to switch attention from one species to another vary. The fisheries off northwest Africa are reviewed as an example of a multispecies, multifishery system. Examples are given of systems in other regions. The impact of having to deal with a multispecies, rather than a single-species situation, on the different stages of fishery management is discussed.


## INTRODUCTION

The basic biological or economic theories actually used to advise fishery managers deal mostly with the simple case of a single fishery exploiting a single monospecific and stable stock of fish. In practice, the same stock of fish may fluctuate and be harvested intentionally or accidentally by a wide range of vessels, from canoes to factory vessels, and a given vessel usually catches during the year, or during a single fishing operation, a number of different species. The biological interactions between species (competition, predator-prey), including the stability of the community structure and the operational interactions between different groups of vessels targeting a particular species, need to be assessed and taken into account, as do the effects on shore, e.g., the interactions between the markets for different species.

The question of interaction and stability in multispecies fisheries has therefore become recognized as a matter deserving of increased practical

010019658
and theoretical attention, and a number of studies have addressed this problem (14, 30, 40, 41), but these have done little more than open the door on a complex maze of interrelated problems. An important initial difficulty is that there are many types of multispecies fishery, and of multispecies problems, and many different scales at which they can be examined. Simple cases, such as the krill-whale system with one fishery on a predator and another on its prey, are in the minority in the sea. It is probably premature to attempt a definitive taxonomy of multispecies systems, but this paper will attempt to identify some of the main types.
"Patterns and problems characteristic of multispecies fisheries will be shown in some detail through the example of West Africa where most of the classical events and some exceptional ones have occurred. This will be followed by a selected review of examples of different types of problems in various parts of the world. The final section deals with the types of question that need to be answered; for convenience this has been arranged following the stages of management identified by the ACMRR Working Party on the Scientific Basis of Determining Management Measures (15).

## CHARACTERISTIC MULTISPECIES PATTERNS: THE EXAMPLE OF WEST AFRICA

The fisheries off West Africa can be considered as a good example of tropical multispecies fisheries. They have all the necessary classical characteristics of these types of resources, and above all, they have undergone in the last ten years a series of dramatic (apparent and actual) changes in species composition and distribution that can be used to illustrate some of the patterns encountered in the exploited multispecies fisheries. The environments range from equatorial lagoons with high rainfall to tropical upwelling systems. The fisheries range from subsistence artisanal ones with canoes to highly industrialized ones with modern long-range factory ships.

## The Resource Is Multispecific

Catches are everywhere characterized by very high numbers of species, the highest diversity being observed in the biogeographical transition zone between the warm temperate and the strictly equatorial areas between Cape Verga and Cape Bojador.

In the Senegal-Mauritania shelf demersal resource as many as 174 species can be identified (10), and any single trawl haul can contain $20-50$ species in the coastal area of Cape Timiris. The pelagic resources comprise
less species, and most of the pelagic biomass over the shelf of Mauritania is made up of eight species of carangids, clupeids, squids, and cuttlefish.

The official statistics tend to group catches into commercial categories consisting often of several species, but still 48 species are identified in the general statistics of Senegal $(24,34)$. These species can fortunately be grouped in a limited number of species assemblages ( 10,37 ) on the basis of co-occurrence on biotypes characterized by depth and bottom type. It is interesting to note that according to Longhurst, similar assemblages containing similar species can be found in many other intertropical areas of the world.

The high species diversity is associated with an important space/time heterogeneity in the resource (Fig. 1), according to bottom type, depth, or position of the thermocline. The species composition tends to vary in a given place seasonally in relation to bathymetric movements of


FIG. 1 - Differences in annual species composition of catches of bottom set gill nets in two different villages of Senegal (52).
fish with changes in river discharge (monsoon migrations) or upwelling strength. Important seasonal feeding and spawning migrations occur around the tropics (between 10 and $22^{\circ}$ north, for instance), changing also drastically the composition of the resource available to the artisanal fishery, off Senegal, for instance (Fig. 2) (7, 26).

The combination of all these sources of heterogeneity affects the fisheries and leads to high variability in the catches which are often increased by changes in fishing strategy.

## The Catch Composition Depends on the Fishing Strategy

Species composition of catches differs greatly according to the targets sought. It may vary greatly between two fleets exploiting the same area (Table 1). It may also vary with time for the same fishery. The trawl fishery of Senegal is a good example of this as seen in Fig. 3 which


FIG. 2 - Seasonal changes in species composition of landings (A) and annual species composition (B) in the handline/canoe fishery of Kayar, Senegal (52).

TABLE 1 - Comparison of species composition of landings of two longrange trawl fleets on the Guinea Bissau shelf.

| Species | Japanese fleet | Russian fleet |
| :--- | :---: | :---: |
| Sciaenids | $3 \%$ | $61 \%$ |
| Sparids | $50 \%$ | $16 \%$ |
| Carangids and clupeids | $22 \%$ | $9 \%$ |
| Lutjanids | $8 \%$ | $0.02 \%$ |
| Balistes | $0.3 \%$ | $0 \%$ |



FIG. 3 - Changes in percentage species composition of landings in the Senegalese trawl fishery. The arrows indicate the appearance of new targets in the fishery (27).
depicts the drastic modifications in species composition of landings resulting from changes in the export market opportunities and discovery of new resources. It illustrates nicely a process which probably always occurs as a fishery develops and progressively "colonizes" the whole spectrum of available resources. If not properly documented, these changes in landings can be confused with actual changes in abundance.

## Discards Are a Characteristic Feature

They are a direct consequence of species diversity contained with unequal market value. They are widespread in all tropical areas and are particularly important off northwest Africa. In Senegal, for instance, Monnoyer (43) reported that discards in the trawl fishery ranged between $65 \%$ (for the fishery targeted on red mullet) to $75 \%$ (on shrimps) with the discards when fishing on sparids and cephalopods varying from $60-70 \%$.

The total quantity discarded is roughly estimated as $90,000 \mathrm{t}$, compared with landings of $40,000 \mathrm{t}$. Even in the "poor" Mediterranean area, it is noted that 44 to $72 \%$ of the catch is discarded (1).

Discarding practices generally change with time and, if not properly documented, may be confused with trends in abundance. An example is given in Fig. 4.


FIG. 4 - Changes in CPUE (catch per hour of a $400 \mathrm{~h} . \mathrm{p}$. trawler) of characteristic species landed by Ivory Coast trawlers off Sierra Leone (Sherbro division) and Senegal (Cape Verde Coastal division) related to change in discarding practices (6).

## The Species Composition of the Resource Changes

One basic question about multispecies resources is the stability of their composition. While undocumented changes in fishing strategy or discarding practices may be confused with real changes in species composition or abundance, the West African resources offer a few striking examples of real and large-scale changes.

## The Collapse of Sardinella aurita

The pelagic community of the Ivory Coast, Ghana, and Togo dominated by sardinellas, horsemackerels, and mackerels has suffered from a collapse of its major component, the Sardinella aurita, in 1973 after a $3-4$-fold relative increase in catch in 1972 and recovered, apparently, 3-6 years later (Fig. 5B). The phenomenon has been analyzed many times (4, 20, 25). It seems true, from the results presented by Binet and despite the limited number of data points, that before the collapse the catch used to vary with upwelling strength and river outflow (Fig. 5A, Curve A), these two environmental variables being themselves (loosely) inversely related. When river outflow decreased sharply during the 1970s and upwelling strength increased, it seemed that plankton abundance (and food availability) decreased (4) and that stock availability inshore increased, thus potentially affecting larval survival while increasing fishing mortality.

The high 1972 catches due to drastic increase of catchability of sardines to artisanal purse seining, because of exceptionally low river flow, led to collapse, probably aggravated by low larval survival due to poor feeding conditions and low fecundity of the collapsed stock which consisted almost entirely of the $0+$ age group. Since the collapse, some faint relationship between catches and environment may exist, but at a much lower level of catches (Fig. 5A, Curve B). The separation of the two sets of data in Fig. 5 is probably a bit artificial, and it is more likely that there exists a continuum in the data set from Curves B to A related to the changes of underlying biomass under the effect of both recruitment and fishing mortality changes during the recovery phase.

It must finally be noted that in this case biomass is affected by environmental changes through changes in recruitment as well as in fishing mortality (despite a relatively constant effort) rendering impossible the separation of the two effects with the data available. A schematic interpretation of Fig. 5A is given in Fig. 5C. This figure may imply that the environment was the only driving factor. However, as catchability is modified by the environment quite drastically in this particular case, the data could
just as well be interpreted with the classical production model theory as in Fig. 5D following MacCall (38).


FIG. 5 - The collapse of the Sardinella aurita stock off Ivory Coast/Ghana/ Togo.
5A - Relationship between environmental variables and catches before and after the major 1972 overfishing. Curves are drawn by eye. Modified from (4). Black circles $=$ normal, pre-collapse situation; open circles $=$ post-collapse; open squares $=$ recovery.
5B-Catch time series.
5C - "Environmental" interpretation of the phenomenon shown in Fig. 5 A and 5 B , showing time series of catches under moderate fishing (full line), and overfishing (broken line).
5D - The combination of environmentally driven changes of biological productivity and catchability under constant fishing effort: an example of environmentally induced overfishing.

TABLE 2 - Changes in catch composition of the Soviet pelagic trawl fishery off Guinea Bissau (22).

| Species | 1978-79 (\%) | 1982 (\%) |
| :--- | :---: | :---: |
| Sardinella | 55 | 0.05 |
| Trachurus | 38 | 29 |
| Decapterus | 7 | - |
| Caranx | 0.6 | - |
| Mackerel | 0.2 | - |
| Balistes | 0 | 64 |
| Others | 31 | 20 |

## The "Invasion" of Balistes carolinensis

This species was present in the hard bottom shelf/sparid fish community in insignificant quantities during the 1960 s in the Gulf of Guinea (rarely more than $10 \mathrm{~kg} / \mathrm{h}$ ) while 20 t /hour could be caught by trawling in GuineaBissagos at the beginning of the 1980s (Table 2). According to Caverivière (6), the biomass increased from 1971-72* off the Ivory Coast-Ghana and from 1974-75 off Guinea/Guinea-Bissau, leading to two very important stocks now existing (Fig. 6) whose biomass is estimated to be around $5 \times 10^{5} \mathrm{t}$ in the Ivory Coast-Ghana and $0.4-1.3 \times 10^{5} \mathrm{t}$ off the Guineas, and represents in some sectors $80 \%$ of the pelagic biomass (53). From 1978 the "Guinean" stock of Balistes started to invade seasonally in summer the Senegalese waters north of Cape Verde and up to southern Mauritania.

The possible reasons for this most spectacular phenomenon are not known. It occurred in Ivory Coast-Ghana before the overfishing of Sardinella aurita and was apparently associated with a decrease in biomass of the traditional species caught by the Ivorian trawl fishery (6). The data show in fact that the data points for catch and effort in this fishery for 1966-80 are well below the production model fitted to the data of 1959-65. We have calculated the yearly anomalies as percent of the expected CPUE and plotted the time series together with river overflow, salinity anomaly, and plankton abundance (Fig. 7). There is evidence in the figure that the trends are comparable, and that the decrease in temperature, river output, food availability, and the increase in upwelling and salinity may have reduced the carrying capacity of the area for the

[^0]

FIG. 6 - Distribution of triggerfish, Balistes carolinensis, from Dakar to Lome in June 1981 (53). Data about expansion periods have been added.
_ Cpue anomaly in percent(Balistes excl.)

- Plankton abundance
_ River output


FIG. 7 - Trends in CPUE anomalies in the trawl fishery, river output, plankton abundance, salinity anomalies, and fishery events in the Ivory Coast in relation to the changes in species composition of the resource (Sardinella collapse, Balistes eruption). Environmental data from (4); fishery data original, extracted from (6).
warm water, low salinity sciaenid superthermoclinal community traditionally exploited by the trawl fishery while increasing it for the cool water, high salinity infrathermoclinal sparid community to which the Balistes belongs (37). It can be noted that Fig. 7 seems to show some return to "normal" conditions for the environment and the trawl fishery productivity, while Balistes is still abundant as far as it is known. This may indicate either a lack of relationship or some hysteresis or nonreversibility in the phenomenons involved.

Finally, it is interesting to note that an increase in abundance of the flying gurnard (Cephalacantus volitans) belonging to the same sparid community has apparently occurred at the same time as for Balistes. This is indicated for the Ghanaian area (48) and is seen also to be the case in Guinea Bissau.

## The "Replacement" of Sparids by Cephalopods

Between Cape Blanc and Cape Garnett off the coast of the Sahara lies one of the most famous fishing grounds for demersal fish of northwest Africa. The fish communities have been studied since the 1940 s and a good review exists (39). The fishery fauna has been traditionally largely dominated by gray (in the littoral area) and red (on the shelf) sparids of the genera Pagellus, Pagrus, Dentex, Diplodus, Sparus, etc. However, cephalopods and especially cuttlefish (Sepia) and squids have always been a permanent feature of these species assemblages in this region. Octopus, however, was rarely mentioned in most earlier works (28) and is mentioned as a significant element only in 1962 ((39), p. 63). In various scientific expeditions the relative abundance of cephalopods among the rest of the commercial resources raised from about nothing in 196162 to about $30 \%$ in 1968 and $90 \%$ in 1971 (46). According to GarciaCabrera (28), however, the proportion was already $80 \%$ in 1967 ( 17 t of fish for 66 t of cephalopods). Even if the scientific evidence is still weak, the Canarian fishermen who exploited the area for centuries definitely consider the buildup of the cephalopod stock in the early 1960 s as a fact. The available recent information on the subject has been summarized in Fig. 8A to 8D.

Figure 8A illustrates the relative changes in catches of sparids and cephalopods since 1964-65 and shows the dates when the stocks have been declared overfished. Figure 8 B shows trends in recruitment indexes of octopus and catch rates of big and medium-sized cuttlefish. This figure indicates the drastic increase of recruitments in 1965-66 for both species. Figure 8C shows the decrease of abundance of big and medium-


FIG. 8 - Some indexes for monitoring the evolution of the sparid/cephalopod community in the Sahara (Coastal) division.

8A - Evolution of catches of sparids (A) and cephalopods (B). Data source (A) $(9,21)$, and (B) $(16,17)$.

8B - Recruitment indexes for octopus (A) in Cape Blanc (21) and abundance of big size (....) and medium size ( - ) cuttlefish as measured by CPUE (B) (32).

8C - Development of fishing effort on octopus as an indicator of the whole cephalopod fishery (19) and abundance of big and medium-sized Pagellus (33).
8D - Variations in abundance of sparids ( $A_{1}, A_{2}$ ) and octopus (B). $A_{1}$ modified from FAO (12), $A_{2}$ from FAO (13): see text $B$ from (2). C proportion of cephalopods in commercial catches during trawl surveys (46).
sized sparids and the simultaneous increase in fishing effort for octopus (it is believed that the effort increased as well on all cephalopods). As all these figures start from 1965 while the fishery for sparids started after the Second World War at much higher levels of abundance, we have grouped on the same Fig. 8D changes in sparid abundance in northwest Africa in 1955-66 (a period when catch statistics were only grossly geographically allocated) with changes of abundance in the Sahara (littoral) statistical division (1965-73). Both series have been expressed relative to the average CPUE for 1965 and 1966. This figure is only intended to show that sparids have been apparently driven to close to extinction level and that cephalopods increased when sparid abundance was about $30 \%$ of their 1955 level.

The figure also shows that, in fact, both sparid and cepholopod stocks have been driven down drastically by fishing. An important fact, not shown in the figures, is that the proportion of small-sized sparids increased drastically in the 1970 s, possibly as the fishery moved further inshore searching for spawning concentrations of octopus. According to GarciaCabrera (28), huge amounts were reduced into fish meal and later on were discarded when the fishery specialized on cephalopods. These data show that $94 \%$ of the fish catch was discarded in 1967 and this observation is largely valid today.

It seems, therefore, clear that the Saharan sparid community has been drastically affected by fishing which reduced the biomass and average individual size of sparids inducing a transfer of effort to cephalopods at the same time as their biomass, especially for octopus, increased. Later, heavy fishing reduced also the biomass and average size of cephalopods. Garcia-Cabrera (28) indicates that the thinning down of sparids suppressed an important source of larval mortality of octopus in the short pelagic phase and that in addition the huge quantities of fish discarded were a good source of food supply for cephalopods. It should probably also be noted that a long-term upward trend in upwelling has been identified in the region between 1967 and 1980 (3) and that we do not know how the continuous cooling down of the region has affected also the larval survival of the sparid community by Pagellus bellotti and other sparids of "Guinean" affinity whose concentrations off the Sahara are at the extreme northern limit of the distribution of these species in West Africa. Some possible mechanisms for such replacements are discussed by Caddy (5).

## The Sardine Expansion

Off West Africa, between $20-36^{\circ} \mathrm{N}$, there are three important fishing areas for Sardina pilchardus: in the North $\left(36-33^{\circ} \mathrm{N}\right)$, the Center ( $32^{\circ} 30$ to $27^{\circ} \mathrm{N}$ ), and the South ( $26^{\circ}$ to $21^{\circ} \mathrm{N}$ ). It is assumed that they correspond to separate stocks, but some seasonal partial mixing might well occur. The biomass in the central and southern concentrations has widely fluctuated in the last twenty years (3), drastically modifying the catch composition (Table 3).

In the central area, long-term changes in availability to Moroccan traditional fleets and in recruitment have been related either to extreme droughts and/or fluctuation in upwelling strength (Fig. 9). In the southern area the spectacular expansion of Sardina pilchardus catches from $37 \times 10^{3}$ to $1 \times 10^{6} \mathrm{t}$ in seven years was related to the strengthening of the upwelling in the early 1970 s (11, 31). In this area the sardine has been progressively disappearing again since 1973 (35), and it can be seen in Fig. 10 that this seems to correspond with the decrease of the upwelling. These changes have, of course, affected the whole pelagic fish community, and Fig. 10 gives a representation of changes occurring in the catch composition and showing the apparent "replacement" of the tropical species Scomber and Sardinella by the warm temperate Sardina, while the effect on horsemackerel is less clear. The "replacement" of Sardina by Scomber in the central area has also been described and is related to changes in coastal water masses (3).

TABLE 3 - Changes in species composition of Polish fishery in the northern sector of CECAF (22). (The same changes can be observed in Bulgarian catches.)

| Species | $1968-72(\%)$ | $1975-77(\%)$ |
| :--- | :---: | :---: |
| Sardine | 2 | 87 |
| Horsemackerel | 30 | 5 |
| Mackerel | 20 | 5 |
| Hairtails | 5 | 0 |
| Bluefish | 7 | 0 |
| Sparids | 4 | 0 |
| Sardinella | 6 | 3 |



FIG. 9 - Relationship between annual catches and upwelling in the central area (3).


FIG. 10 - A) Variations in upwelling strength in the central area (3). B) Variations in upwelling strength in the southern area (50). C) Changes in species composition of catches (data sources (13, 17)).

Regarding the fishery it is, however, interesting to note a coincidence during the period 1967-68 between the increase of Sardina stock and the shift of important Eastern European fleets from bottom trawling with high opening trawl to pelagic trawling (22). It is also interesting to note that the mackerel stock was found to be apparently exploited beyond $f_{\text {MSY }}$ since $1970-71$ (18), while the horsemackerel appeared to be close to full exploitation at the same time. The expansion of sardine could therefore have been mistaken for a consequence of heavy or overfishing, while the picture given above demonstrates clearly enough the effect of environment and leads to the conclusion that, owing to the difficulty of measuring effort on pelagic fisheries, the stock assessment of mackerel and horsemackerel and particularly their apparent "fishing: down" in the 1970 s ought to be reassessed in view of the long-term changes in biomass of sardine and availability of mackerels. (This possibility was in fact mentioned in the papers quoted above.)

## The Various Fisheries Interact (Competition, By-catch)

As the number of species increase, so do the number of potential interactions between neighboring fisheries. These interactions complicate the assessment as well as management by rendering difficult the monitoring and regulation of fishing mortality. In Senegal, for instance, strong interactions exist within specialized sectors of the trawl fishery as well as between different fisheries. Figure 11 shows the distribution of the relative weight (in percent) of the species sought in a great number of well identified trips aimed at a particular target*. The wide range of percentages observed precludes any accurate a posteriori definition of the target from an examination of catch composition, and Captain's interviews are necessary. Experience also shows that as diversification of targets increases and markets are open, the specialization of the boats decreased. Table 4 shows the degree to which most species occurring off Senegal are caught in a number of fisheries and illustrates the difficulty of regulating effort or size at first capture for a given species and afortiori for a combination of species with different population parameters under these conditions. It is in order to ease this last difficulty and to facilitate enforcement as well that the CECAF Committee recommended the adoption of a compromise and unique mesh size of 60 mm for all demersal fisheries on the shelf, from Gibraltar to the Congo River. These sorts of compromises are, however, difficult to work out when the species

[^1]TABLE 4 - Interactions between various fishing gears in the Senegalese fisheries ( $\mathrm{x}=\mathrm{present}$; $\mathrm{xx}=\mathrm{important}$; $\mathrm{xxx}=\mathrm{very}$ inportant).

| SPECIES | Purseseine | Ring net | Artisanal fishing |  |  | $\mathrm{A} R \mathrm{~S}$ | hadustrial fishing |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | Handline (trad. \& modern) | Shrimp fishery | Urift net | Bottom set net | Beach seine | Tuna Purseseine | Coastal <br> Purseseine | 'Traw |
| PELAGIC SPECIES |  |  |  |  |  |  |  |  |  |  |
| Thumus albacares |  |  |  |  |  |  |  | Xxx |  |  |
| Thunnus obesus big tunas |  |  |  |  |  |  |  | Xxx |  |  |
| Katsuwonus pelamys |  |  |  |  |  |  |  | XXX |  |  |
| Euthynnus alletteratus | X |  |  |  |  |  | X |  |  |  |
| Sphyraena spp. | x |  |  |  |  |  | X |  | X | X |
| Caranx spp. | xxx |  | X |  | X |  | Xxx |  | XxX | X |
| Trachurus spp. |  |  | xxx |  |  |  |  |  | XXX | xNX |
| Surdinella maderensis | $x$ | xxx |  |  | xxx |  | xxx | buit | XxX | K |
| Sardinella aurita | Xxx | XXX |  |  | x |  | xxx | bait | x | X |
| Ethmalosa fimbriata | XXX | XXX |  |  | x |  |  |  | x |  |
| Brachydeuterus auritus | $x$ |  | x |  | x |  | $x \mathrm{x}$ |  |  | XX |
| Pomadasys spp. | x |  |  |  |  |  | XxX |  | xXx | xxx |
| Loligo |  |  | XXX |  |  |  |  |  |  | x |
| BOTTOM SPECIES |  |  |  |  |  |  |  |  |  |  |
| Pagellus bellottii |  |  | XXX |  |  |  | x |  |  | XXX |
| Pseudupeneus prayensis |  |  |  |  |  |  |  |  |  | XXX |
| Sepia officinalis |  |  | xxx jig |  |  |  | $x$ |  |  | XXK |
| Epinephelus aeneus |  |  | XXX |  |  |  |  |  |  | xxx |
| Palinurus spp. |  |  |  |  |  | XxX |  |  |  | x |
| Fseudotolithus spp. |  |  |  |  |  | X | X |  |  | xxx |
| Arius spp. | $x$ | XXX | x |  |  | XXX |  |  |  | xrx |
| Cymbium spp., Murex spp. |  |  |  |  |  | xxx | XxX |  |  | x |
| Penaeus notialis |  |  |  | x |  |  |  |  |  | xxx |

Data Sources: (24, 34). Only a limited and typical sample of the 64 species or gróups of species identified in Senegalese statistics.


FIG. 11 - Distribution of the relative weight (in percent) represented by the species sought in landings from individual trips with a priori clearly identified targets. Trawl fishery of Senegal.
caught together differ drastically in value as well as in biological characteristics (e.g., hake and deep sea shrimps).

The by-catch mortality is an important problem in multispecies fisheries. The sparid stock off the Sahara is probably held down by at least growth overfishing, despite the nonexistence of an aimed fishery for sparids. The effect of the horsemackerel pelagic fisheries on the stocks of hakes are certainly important due to the high mortality they can generate on juvenile hakes. The direct effect of increased "by-catches" is a change in total mortality as well as in age-specific fishing mortality vectors with the result that the use of production models for management by quotas becomes at least questionable.

## TYPES OF MULTISPECIES FISHERIES

## The Exploitation of a Simple Predator-prey System

Apart from relatively minor fisheries (maximum 400,000 tons in any one season) for finfish (notothenids) and icefish (Champsocephalus) in restricted areas (mostly round South Georgia and Kerguelen), the Southern Ocean presents the best, and possibly the only, example of the simple system of the exploitation of either the prey (krill) or of one or more competing prey species (whales, seals, etc.) (40). Although much the
same countries are concerned in harvesting whales and krill, the vessels used are distinct, and the problems are those of biological interaction. Important questions are whether, and to what extent, the recovery of whale stocks could be affected by an increased krill harvest or whether the depletion of the stocks of larger whales has caused an irreversible change in balance between these whales and their competitors (seals, penguins, and possibly minke whales) $(36,42)$.

## The Exploitation of Unstable Resources

The upwelling system from central Chile to northern Peru is enormously productive. This production supports correspondingly enormous fisheries, and at its peak around 1970 the Peruvian anchoveta fishery was by far the largest single-species fishery in the world. Since then it has collapsed, and 1984 catches are likely to be near to zero, but there has been an almost equally dramatic rise in the catches of sardine (Table 5). While other species, e.g., hake, contribute to the fisheries in Chile and Peru, especially for the inshore fleet, the main commercial fisheries in both countries are dominated by small shoaling pelagic species (anchoveta, sardine, and horsemackerel). Though the catches by the local fisheries are nearly all taken by purse seiners and turned into fish meal, the fisheries are not wholly indifferent to the species composition. The larger and more active sardines and horsemackerel cannot easily be caught with the same gear used for anchovy, while horsemackerel is usually found in deeper waters, out of reach of purse seiners. These species also can be used for direct human consumption (canning or freezing) and have a potentially higher unit value.

While there has been a definite switch in target species, independent observations (e.g., surveys of fish eggs and larvae) show that there has been a real increase in sardine abundance. This has occurred at about the same time as the collapse of the anchoveta, which is presumed to have been due to a combination of heavy fishing and unusual environmental effects (especially the El Niños in 1972, 1976, and 1982/3). The big biological question is the extent to which the sardine increase was caused by the anchoveta collapse. This then raises the operational questions of whether the abundance of anchovy can be adjusted by controls on the fishing for sardine, and vice versa, and if so, what would be the optimum balance of sardine and anchovy.

Similar situations associated with heavy fishing and environmental changes arise in the other major upwelling areas of the world - off northwest and southwest Africa, off California (where it has been shown that there

TABLE 5 - Catches of major species in the Southeast Pacific ( $10^{5}$ tons).

| Species | 1955 | 1960 | 1965 | 1970 | 1971 | 1972 | 1973 | 1974 | 1975 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Anchoveta | 1 | 35 | 77 | 131 | 112 | 48 | 20 | 40 | 33 |
| Sardine | + | + | 1 | 1 | 2 | 1 | 2 | 5 | 3 |
| Jack Mackerel | + | + | $+$ | 1 | 2 | 1 | 2 | 3 | 3 |
| Other Species | 3 | 4 | 4 | 5 | 4 | 5 | 6 | 5 | 4 |
| Total | 4 | 39 | 82 | 137 | 120 | 56 | 30 | 53 | 44 |
|  | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 | 1983 |  |
| Anchoveta | 43 | 8 | 14 | 14 | 8 | 16 | 18 | $\begin{gathered} 3(a) \\ 35(a) \end{gathered}$ |  |
| Sardine | 5 | 15 | 20 | 33 | 33 | 28 | 33 |  |  |
| Jack Mackerel | 4 | 8 | 10 | 13 | 12 | 17 | 22 |  |  |
| Other Species | 4 | 6 | 7 | 11 | 8 | 9 | 8 |  |  |
| Total | 58 | 39 | 56 | 69 | 62 | 69 | 78 |  |  |

Notes: + quantity less than 0.5 ; (a) preliminary estimates.
have been long-term changes in the balance between sardine and anchovy quite independent of fishing (51)), as well as in the fisheries for small pelagic fish around Japan (30, 44, 54). It is interesting to note that similar changes (from sardine to anchovy) have been observed in the last few years all over the western Mediterranean either in the presence of heavy fishing (Spain) or not (Algeria, Morocco).

## Progressively Diversifying Fisheries

Changes in species in the catches do not always reflect equivalent changes in the sea. Until the early 1960s, harvesting of the rich resources of the Bering Sea was confined to a few high-valued species (fur seal, salmon, and halibut) and the total weight caught, and the impact on the ecosystem as a whole was small. After 1960, large-scale trawling was carried out, mainly by Japan, targeting in succession on flounders, Pacific Ocean perch, and Alaska pollock. While all these species are caught by trawl, the way the gear is rigged and the areas fished are different, so that the rise in catches of the second and third species is in fact no evidence that these species increased. Indeed, the first "multispecies" question is whether there is any "multispecies" problem at all, other than determining the true effort on one or other species. It is possible that, given proper "effort" data, the dynamics of each species could be described by a simple single-species model, with the decline of the flounder and Pacific Ocean perch catches being due more to the fishing out of accumulated stocks of very long-lived fish, i.e., the so-called "pulse-fishing"
than to any real decline in the productivity of the populations.
Similar situations, where the main problem is knowing the species on which the fishery is targeted at a particular stage of its evolution, have occurred on a number of occasions as industrial fishing has spread into new areas, e.g., the changes between sparids and cephalopods off northwest Africa, between plaice, haddock, and cod in the English trawl fishery off Iceland and northern Russia in the first half of this century, and even the changes from blue whale to fin, sei, and minke whales in the Antarctic. In some cases it is clear that the rise in catches of an alternative species is due purely to a switch in attention (e.g., Senegal), in relation to changes in gear technology (wide opening trawl) or market opportunities. In the Antarctic the minke whales are the only species of whales suspected of increasing because of the depletion of the larger species. In other cases, there may have been a real increase of the new target biomass, e.g., in the northwest African cephalopods, Balistes, and sardines.

## Multi-Single-Target Fisheries

The North Sea contains 50 or more species of fish and invertebrates of commercial interest, of which about a dozen can support major fisheries. While some vessels, especially trawlers, may catch several species in a single haul, and there is some switching of attention by individual vessels at different seasons of the year, the simplified picture of the North Sea fisheries as consisting of a set of individual fleets, each targeting all year round on one species, or a narrow group of related species, is fairly realistic. Thus it is possible to distinguish the Danish trawl fishery for small fish (sandeels, Norway pout, and, in the past at least, small herring) for reduction to meal and the Dutch beamtrawl fishery for sole and other species; the Scottish seine-net fishery for haddock, whiting, and cod; various national fisheries for herring for human consumption, and so on. On a different scale, the first diversification period of the Senegalese trawl fishery was undertaken as a multi-single-target fishery as the various types of the heterogeneous fleet tended to target consistently to particular groups of targets: traditional Mediterranean type of wooden trawlers on red mullet and Japanese type of steel stern trawlers on sparids and cephalopods. This specialization, however, may disappear with time.

For most of the major species it is possible to find one, and often several, fisheries (i.e., a fleet, or identifiable group of vessels of roughly similar type coming from a particular country or fishing port) whose activities have remained consistently targeted on that species. The catch and effort statistics of this fleet or fleets therefore provide a reasonable
measure of the abundance of the species, and thus within the limitations of the models, each major species can be analyzed with the standard single-species techniques. This has been to a large extent the standard practice in ICES, particularly in respect to its numerous stock assessment working parties.

Multi-single-target fisheries might be considered as a necessary intermediate stage of evolution of fisheries in their development process from the stage of artisanal, highly diversified fishing strategy of the littoral zone to the full exploitation of the high seas. It can be foreseen that for global economic reasons each element of the fishery will not stay targeted on one species but, at least in the long term, will switch targets in response to trends in relative abundance, changes in market preference, and in response to management measures. As the new opportunities open, as markets become used to the different varieties of targets coming from the open sea, as the fish processing techniques evolve, and as effort limitations are imposed on traditional species, the boats will develop flexibility, the multipurpose boat being one way to reduce the cost of uncertainty raised by heavy fishing and subsequent stock fluctuations. The fishery might then evolve into what we may call a single-multitarget fishery.

## Single-Multi-Target Fisheries

This is the case when a wide range of targets is exploited by a limited number of types of multipurpose boats shifting seasonally or from one trip to another, or from one group of targets to another in order to stabilize the revenues despite variations in the resource.

We described it above as the likely ultimate stage of development of fisheries, and paradoxically it can also be the departure stage of a fishery because artisanal fishing falls very often in this category.

A lot of medium-range demersal fisheries on the shelf fall in this category. The present state of the Senegalese trawl fishery is close to it as well as most of the traditional trawling on the Mediterranean shelf and especially in the Adriatic Sea. There a limited number of multipurpose boat types using a range of selective (dredge) to nonselective (Italian trawl) gears exploit at one time or another most of the available species for a market able to accept with minor adjustments whatever species mix is offered (very often mixtures of species and sizes are sold in batch, unsorted). There the scientists and the fishermen tend to consider the high space-time variability of the resource (few fish are older than one
year) as noise. While no drastic change in species composition has apparently been observed, the overall fishery has a stable production, and the essential concern seems to be in terms of total value of the catch, species interactions being of relatively minor immediate practical interest. However, as trawlers are directing purposely more and more effort to pelagic species by using high opening trawls (in the Gulf of Lions, for instance), conflicts between the pelagic and demersal fisheries can already be perceived.

A similar situation arises in a number of tropical trawl fisheries where it is not clear to what extent the fisherman can alter his fishing practices to change emphasis on one species or another. Since the rapid expansion of the Thai trawl fisheries, whose catches grew from near zero in 1960 to over a million tons a decade later, there have been big decreases in overall biomass ( $45,49,55$ ), as well as changes in species composition. Since these results come from surveys by research vessels, they probably reflect real changes in abundance, but they are fairly closely matched by changes in commercial landings.

The changes in species composition raise interesting scientific questions, since some, e.g., the severe decline of most long-lived species, fit singlespecies theory, but others, e.g., the increase in absolute abundance of squid, must involve some interaction. However, these questions may be irrelevant for immediate practical purposes, since the fisherman is interested in the total value of his catch, irrespective of the species composition. It seems that for purposes of deciding on current management policy, it may be adequate to use the simplest type of production model, relating the total catch (or CPUE) of all species (preferably expressed as value) to the total amount of fishing.

When analyzing and comparing the effect of fishing on stock composition, the rate of increase of effort should be considered. The biological resource may have some capacity to adapt to increased effort without catastrophic changes, provided the increase is slow enough. In the same way, the fishing strategies and the market can be smoothly adjusted to some slow rate of change of the resource base but not to catastrophic ones. Considering the example of the Adriatic fishery, one may wonder whether a single-multi-target fishery operating for a very diversified market, at high effort levels, is not a valid economic strategy and also a possible biological one, if the problem is considered in terms of global energy balance.

## PROBLEMS AND QUESTIONS

## Definition of Objectives

This is no place to repeat the arguments about MSY, MEY, etc. Most practitioners of the art or science of management would probably follow John Pope's objectives of MSW (Minimum Sustainable Whinge, i.e., that policy which, over a period, leads to least complaints reaching the Director of Fisheries). Most of the theoretical arguments, though based on singlespecies analyses, translate to the multispecies situation without difficulty. The new element is the degree to which the balance between species should be an objective in itself. Assuming, for example, the greatest total return from the North Sea (in weight value, net economic return, or whatever) would be taken by a pattern of fishing that virtually eliminated cod, to what extent should this mean that that pattern of fishing is unacceptable? Since there is no group, as yet, dedicated to the conservation and protection of cod, this question would probably resolve itself into a second question of the degree to which those fishermen currently fishing for cod can switch, with or without compensation, to other species. The problem of species balance is particularly alive where marine mammals are concerned, and the best formal attempt to deal with it is in Article 2 of the new Convention for the Conservation of Antarctic Marine Living Resources*, which inter alia states the following principles of conservation:
(a) prevention of decrease in the size of any harvested population to levels below those which ensure its stable recruitment. For this purpose its size should not be allowed to fall below a level close to that which ensures the greatest net annual increment;
(b) maintenance of the ecological relationships between harvested, dependent and related populations of Antarctic marine living resources and the restoration of depleted populations to the levels defined in subparagraph (a) above; and
(c) prevention of changes or minimization of the risk of changes in the marine ecosystem which are not potentially reversible over two or three decades.

This statement of objectives was undoubtedly a good solution to the immediate obstacles to establishing the Commission, but it will be

[^2]interesting to see how well it will turn out to be a usable guide to management procedures in practice.

In the policy field, the test will be whether the definition of objectives is clear enough to determine specific actions when there is a clash of interests between conservation and harvesting interests. In the scientific field the test will be whether the implied models (of some level of population ensuring greatest recruitment, or of some constant and maintainable set of ecological relationship) come any closer to the reality of the dynamic multispecies systems of the Southern Ocean than did the model underlying the MSY objective to the dynamics of a single species.

## Determination of Boundaries

By recognizing a multispecies problem, the manager has implicitly looked beyond the limited boundaries of a single-species situation. The question is how far should the boundaries of his consideration be extended so as to make it more realistic without making it so wide as to be impossible to handle. In the sea, by considering the movements of currents, and of prey and predators (perhaps at several steps removed), it is possible to connect any one species in a particular place to any other species in any other location. How small an area is it reasonable to look at? Is it in fact possible to set definite geographical boundaries except in a few enclosed areas (e.g., the Baltic, the Adriatic), or must subjective, but operationally acceptable boundaries be chosen for each occasion? Is it possible to use other divisions, e.g., is it realistic in a particular region to consider managing pelagic and demersal systems separately? (Probably not, since in several areas - Mediterranean, Gulf of Thailand trawlers are turning to typically pelagic species - sardines, Rastrelliger spp. - as valuable secondary targets.)

Similar questions arise on the shore side. The arguments about MSY, MEY, etc., have highlighted the fact that the manager must look beyond the biological yield to the producers and consumers of fish. To what extent are there important interactions between species on the market so that management policies on, say, sardine off northwest Africa should have to take into account the events in fisheries for other stocks supplying the same markets (fishmeal, or cheap canned fish) in any part of the world, and not just off Africa?

## Data Needs

The data needed for the biological assessment of single-species fisheries are relatively well-defined and do not need further discussion, though
some items, e.g., on discards, may have increased importance in a multispecies context. There is less explicit agreement on what specific data are needed for economic and social analyses, but that some such data are necessary has become generally accepted. For multispecies fisheries it is sometimes supposed that these data are needed for each important species, plus information on the degree of biological and other interactions, e.g., who eats what; how the demands for different species interact.

When many species occur, the volume of the resultant demand for data is frightening and certainly beyond the capacity of a small fishery department in a typical developing country to supply. There is a need to identify certain key data which will allow analysis of advice about multispecies fisheries.

It is also important to collect data as soon as possible. Experience in single-species fisheries has shown that one piece of good information collected when the fishery was just beginning can be worth volumes of data from a well-developed fishery. Unfortunately, we do not have the models to tell us which are the key data, especially the key data for priority attention in a new fishery. Identification of key data, which may require identification, at least in general terms of the main outline of the models to be used, is therefore a matter of some importance.

Since virtually any kind of data is useful to someone, the real question in practice is how limited resources for data collecting can be best deployed. How should they be divided between data used for stock assessment, economic analyses, or other purposes (bearing in mind some data are useful for several purposes)? Considering just the collection of data for stock assessment, should resources be concentrated on the quantities - catch/effort/age/size - that have been proved useful for single-species work, or should there be a greater concentration on more qualitative observations (food, predators, distribution)? Should they be spread across all species (evenly, or in proportion to their commercial importance), or is it better to concentrate on a few key or typical species? Are there types of data that do not occur in single-species studies, e.g., could the intentions of fishermen when they leave port be valuable information in interpreting catch and effort data in terms of relative species abundance?

## Interpretation and Analysis

The two approaches to analyzing multispecies biological systems are a) to look at each species separately and add, within the analysis of each
species, appropriate terms for the interaction with other species (bottomup approach), or b) to look at the whole system in terms of energy flow, total catch, etc., and separating, e.g., the production of secondary carnivores into species only to the extent that is possible and desirable (topdown approach).

The first approach seems to work comparatively well in the Southern Ocean, with very few species and considerable interest in what happens to individual species, especially the great whales. It runs into problems of increasing data demands and large numbers of degrees of freedom in fitting parameters as soon as the numbers of species increase (47). These problems become extremely difficult even in areas such as the North Sea or the Bering Sea where the number of species are relatively few and the data supply good. They offer little practical help in many tropical areas with many species and little data.

The integrated approach has proved useful in some places. The analysis of total catch, and catch per unit effort of all species combined in the Gulf of Thailand or Ivory Coast (23), has been sufficient to show that there are far too many trawlers, and there is little call for more detailed analysis and advice until action has been taken to reduce the fleet size (in fact, in the Ivory Coast the marine resource program is now limited to a small monitoring program). The total production-energy flow approach applied, say, to the whole North Sea or the Peruvian upwelling system has given results that are compatible with, and supportive of, the species-by-species analysis. However, the practical value of total biomass, Gulf of Thailand approach, is limited to those situations where the fishery is homogeneous and is not sensitive to changes in species composition. Energy flow analyses tend to have wide confidence limits, e.g., in the efficiency of transfer between trophic levels. Thus, while they can distinguish between areas where the production is hardly touched, and areas where the fisheries are taking much of what is available (which can be useful), they are less able to distinguish between situations where the resources are fully or overexploited, and those where some moderate expansion, perhaps even a $50 \%$ increase in catch, is possible. It is also difficult to use this approach to determine what action might be appropriate when stocks are known to be heavily fished.

This implies that, accepting that single-species analyses are inadequate, with both current multispecies approaches having only limited usefulness, fishery scientists have problems. This is true, but there is some relief. Single-species analyses are not completely useless. Most present
management decisions are based on them, and if they were abandoned today, the world's fisheries would be in a worse condition. Indeed, with a narrow enough focus, single-species analyses can be perfectly adequate. For example, accepting for the purposes of illustration that in the North Sea the year-class strength of cod is determined to some extent by the abundance of herring and whiting, and that the abundance of food consumption of cod affects the yield of whiting and other small fish, the present advice on cod, based on a single-species model, may still, in principle, give the optimum fishing pattern for cod so far as cod fishermen are concerned, and if controls are set in terms of catch quotas and these are adjusted in the light of information on current year-class strengths, they will result in the correct cod quotas from the point of view of cod fishermen. The same is true for herring and other species, where the policies for herring, etc., are, in principle, the optimum for the fishermen harvesting these species. (We ignore for the present discussion that in practice the policies actually set correspond to fishing mortalities which are in most cases well above any long-term optimum, and that many of the corresponding quotas are poorly enforced.)

Two cautions should be considered: the cod analysis may not necessarily give the correct advice even for the cod fishery, and pursuing the optimum for individual species for fisheries may result in a pattern for the fishing as a whole that is very much suboptimum. The first caution gives rise to a clear scientific question - under what circumstances will a singlespecies analysis give rise to advice that is bad in terms of that species and the fishery on it? To what extent does the answer depend on the nature of the species (large predator, etc.) and the types of action taken (e.g., the optimum fishing mortality on cod may be insensitive to changes in year-class strength and factors that affect year class, while catch quotas are highly sensitive to these factors). This would seem to be a relatively simple question, and it is tempting to suggest that the answer is that with obvious precaution (e.g., the need to adjust year classes), single-species advice is relatively insensitive in species interactions.

The second caution is more important, and looking only at single species can lead to poor management. It seems, for example, that countries that adopt a flexible opportunistic approach to their pelagic fisheries, taking whatever species is present at the time (e.g., Japan, Chile), are more successful than those focussing on particular species (Californiasardine, Peru-anchovy). Gulland (29) suggested, on some assumptions about the nature of the interactions, that the value of the North Sea catch could be significantly increased by taking advantage of those
interactions, e.g., by deliberately overexploiting some species to let their competitors expand. The first example concerns a possible or partial replacement of one species by another (sardine/anchovy, etc.). The second depends on the fact (which is in part an assumption) that the recruitment of valuable species (i.e., the larger demersal species such as plaice and cod) increases when smaller, less valuable species (Norway pout, herring) are relatively depleted. Also relevant is the fact that the demand for herring is inelastic, and once catches increase above a certain point, they must go to fish meal. There is therefore little economic attraction in a complete rebuilding of the herring stocks.

Two basic biological questions arise that deserve further examination. First, how reasonable is it to expect that if one species declines, it will be replaced (wholly or to some specified extent by another)? Intuitively, replacement seems likely, and there is evidence to suggest that it sometimes happens in practice. However, as Daan (8) points out, the evidence for direct and complete replacement is poor. Replacement is not automatic, and, if it is, the timing and degree of replacement are not predictable. Nevertheless, even partial replacement could well influence management policies. A manager faced with a collapsing anchovy stock would be less inclined to impose drastic measures to preserve the anchovy stock if he thought that if it did completely disappear, there would be a fair chance of getting increased sardine catches.

The second question is of the degree to which recruitment of one stock can be influenced by the abundance of another. To what extent, if at all, was the increased recruitment of gadoids in the North Sea since 1960 linked to the declines of mackerel and herring? This is clearly connected with the important but unsolved single-species problem of the degree to which the adult stock of the typical, highly fecund commercial fish can be reduced before there is a significant fall in the average recruitment.

Answers to the questions in the preceding paragraphs should warn the scientist, and those he is advising, as to when a single-species analysis could be seriously misleading. They do not allow him to avoid doing the individual, and possibly numerous, species analyses. An approach to this is to treat the species in groups, e.g., large predators, detritus feeders, etc. Pauly (45) has done this for the Gulf of Thailand and suggests that the trends in abundance within a group are consistent, whereas there are differences between groups which can be large. This implies that, for example, production modeling could be done for n groups rather than
m species ( $\mathrm{n}<\mathrm{m}$ ), and that it might be sufficient to do detailed analyses (looking at growth, mortality rates, etc.) for only-one or two species within a group.

## Formulation of Action

The problems here do not concern so much the multispecies question as the multifishery question, i.e., the degree to which action concerning one fishery may affect, or be affected by, events in another. These effects may arise from biological interactions between species but are equally likely to be due to operational and economic factors. For example, the implementation of a limited entry scheme for one fishery on a particular species group in a region can have an immediate impact on most other fisheries on other species, as surplus effort is displaced from the controlled fishery and, often, as fishermen seek to establish their rights in the other fisheries in case limited entry is applied to those fisheries, too.

The immediate question is to what extent the choice of management technique to control either the sizes of fish (mesh sizes, minimum market sizes, closure of nursery areas, etc.) or of fishing mortality (catch quotas, licence limitation, etc.) in individual fisheries needs to be modified to take account of species interactions between fisheries.

The more fundamental question is whether it would be desirable, in a multifishery region such as the North Sea or Western Sahara shelf, to put less emphasis on detailed fishery-by-fishery or species-by-species controls, and more on some general overall approach. There are at present far too many fishing vessels in the North Sea, and successes in controlling excess effort in, say, the cod or sandeel fisheries are to a large extent only successes in that they shift the problem to the fisheries on herring or haddock. It may be, and this is a question deserving more careful analysis, that reducing the overall size of the fleet would make the management of the individual species much easier, with less time of research scientists, administrators, and enforcement officers tied up in species-by-species detail.

## Implementation and Enforcement

On first sight it might appear that the legal and administrative activities of implementing and enforcing fishery management programs do not concern scientists and need not be discussed in a scientific paper. This is not completely true. No fishery regulation is easy to enforce, but some are much more difficult to enforce than others. A measure that
might appear optimum on biological or economic grounds may prove impossible to enforce, or enforcement may involve the deployment of so many costly patrol ships or aircraft that the net benefits obtained may be much less than those from a theoretically suboptimum, but more easily enforceable, measure. Since the choice of measure has implications on the work done at each of the preceding stages (models and methods of analysis, data collection), the fishery scientist must take some account of enforcement problems. This is particularly true of multispecies fisheries. Differences in the sizes of the various species caught in a trawl fishery may make some techniques, e.g., mesh regulation, impracticable, while others, which may be inappropriate in respect to a single species, e.g., limits on the total number of fishing vessels, may become attractive when all species become heavily fished.

## REFERENCES

(1) Arena, P. 1978. Indagine qualitativa et quantitativa sui materiali di scarto della pesca e sulle possibilità di una loro conveniente utilizzazione. Mimeo. ESPI.
(2) Belvèze, H., and Bravo de Laguna, J. 1980. Les ressources halieutiques de l'Atlantique Centre-Est. Deuxième partie. Les ressources de la côte ouest-africaine entre $24^{\circ} \mathrm{N}$ et le détroit de Gibraltar. FAO Doc. Tech. Pêches (186.2).
(3) Belvèze, H., and Erzini, K. 1983. The influence of hydro-climatic factors on the availability of the sardine (Sardina pilchardus Walbaum) in the Moroccan Atlantic fishery. FAO Fish. Report 291(2): 285328.
(4) Binet, D. 1982. Influence des variations climatiques sur la pêcherie des Sardinella aurita ivorio-ghanéennes: relation sécheresse-surpêche. Oceanologia acta 5(4): 443-452.
(5) Caddy, J. 1983. The cephalopods: factors relevant to their population dynamics and to the assessment and management of stocks. FAO Fish. Tech. Paper 231.
(6) Caverivière, A. 1982. Les especes démersales du plateau continental ivoirien. Biologie et exploitation. Ph.D. Thesis presented at the University of Aix-Marseilles II.
(7) Champagnat, C., and Domain, F. 1978. Migration des poissons démersaux le long des côtes ouest-africaines de $10^{\circ}$ à $26^{\circ}$ de latitude nord. Cah. ORSTOM ser. oceanogr. 16(3-4): 239-261.
(8) Daan, N. 1980. A review of replacement of depleted stocks by other species and the mechanics underlying such_replacement. Rapp. P-v. Réun. Cons. Int. Explor. Mer 177: 405-421.
(9) Domain, F. 1976. Mauritanie. Les ressources halieutiques de la côte ouest-africaine entre 16 et $24^{\circ}$ lat.N. Rapport, FAO, FI:MAU 73/007/1.
(10) Domain, F. 1980. Contribution à la connaissance de l'écologie des poissons démersaux du plateau continental Sénégalo-mauritanien. Les ressources démersales dans le contexte du golf de Guinée. Ph.D. Thesis presented at the University Pierre et Marie Curie, Paris VII and the Muséum national d'histoire naturelle, Paris.
(11) Domanewsky, L.N., and Borkova, N.A. 1981. Etat du stock de la sardine, Sardina pilchardus Walb. dans la région de l'Afrique du nordouest. COPACE/TECH. 81/31: 19-30.
(12) FAO. 1968. Supplement 1 to the report of the 5 th session of the ACMRR. Report of the ACMRR/ICES Working Party on the Fishery Resources of Eastern Central and Southeast Atlantic. FAO Fish. Report 56(Suppl. 1).
(13) FAO. 1975. Report of the 2nd session of the Fisheries Committee for the Eastern Central Atlantic Fisheries (CECAF) Working Party on Resource Evaluation, Rome, 3-6 December 1973. FAO Fish. Report 158.
(14) FAO. 1978. Some scientific problems of multispecies fisheries. Report of the Expert Consultation on Management of Multispecies Fisheries. Rome, 20-23 September 1977. FAO Fish. Tech. Paper 181.
(15) FAO. 1980. ACMRR Working Party on the Scientific Basis of Determining Management Measures, Report of the ACMRR Working Party on the Scientific Basis of Determining Management Measures. Hong Kong, 10-15 December 1979. FAO Fish. Report 236.
(16) FAO/CECAF. 1976. Nominal catches 1964-74. Statistical Bulletin No. 1.
(17) FAO/CECAF. 1979. Nominal catches 1967-77. Statistical Bulletin No. 2.
(18) FAO/COPACE. 1979a. Rapport du groupe de travail ad hoc sur les poissons pélagiques côtiers ouest-africains de la Mauritanie au Liberia ( $26^{\circ} \mathrm{N}$ à $5^{\circ} \mathrm{N}$ ). COPACE:PACE Series 78/10.
(19) FAO/COPACE. 1979b. Rapport du groupe de travail spécial sur les stocks de céphalopodes. COPACE:PACE Series 78/11.
(20) FAO/COPACE. 1980. Rapport du groupe de travail ad hoc sur les sardinelles des côtes de Côte d'Ivoire-Ghana-Togo. COPACE:PACE Series 80/21.
(21) FAO/COPACE. 1982. Rapport du groupe de travail spéciale sur les stocks de céphalopodes de la région nord du COPACE. COPACE:PACE Series 82/24.
(22) FAO/COPACE. 1984. Rapport du groupe de travail ad hoc sur les chinchards et les maquereaux de la zone nord du COPACE. COPACE:PACE Series 84, in press.
(23) Fonteneau, A., and Bouillon, P. 1971. Analyse des rendements des chalutiers ivoiriens. Définition d'un effort de pêche. Doc. Scient. Centre Rech. oceanogr. Abidjan ORSTOM 21(1-2): 1-10.
(24) Fontana, A., and Weber, J. 1983. Apperçu de la situation de la pêche maritime sénégalaise (Déc. 1982). Dakar: CRODT/ISRA (Miméo).
(25) FRU/CRO/ORSTOM. 1976. Rapport du groupe de travail sur la sardinelle (S. aurita) de Côte d'Ivoire-Abidjan, 28/6-3/7/1976. Dakar: ORSTOM.
(26) Garcia, S. 1982. Distribution, migration and spawning of the main fishery resources in the northern CECAF area. CECAF/ECAF Series $82 / 25$, and 10 sets of maps.
(27) Garcia, S.; Lhomme, F.; Chabanne, J.; and Franquerville, C. 1979. La pêche démersale au Sénégal: historique et potentiel. COPACE:PACE Series 78/8: 59-88.
(28) Garcia-Cabrera, C. 1968. Pulpo. Biologia y pesca del pulpo (Octopus vulgaris) en aguas del Sahara español. Publ. Tech. Junta Estud. Pesca, Madrid 7: 161-198.
(29) Gulland, J.A. 1981. Long-term potential effects from the management of the fish resources of the North Atlantic. J. Cons. Int. Explor. Mer 40(1): 8-16.
(30) Hayasi, S. 1984. Some explanation for changes in abundance of major neritic pelagic stocks in the northwestern Pacific Ocean. In Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, eds.
G.D. Sharp and J. Csirke. FAO Fish. Report 291(1): 37-56.
(31) Holzlohner, S. 1975. On the recent stock development of Sardina pilchardus Walbaum off Spanish Sahara. ICES C.M. 1975/J: 13.
(32) Ikeda, I. 1971. Observations sur les stocks de seiches au large de la côte ouest de l'Afrique. FAO Rapp. Pêches 103: 92-100.
(33) Ikeda, I., and Sato, T. 1971. Renseignements biologiques sur Pagellus bellotti Steindochner au large de la côte nord ouest de l'Afrique avec une evaluation préliminaire des stocks. FAO Rapp. Pêches 103: 100-104.
(34) Institut Sénégalais de recherches agricoles (ISRA). 1982. Statistiques de la pêche maritime sénégalaise en 1982. Achives No. 120. Dakar: CRODT.
(35) Lambouef, M.; Burczynsky, J.; Bencherifi, S.; and Chbani, M. 1981. Campagne de prospection des stocks pélagiques du cap Cantin (Maroc) au cap Timiris (Mauritanie) en juillet 1980 (résultats préliminaires). Trav. Doc. Dev. Pêche. Maroc 28.
(36) Laws, R.M. 1977. Seals and whales of the Southern Ocean. Phil. Trans. Roy. Soc. London (B) 279: 81-96.
(37) Longhurst, A.R. 1969. Species assemblages in tropical demersal fisheries. Actes sycup. oceanogr. Res. halieutiques Atlant. Trop. Unesco, pp. 167-170.
(38) MacCall, A. 1980. Population models for the northern anchovy (Engraulis mordax). Rapp. P.-v. Réun. Cons. Int. Explor. Mer 177: 292-306.
(39) Maurin, C. 1968. Ecologie ichthyologique des fonds chalutables atlantiques (de la baie ibéro-marocaine à la Mauritanie) et de la mediterranée occidentale. Rev. Trav. ISTPM 22(1).
(40) May, R.M.; Beddington, J.R.; Clark, C.W.; Holt, S.J.; and Laws, R.M. 1979. Management of multispecies fisheries. Science 205(4403): 267-277.
(41) Mercer, M., ed. 1982. Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.
(42) Mitchell, B., and Sandbrook, R. 1982. The Management of the Southern Ocean. London: International Institute for Environment and Development.
(43) Monnoyer, P. 1979. Contribution à l'étude des rejets à la mer de la faune ichthyologique capturée par les chalutiers commerciaux dans la zone 34.3.1. Rapport dactylographié du COPACE. Non publié.
(44) Nagasaki, F. 1973. Long-term and short-term fluctuations in the catches of pelagic fisheries around Japan. J. Fish. Res. Board Can. 30(12)Pt. 2: 2361-2367.
(45) Pauly, D. 1979. Theory and management of multispecies stocks. ICLARM Stud. Rev. 1: 1-35.
(46) Pereiro, J.A., and Bravo de Laguna, J. 1980. Dinamica de la población y evaluación de los recursos del pulpo del Atlantico centro oriental. Serie CPACO/PACO 80/18.
(47) Pope, J. 1979. Stock assessment in multispecies fisheries, with special reference to the trawl fishery in the Gulf of Thailand. FAO/ UNDP South China Sea Fisheries Development and Coordination Programme, Manila. Doc. SCS/DEV/79/19.
(48) Pupyschev, V.A. 1982. To the increase in the abundance of Balistes capriscus (Gmel. 1789) and Cephalacanthus volitans in the Gulf of Guinea in VNIRO fishery investigations in the east tropical Atlantic. Proceedings, Lyoghaya I Pishchevayo Promyshlennost, pp. 50-60.
(49) Ritsraga, S. 1976. Results of the studies on the status of demersal fish resources in the Gulf of Thailand from trawling surveys 19631972. In Fishery Resources and Their Management in Southeast Asia, ed. K. Tiews, pp. 198-223. Berlin: German Foundation for International Development.
(50) Sedykh, K.A. 1979. Etude de l'upwelling près de la Côte de l'Afrique du Nord ouest per l'Atlant-NIRO. COPACE:PACE Series 78/11: 93-99.
(51) Soutar, A., and Isaacs, J.D. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. Fish. Bull. NOAA/NMFS 72: 257-275.
(52) Stequert, B.; Brugge, W.J.; Bergerard, P.; Fréon, P.; and Samba, A. 1979. La pêche artisanale maritime au Sénégal. Etudes des résultats de la pêche en 1976 et 1977. Aspects biologiques et économiques. Doc. Sci. Centre Rech. océanogr. Dakar-Thiaroye 73.
(53) Strømme, T. 1983. Final report of the R/V DR. FRIDTJOF NANSEN fish resource surveys off West Africa from Agadir to Ghana. May

1981-March 1982, Bergen, Norway.
(54) Tanaka, S. 1984. Variation of pelagic fish stocks in waters around Japan. In Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, eds. G.D. Sharp and J. Csirke. FAO Fish. Report 291(2): 17-36.
(55) Tiews, K.; Sucondhamarn, P.; and Isrankura, A. 1967. On the change in the abundance of demersal fish stocks in the Gulf of Thailand from $1963 / 1964$ to 1966 as a consequence of the trawl fishery development. Contrib. Dep. Fish. 8 .


[^0]:    * Because of the average ages in the catches (about two years) it must, however, be assumed that the recruitment started to increase around 1969-70.

[^1]:    * A small percentage of trips aimed at a mix of targets was discarded.

[^2]:    * Text of Convention available from the Commission for Conservation of Antarctic Marine Living Resources, 25 Old Wharf, Hobart, Tasmania 7000, Australia.

