Food and population variability in five regions supporting large stocks of anchovy, sardine and horse mackerel

R. J. M. Crawford

FOOD AND POPULATION VARIABILITY IN FIVE REGIONS SUPPORTING LARGE STOCKS OF ANCHOVY, SARDINE AND HORSE MACKEREL

R. J. M. CRAWFORD*

The Benguela, California, Humboldt and Canary currents and the coastal waters of Japan support large stocks of sardine or pilchard *Sardinops* spp. and *Sardina* sp., anchovy *Engraulis* spp., horse mackerel *Trachurus* spp. and chub mackerel *Scomber japonicus*, with hake *Merluccius* spp. also abundant in each of the systems except off Japan. In these systems many of the more numerous fish, birds and mammals are opportunistic feeders having catholic diets. As a result species often have overlapping diets, and when a particular food item is plentiful it may be consumed by a wide variety of organisms at higher trophic levels. Frequently the performances of predator populations have been related to the availability of forage species, but predators have not always been influenced similarly by gross changes in the systems. Predators with the most generalized feeding strategies appear best buffered against collapses of particular prey resources. Although seabirds are generally opportunistic feeders, limitations in their foraging range may make them more susceptible than most other predators to system perturbations. Opportunistic feeding by species at lower trophic levels suggests that they could be advantaged by an increased food supply, and it may not be unreasonable to interpret species replacements in catches as reflecting shifts in the dominance of species. Overall catches from the systems have usually been more stable than the catches of individual species, which have shown wide fluctuations. Shifts in the dominance of species in the catches have often been sustained over a number of years. Generalized feeding creates the possibility that more than one species may benefit from energy made available by the collapse of an abundant resource, and there is evidence that species more abundant in former years have in some instances been partially replaced by a number of organisms. The likelihood of a particular organism becoming the main replacing species will probably be influenced by the degree to which it is utilized during and after the collapse of the originally dominant resource.

Die Benguela-, Kaliforniese, Humboldt- en Kanariese seestroom en die kuswaters van Japan dra groot stapels van sardyn of sardientjies *Sardinops* spp. en *Sardina* sp., ansjovis *Engraulis* spp., marsbanker *Trachurus* spp. en makriel *Scomber japonicus*, en stokvis *Merluccius* spp. is ook volop in elke stelsel behalwe teenoor Japan. In hierdie stelsels is vele van die talryker visse, voëls en soogdiere opportunistiese vreters met katolieke diëte. Gevolglik oorvleuel die diëte van spesies dikwels, en as 'n sekere voedsel-item volop is, mag dit deur 'n wye verskeidenheid organismes op hoër trofiese vlak verbruik word. Die prestasie van roofbevolkings is al dikwels in verband gebring met die beskikbaarheid van prooispesies, maar roofdiere is nie altyd op soortgelyke wyse deur groot veranderinge in die stelsels geraak nie. Dit lyk of die roofdiere met die veelsydigste voedingstrategie die beste teen instortings van bepaalde prooihulpbronne gebuffer is. Hoewel seevoëls oor die algemeen opportunisties vreet, mag die beperkte afstand waaroor hul kos kan soek hul kwesbaarder as die meeste ander roofdiere maak t.o.v. stelselversteurings. Op laer trofiese vlakke dui opportunistiese voeding deur spesies daarop dat hul bevoordeel mag word deur 'n toename in die voedselvoorraad; dit is seker nie onredelik om spesievervanging in vangste te vertolk as die weerspieëling van verskuiwings in die dominasie van spesies nie. Die totale vangste uit stelsels was gewoonlik stabieler as dié van afsonderlike spesies, wat groot skommelings vertoon het. Verskuiwings in die oorheersing van spesies in die vangste is dikwels oor 'n aantal jare volgehou. Veralgemeende voeding skep die moontlikheid dat meer as een spesie voordeel kan trek uit die energie wat deur die instorting van 'n volop hulpbron beskikbaar gestel word, en daar is bewys dat spesies wat vroeër jare volopper was, in sommige gevalle deels deur verskeie ander organismes verplaas is. Die waarskynlikheid dat 'n gegewe spesie die hoofverplaser sal word, word moontlik beïnvloed deur die mate waartoe dit tydens en na die instorting van die oorspronklike oorheersende hulpbron benut word.

Four major eastern boundary current systems, those of the California, Humboldt, Canary and Benguela currents, contain similar ichthyofaunal assemblages, in which hake *Merluccius* spp., horse mackerel *Trachurus* spp., chub mackerel *Scomber japonicus* and the clupeoid pairing of anchovy *Engraulis* spp. and sardine/pilchard *Sardinops* spp. or *Sardina* sp. are prominent (Parrish *et al.* 1983). These groupings, with the exception of hakes, are also abundant in a fifth region, the coastal waters of Japan on the western boundary of the Pacific (cf. Blaxter and Hunter 1982, Hayasi 1983). In all five regions (see Fig. 1), many of the stocks have undergone large-scale changes in abundance. For example, Japanese catches of sardine *Sardinops melanosticta* were more than 2 million metric tons between 1934 and 1939 but fell to under 10 000 tons in 1961, before again rising to over 2 million tons in 1980 (Kondo

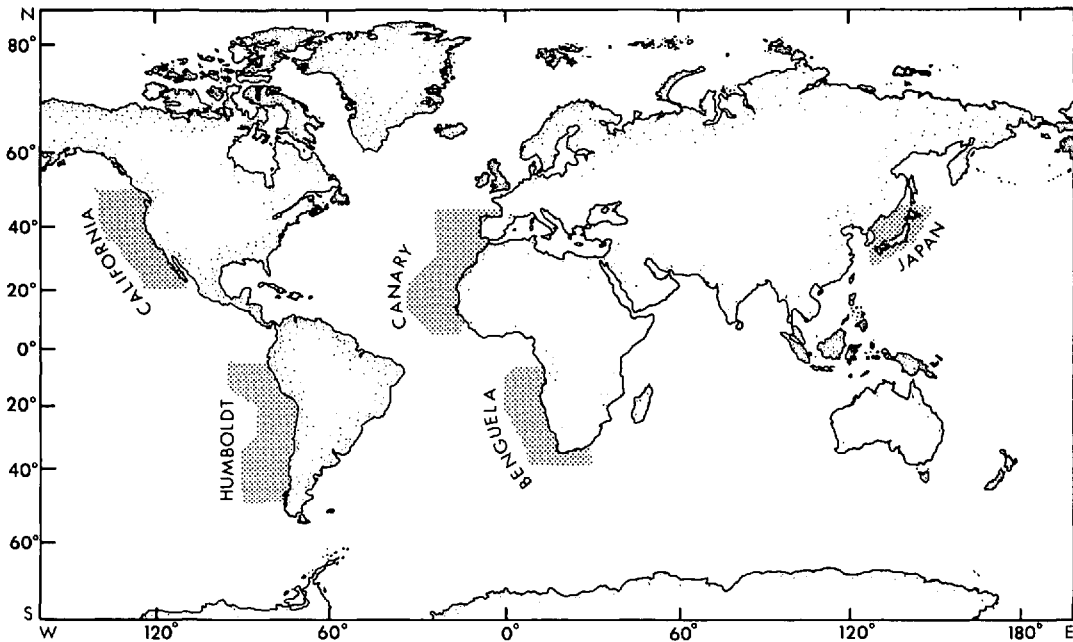* Sea Fisheries Research Institute, Private Bag X2, Rogge Bay, 8012, Cape Town

Fig. 1: Map illustrating the five regions supporting large resources of sardine or pilchard, anchovy and horse mackerel

1980, Hayasi op. cit.). In the Humboldt system, catches of anchovy *Engraulis ringens* exceeded 13 million tons in 1970 but fell to only 126 000 tons in 1983 (Jordán 1983).

The biomass of fish species probably fluctuated widely even before the establishment of commercial fisheries (e.g. Crawford and Shelton 1978, Blaxter and Hunter 1982), and the causes of such changes are of considerable interest. The proposal for the International Recruitment Experiment (IREX) identified six factors which were thought to account for most of the biological variability observed in exploited fish populations, namely temperature, turbulence, transport, food, predation and population density (Parrish *et al.* 1983).

The possible influence of these various factors on marine animal populations may be investigated in a number of ways. One might be to make deductions on the basis of empirical observations. For example, Bailey (1981) showed that, between 1950 and 1979, the three strongest year-classes of Pacific hake *Merluccius productus* were recruited from spawning that took place in winters of those years in which strongest onshore transport was recorded. He demonstrated a significant negative correlation between Ekman transport in winter, the season of greatest spawning, and

an index of year-class abundance. However, empirical information is frequently inadequate for this type of analysis (Bakun 1985). For some fish species in the Benguela system, recent analyses have cast doubt on the validity of formerly accepted time-series of estimates of biomass (e.g. Armstrong *et al.* 1985, Shelton *et al.* 1985, Leslie 1986), resulting in population data series generally too short for empirical analyses.

Even when reliable estimates of population parameters and other variables are available over a sufficiently long time horizon, it may not be possible to distinguish between two possible influences on the population. Have the collapses of the various sardine fisheries (Fig. 2) been caused by exploitation or by environmental changes? Kawasaki (1983) noted that Clark and Marr (1955), arguing in a joint paper from the same data, each arrived at different conclusions regarding the relative importance of these factors for the collapse of the Californian fishery for sardine *Sardinops sagax*. Lasker and MacCall (1983) stated that scientists who had studied the fluctuation of fish populations had not come to a definitive conclusion as to what degree fishing was the source of any clupeoid collapse. MacCall (1984) remarked that the interpretation of fishery effects is made difficult by
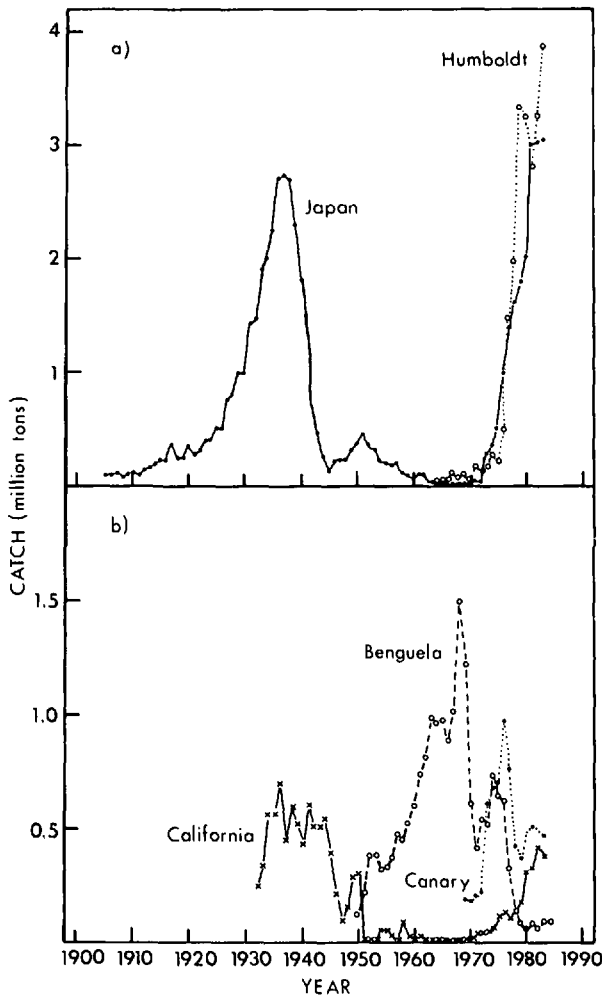
Fig. 2: Trends in the catches of sardines or pilchards from five regions, modified from Kawasaki (1983) and Parrish *et al.* (1983). For the Californian system F.A.O. records have been used for recent years, probably including large amounts of *Opisthonema* and *Cetengraulis* and some *Etrumeus* taken by the Mexican fishery (R. H. Parrish *in litt.*)

the lack of replication and of experimental control. Bakun (1985) commented that a high degree of variability in recruitment largely obscured signals, such as a stock-recruitment relationship, essential for managing human impacts on a biological system.

A second approach to investigating the possible influence of factors on population variability is to make deductions from what is known of the biology of the species concerned. For example, Parrish *et al.*

(1983) compared the spawning habitats of sardines and anchovies in four eastern boundary current systems and showed that these clupeoids tended not to spawn in highly turbulent areas or areas of strong offshore transport. Given this basis, one might postulate that the survival of reproductive products would be disadvantaged in years of abnormally high offshore transport or of excessively turbulent conditions over the main spawning grounds.

Simulation modelling provides a third alternative by which causes of variability in marine stocks can be examined, and the method was used by MacCall (1984) to suggest that a variable food supply for seabirds would result in a variable seabird abundance. Models simplify reality, often grossly (Stewart 1980), but allow for the control of variables and for replication (MacCall op. cit.).

The likely influences of temperature, transport and turbulence on the population variability of anchovy and sardine have been addressed in depth by Parrish *et al.* (1983). The aim of this paper is to explore, for systems supporting large stocks of these clupeoids, some possible effects of one other factor identified by IREX as likely to influence population variability: food. In doing so, recourse is made to all three of the approaches outlined above and the discussion is extended to include not only the clupeoids, but other marine animal populations too. Since the study is preliminary, no attempt is made to comprehensively review all available information, though of necessity the literature referred to is extensive. Aspects of feeding in the Benguela have been considered by Crawford *et al.* (1987).

OPPORTUNISTIC FEEDING

Many of the more abundant species in the eastern boundary current systems have a broadly based diet and are generalist, rather than specialist, feeders (cf. Crawford *et al.* 1987). The food of these species is largely determined by what is available at any particular time and place, and it may vary considerably between areas and seasons or years.

In the Benguela system, the diet of the shallow-water Cape hake *Merluccius capensis* has been investigated at various localities, and it provides an example of large inter-regional changes in diet (Fig. 3). During the 1970s, hake of similar sizes fed on pelagic goby *Sufflogobius bibarbatus* off the Namib coast, Cape hakes *M. capensis* and *M. paradoxus* off the Western Cape, and cephalopods, pilchard *Sardinops ocellatus* and anchovy *Engraulis capensis* over the Agulhas Bank (Hecht 1976, Botha 1980,
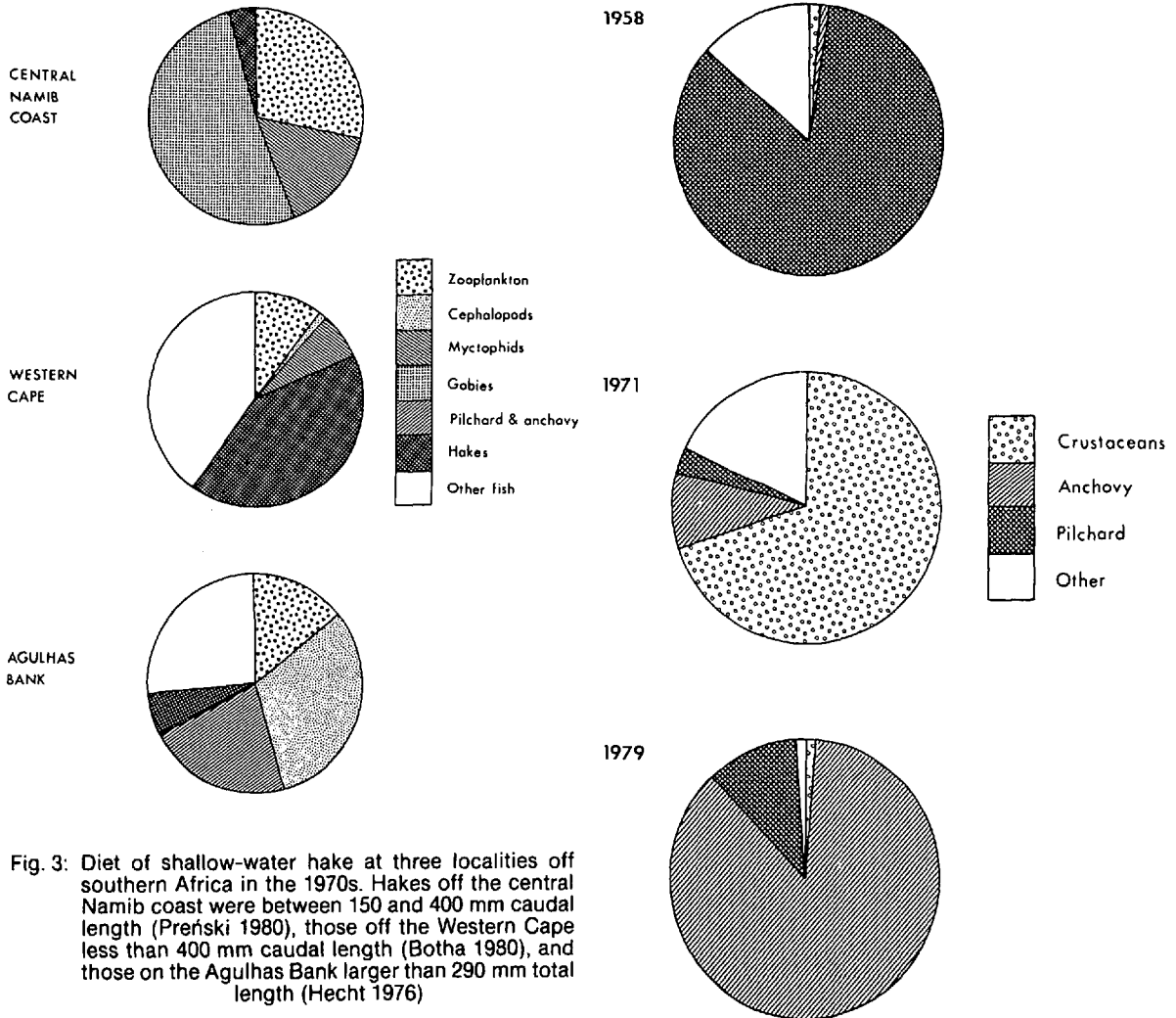
Fig. 3: Diet of shallow-water hake at three localities off southern Africa in the 1970s. Hakes off the central Namib coast were between 150 and 400 mm caudal length (Preński 1980), those off the Western Cape less than 400 mm caudal length (Botha 1980), and those on the Agulhas Bank larger than 290 mm total length (Hecht 1976)

Fig. 4: Diet of snoek caught by handline off the Western Cape during three different periods (information from Nepgen 1979, 1982)

Preński 1980, Payne 1986). Myctophids of varying genera were consumed off both the Namib and the Western Cape coasts. Various researchers have concluded that the Cape hakes are opportunistic feeders (Botha op. cit., Payne op. cit., Payne *et al.* 1987).

The diet of snoek *Thyrsites atun* caught inshore by handline off the Western Cape during three selected years illustrates inter-annual changes in diet (Fig. 4). In 1958 pilchard was the most important prey, whereas crustaceans dominated in 1971 and anchovy in 1979, trends that largely reflected changes in the relative abundances of these organisms (Nepgen 1979, 1982). Round herring *Etrumeus whiteheadi*, lanternfish *Lampanyctodes hectoris*, lightfish *Mauro-licus muelleri*, Cape hake, saury *Scomberesox saurus* and euphausiids were important in the diet of snoek

caught off the Western Cape farther out to sea by demersal trawlers in the 1980s, so that composition of the food of snoek is also influenced by location (Prosch 1986, Crawford *et al.* 1987).

In the Benguela, researchers have concluded that a number of abundant species are non-selective feeders, for example pilchard, anchovy (King and Macleod 1976) and horse mackerel (Hecht 1976, Konchina 1986). Euphausiids and copepods occur widely in the diet of Cape horse mackerel *Trachurus capensis* (e.g. Hecht op. cit., Krzeptowski 1982, Andronov 1983,

1985), but certain prey items are of importance in specific regions. Pelagic gobies are eaten off the Namib coast, lightfish off the Western Cape and cephalopods on the Agulhas Bank (Venter 1976, Hatanaka *et al.* 1983, Uozumi *et al.* 1984, 1985, Prosch 1986). Many other species have been shown to have a catholic diet. Between 1969 and 1971, chub mackerel off the Western Cape fed mainly on amphipods, euphausiids and lanternfish (Baird 1978), whereas in False Bay in 1979 and 1980 anchovy occurred in more than half the stomachs investigated (Nepgen 1982). Off South West Africa (Namibia), food of kingklip *Genypterus capensis* varied in accordance with the geographical composition of prey species in the early 1980s (Macpherson 1983). For kingklip the dragonet *Paracallionymus costatus* was an important source of food off the Western Cape (Rattray 1947, Davies 1949) and over the Agulhas Bank (Payne 1986), but not off South West Africa (Macpherson op. cit.).

Cape gannets *Morus capensis*, Cape cormorants *Phalacrocorax capensis* and jackass penguins *Spheniscus demersus* fed largely on pilchard in the 1950s, but more recently other species including hakes, saury, pelagic goby, anchovy and round herring have assumed increased importance in some areas (Davies 1955, 1956, Rand 1959b, 1960a, b, Matthews 1961, Berry 1975, Crawford and Shelton 1978, 1981, Batchelor 1982, Matthews and Berruti 1983, Randall 1983, Batchelor and Ross 1984, Cooper 1985, Crawford *et al.* 1985, Duffy *et al.* 1985, Wilson 1985, Randall and Randall 1986). Between 1954 and 1956, horse mackerel and pilchard were important in the diet of Cape fur seals *Arctocephalus pusillus* off the Western Cape, whereas in the late 1970s and early 1980s the pelagic goby was frequently eaten off the Namib coast and hakes and anchovy to the south of the Orange River (Rand 1959a, David 1987).

Opportunistic feeding is not confined to the Benguela system. Bernard *et al.* (1985) demonstrated considerable differences between years and regions in the diets of three scombrids (albacore *Thunnus alalunga*, skipjack *Katsuwonus pelamis* and bonito *Sarda chiliensis*) from the north and central Pacific, including the Calfornia Current, and concluded that these scombrids were likely to be opportunistic predators. Gotshall (1969) was of the opinion that the food habits of Pacific hake depended on the availability of a particular organism. Best (1963) considered the Pacific hake to be an opportunistic feeder, and studies have shown geographic, seasonal and annual differences in feeding behaviour between British Columbia and California (Gotshall op. cit., Outram and Haegele 1972, Bailey *et al.* 1982, Livingston and Alton 1982).
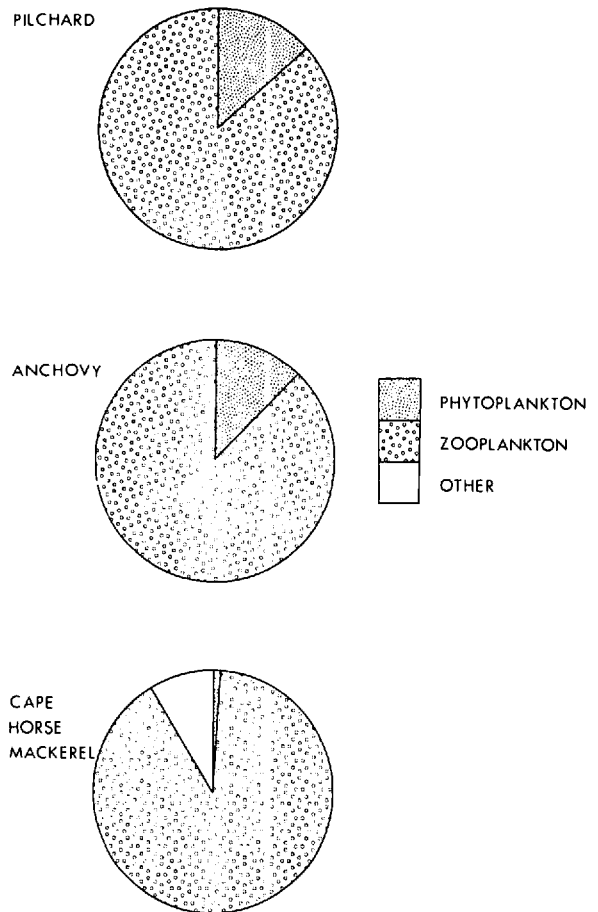

Fig. 5: Contribution of major groupings to the diet of juvenile pilchard, anchovy and horse mackerel off South West Africa in the early 1970s. In each instance the copepods *Calanoides carinatus* and *Centropages brachiatus* were important contributors to the zooplankton eaten (information from King and Macleod 1976 and Venter 1976)

Off California the blue shark *Prionace glauca*, a common species, feeds on a variety of abundant invertebrates and fishes, and changes in its diet are likely to be related to the seasonal availability of prey items (Horn 1980). The food of western gulls *Larus occidentalis* varies between colonies in accordance with the relative availability of foods (Hunt and Butler 1980). California sea lions *Zalophus californianus* feed opportunistically on a number of prey species, their diet often reflecting trends in the seasonal or interannual availability of schooling fishes and squids (Antonelis and Fiscus 1980, Bailey
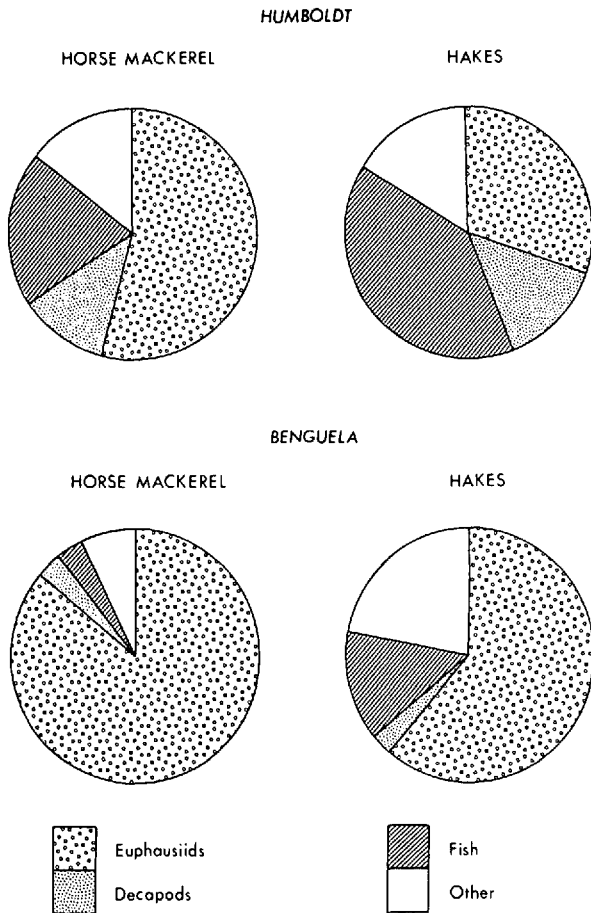
Fig. 6: Diets of horse mackerel larger than 200 mm and of hakes of approximate size 150-250 mm in the Humboldt and northern Benguela systems (information from Andronov 1983 and Konchina 1983)
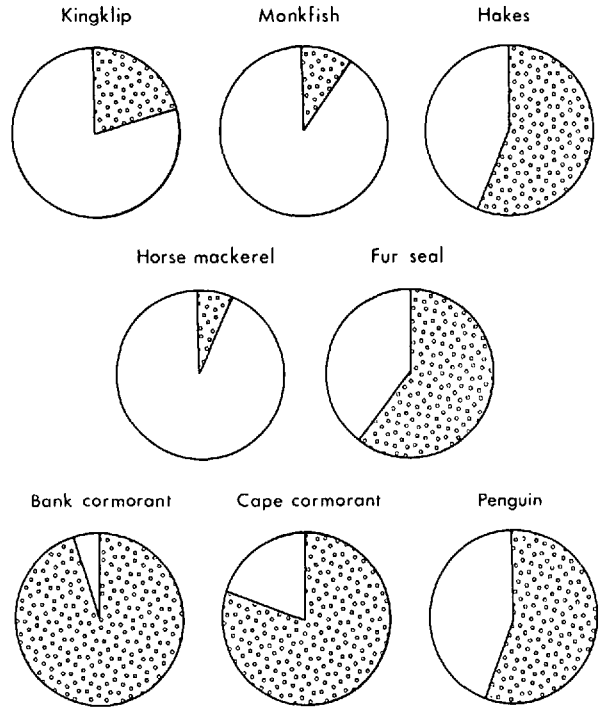

Fig. 7: Contribution of the pelagic goby to the diets of several species off South West Africa in the 1970s (information from Venter 1976, Preński 1980, Macpherson 1983, 1985, Crawford et al. 1985 and David 1987)

and Ainley 1982, Antonelis et al. 1984). Other pinnipeds, including the northern sea lion Eumetopias jubatus, the northern fur seal Callorhinus ursinus, the harbour seal Phoca vitulina, and the northern elephant seal Mirounga angustirostris, also have broadly based diets and feed opportunistically (Antonelis and Fiscus op. cit.). Other opportunistic feeders include two cetaceans, Pacific white-sided dolphin Lagenorhynchus obliquidens and Dall's porpoise Phocoenoides dalli (Stroud et al. 1981).

Konchina (1983) regarded both hake Merluccius gayi and horse mackerel Trachurus symmetricus in the Humboldt system to be facultative predators, deriving the bulk of their food from euphausiids and fish, and able to adapt their feeding to utilize a wide variety of potential food items. As in the Benguela,

hakes fed on their own young, suggestive of opportunistic feeding. The diet of Peruvian fur seals Arctocephalus australis changed from almost exclusively anchovy to one based on sardine S. sagax and horse mackerel T. symmetricus following the collapse of the anchovy resource (Muck and Fuentes 1984).

In the Canary system, Kinzer (1982) concluded that four species of myctophids were opportunistic predators. The sardinellas Sardinella aurita and S. eba appear to be non-selective feeders (Nieland 1982). Hoffmann (1982) demonstrated differences between regions or depths in the diets of a number of fish species, including the grenadiers Coelorhynchus coelorhynchus and Malacocephalus occidentalis, the rosy soldier fish Hoplostethus mediterraneus and the rockfish Helicolenus dactylopterus.

In Japanese waters Tanaka (1983) considered that competition for food between sardine, anchovy E. japonicus, horse mackerel Trachurus japonicus and chub mackerel was probable. Kawasaki and Omori (in press) showed similarity in the diet of sardine and anchovy sampled simultaneously, but inverse trends in the catches of these species from a number of
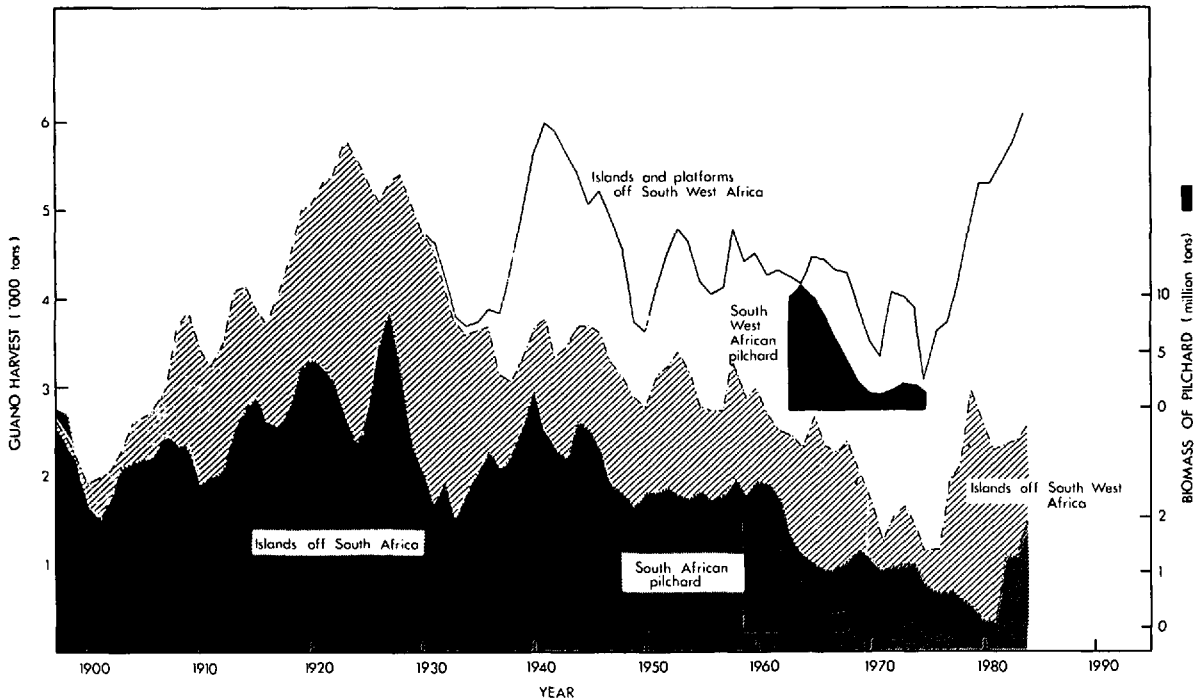
Fig. 8: Trends in the production of seabird guano at islands and platforms off South and South West Africa, and in the biomass of the respective pilchard stocks (after Crawford *et al.* 1987)

regions. They concluded that there was severe competition for food between the two species.

A likely consequence of non-selectivity in the diets of consumers is that similarity will exist in their diets. In the Benguela, this has been shown in the diets of pilchard, anchovy and small horse mackerel (Fig. 5, King and Macleod 1976, Venter 1976), as well as in those of larger horse mackerel and Cape hakes (Fig. 6, Krzeptowski 1982, Andronov 1983), of snoek and chub mackerel (e.g. Nepgen 1982), and of various seabirds (e.g. Crawford and Shelton 1978). Off California seabirds frequently forage on the same species base (Ainley 1980), and, when there is an abundant food supply, foraging areas of different pinnipeds overlap (Antonelis and Fiscus 1980). In the Humboldt system there appears to be some overlap in the major prey groups of hake and horse mackerel of certain sizes (Fig. 6, Konchina 1983).

Where opportunistic feeding is commonly undertaken and a prey organism is abundant, that particular organism may be expected to contribute to the food of a number of consumers at higher trophic levels. The pelagic goby was important in the diets of many species off the Namib coast during the 1970s (Fig. 7), being eaten by a variety of organisms

ranging from groundfish such as the West Coast sole *Austroglossus microlepis* (A. Badenhorst, Sea Fisheries Research Institute, pers. comm.), Cape hakes (Preński 1980), monkfish *Lophius* spp. (Macpherson 1985), kingklip (Macpherson 1983) and large-eye dentex *Dentex macrophthalmus* (Kuderskaya 1985), through Cape horse mackerel (Venter 1976) to the Cape fur seal (David 1987) and seabirds (Crawford *et al.* 1985). Similarly, lanternfish are believed to play an important ecological role in pelagic food webs off California, and to be fed on by squids, sharks, rockfishes, salmon, tunas, billfishes, seabirds, seals and whales (Horn 1980). In Californian waters, Pacific saury *Cololabis saira* are fed on by squids, sharks, albacore, marlin, western gulls, dolphins and porpoises (Horn op. cit.). Other examples of abundant forage species being widely preyed upon are plentiful (cf. Crawford *et al.* 1987).

DEPENDENCE OF PREDATORS ON PREY AVAILABILITY

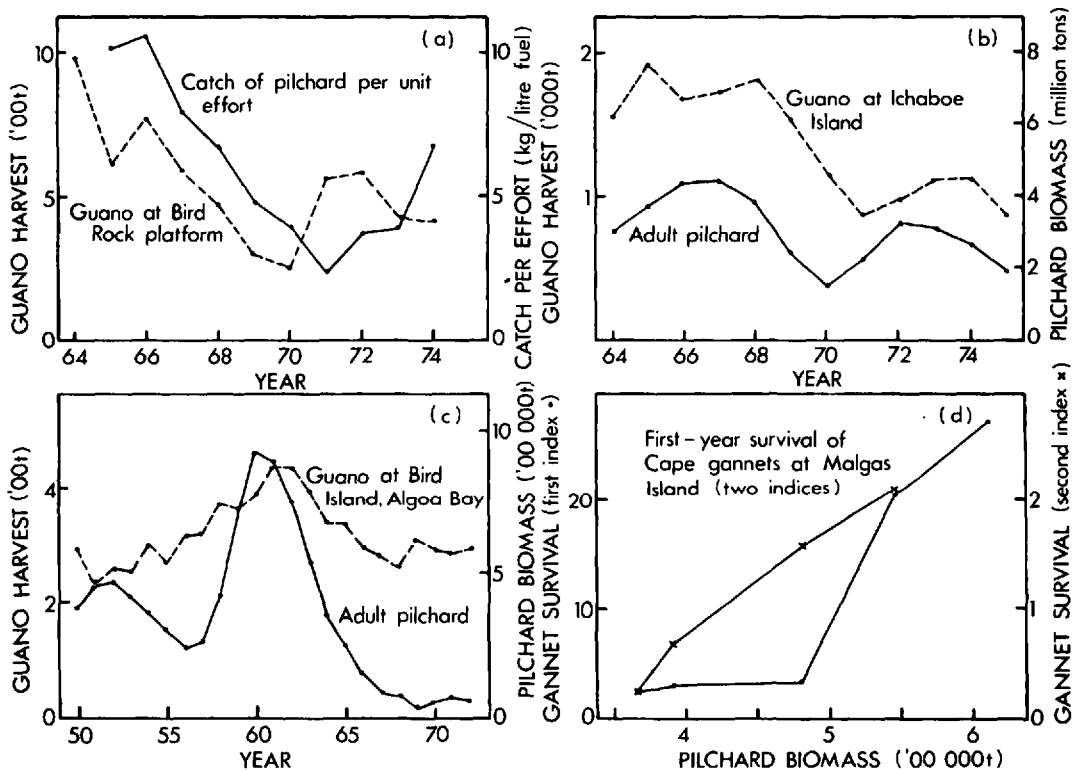In systems with large resources of anchovy, sardine

Fig. 9: Relationship between indices of abundance of pilchard and the production of guano at (a) a seabird platform near Walvis Bay, (b) a seabird island slightly north of Lüderitz and (c) a seabird island near Port Elizabeth, and (d) between biomass of pilchard and indices of first-year survival of Cape gannets at a seabird island off South Africa's Western Cape (after Crawford *et al.* 1987)

and horse mackerel, the performance of predator populations has often been related to the availability of forage organisms. The predators for which such relationships have been best demonstrated have been coastal-breeding seabirds, for which indices of abundance are relatively easily obtained, though other examples exist.

The dependence of predators on their prey has recently been reviewed for the Benguela system (Crawford *et al.* 1987), and only a few examples are given here. Crawford and Shelton (1978) showed that guano harvests could be reliably used as an index of numbers of breeding seabirds, and that in many instances trends in the production of guano were closely related to estimates of the local abundance of forage fish. Yields of guano at both islands and platforms plummeted following collapses of the pilchard fisheries off South and South West Africa (Fig. 8). At various localities, guano harvests were significantly related to estimates of the local biomass

of pilchard (Fig. 9a, b, c). For the early 1950s, two indices of survival of juvenile Cape gannets at an island off the Western Cape could be related significantly to estimates of the biomass of pilchard in the region (Fig. 9d), as well as to estimates of the combined biomass of pilchard and horse mackerel (Crawford *et al.* 1987). These two species were, at that time, dominant in the diet of gannets (Davies 1955, 1956, Rand 1959b). Three large increases in the availability of snoek to handline fishermen off the Western Cape since the 1890s have each been significantly related to estimates of the abundance of prey or of other predators of shoaling epipelagic fishes (Crawford and De Villiers 1985). Availability of snoek off the Namib coast has also been correlated with an index of prey abundance (Crawford *et al.* 1987).

Off California, a significant relationship has been demonstrated between numbers of breeding western gulls and an index of the abundance of anchovy
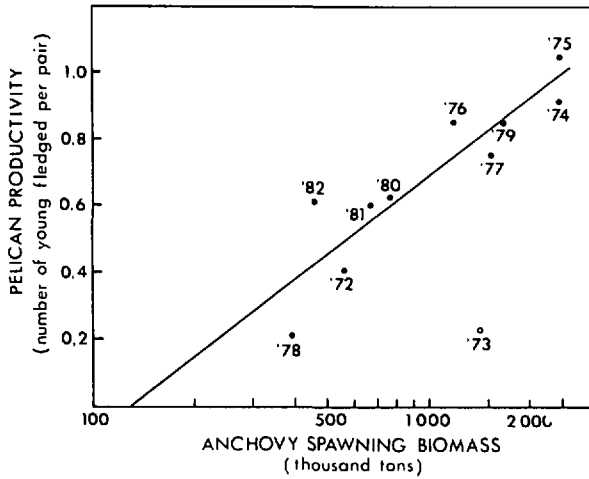
Fig. 10: Relation between brown pelican productivity and anchovy spawning biomass off California (after MacCall 1986)

Fig. 11: Trends in numbers of seabirds and marine mammals and in the catch of anchovy in the Humboldt system, 1956–1983 (after Jordán 1983, Tovar 1983 and Muck and Fuentes 1984)

E. mordax (Hunt and Butler 1980). Pelican productivity has also been shown to be related to the abundance of anchovy (Fig. 10, Anderson *et al.* 1980, MacCall 1986). Ainley and Lewis (1974) hypothesized that the disappearance of Pacific sardine precluded recovery of several Californian populations of seabirds previously reduced by unrelated factors. At the Farallon Islands, numbers of California sea lions increased following termination of the fishery for Pacific hake off central California, possibly because of an enhanced food supply (Ainley *et al.* 1982).

In the Humboldt system there is little doubt that the collapse of the anchovy resulted in a drastic decrease in seabird populations (Jordán 1967, Idyll 1973, Ainley 1980). Numbers of adult seabirds decreased from 18 million in 1962/63 to less than two million in 1972/73, a period in which large commercial catches of anchovy were effected (Fig. 11, Tovar 1983). Earlier, temporary decreases in numbers of seabirds had occurred when oceanographic conditions caused reduced availability of anchovy (Jordán op. cit.), but the heavy commercial exploitation and eventual collapse of anchovy resulted in a decrease in seabird numbers to levels lower than ever previously recorded there. Then, until the early 1980s, seabird numbers remained depressed at below ± 25 per cent of their maximum abundance.

With the exception of the yellow-legged herring gull *Larus cachinnans*, numbers of all seabird species at the Macaronesian Islands in the Canary system are thought to have decreased in recent years, with commercial fishing one likely cause of the decreases
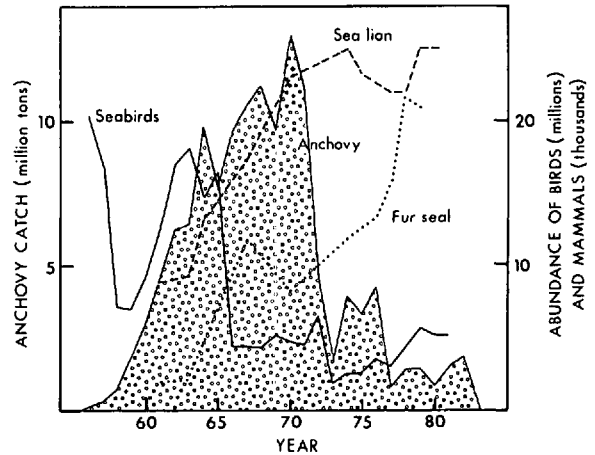
(Le Grand *et al.* 1984). Off the Atlantic sector of the Iberian Peninsula, competition with commercial fisheries may also have affected seabird numbers, and it may have been one of the major contributors to the decrease in numbers of common guillemots from about 20 000 birds in the 1950s to about 300 in the early 1980s (Bárcena *et al.* 1984).

DIFFERENT RESPONSES BY PREDATORS TO SYSTEM PERTURBATIONS

Populations of some predators have been closely related to the abundance or availability of particular forage organisms, so that, for example, changes in the dominance of fish species have sometimes been reflected at the seabird level (Crawford *et al.* 1985). However, other predators have been little influenced by gross changes in the ecosystems. In the Benguela and Humboldt systems, populations of pinnipeds have increased after being reduced to low levels by exploitation, trends that have been maintained in spite of severe depletion of some prey resources, and that are at variance with continued decreases in the sizes of some seabird populations.

Trends in numbers of Cape fur seals in the Benguela region have been documented by Shaughnessy and Butterworth (1981). As a result of sealing, the overall population was at a low level at the beginning of the twentieth century, but it subsequently recovered. There was an increase in seal
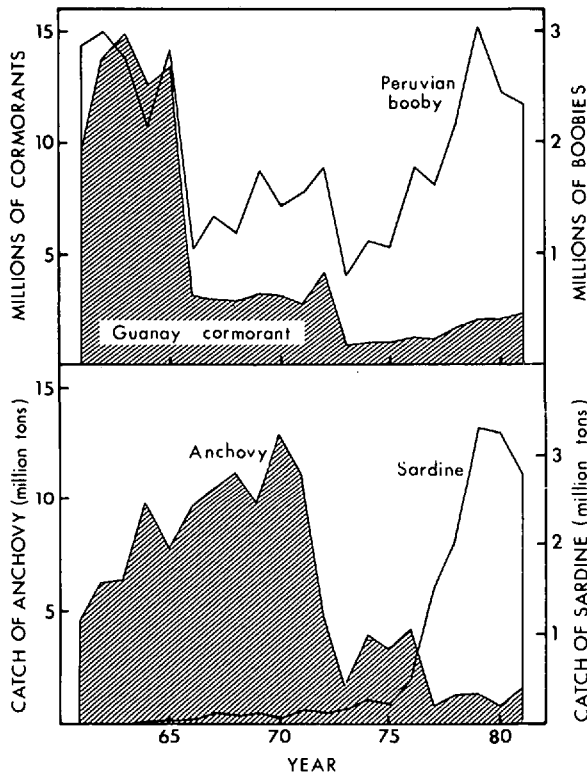
Fig. 12: Trends in numbers of Peruvian boobies and guanay cormorants and in catches of anchovy and sardine in the Peruvian system, 1961–1981 (after Jordán 1983 and Tovar 1983)

herds in the late 1930s, and a maximum estimate of the pup population in 1940 was 155 500 (Shaughnessy and Butterworth op. cit.). In 1971 there were an estimated 196 000 pups and, in 1983, 310 000 (Butterworth *et al.* 1987). The increases since 1940 were despite the collapses of pilchard and horse-mackerel resources off South Africa, and of the pilchard resource off the Namib coast. Pilchard and horse mackerel formed almost 60 per cent by volume of the food of seals off the Western Cape in the period 1954–1956 (Rand 1959a). More recently anchovy and hake have been dominating the diet of seals off the South African coast (David 1987). Numbers of Cape gannets decreased from about 150 000 breeding pairs in 1956 to less than 100 000 in 1980 (Crawford *et al.* 1983). Numbers of jackass penguins concomitantly decreased from some 300 000 breeding adults in 1956 to about 130 000 in the late 1970s (Shelton *et al.* 1984). Both these decreases are believed to have resulted from the collapses of the pilchard resources

(Crawford and Shelton 1981). However, not all seabirds have shown the same response to changes in the abundance of fish species. For example, in the 1970s in the region between Walvis Bay and Lüderitz along the Namib coast, numbers of Cape gannets decreased while numbers of bank cormorants *Phalacrocorax neglectus* increased. In the same region the abundance of pilchard, eaten by gannets, diminished. Pelagic goby, eaten by bank cormorants, became more plentiful (Crawford *et al.* 1985).

Off Peru, the numbers of fur seals and sea lions *Otaria flavescens* have increased since the early 1960s (Fig. 11, Muck and Fuentes 1984). Numbers of sea lions appear to have stabilized following the collapse of the anchovy, but the population of fur seals has continued increasing. Muck and Fuentes (op. cit.) noted that sardine and horse mackerel had replaced anchovy as the main pinniped food resource and concluded that growth of the pinniped populations had not been affected by the collapse of the anchovy. Numbers of Peruvian boobies *Sula variegata* (boobies and gannets are both members of the family Sulidae) and guanay cormorants *Phalacrocorax bougainvillii* both decreased after 1965 during a period of heavy exploitation and subsequent collapse of the anchovy. Although those of boobies subsequently recovered, the numbers of cormorants remained at a low level (Tovar 1983). The recovery of the booby population is associated with increased harvests of sardine from the region (Fig. 12), suggesting that boobies were more successful than cormorants in utilizing sardine as an alternative prey resource to anchovy. However, recent feeding studies have not been conducted (Duffy *et al.* 1984b).

One may conclude that the more generalized the feeding of a particular species, the better buffered it will be against large changes in the species composition of organisms at lower trophic levels. Indeed, generalized feeders in systems having variable food resources may maintain relatively stable populations, as has been the case for the sea lion off Peru since 1970. Conversely, where there are few prey species, the performance of predators may be dependent on the states of particular forage resources. In the southern California Bight, the diversity of prey species for seabirds, such as the brown pelican *Pelecanus occidentalis*, is low and the breeding success and winter populations of this species increase or decrease with population size of the dominant prey, anchovy (Anderson and Gress 1984). The guanay cormorant appears to have been similarly dependent on anchovy off Peru.

Should the behaviour of a particular prey species change with time or locality, a specialist predator may be influenced by this change even if the density
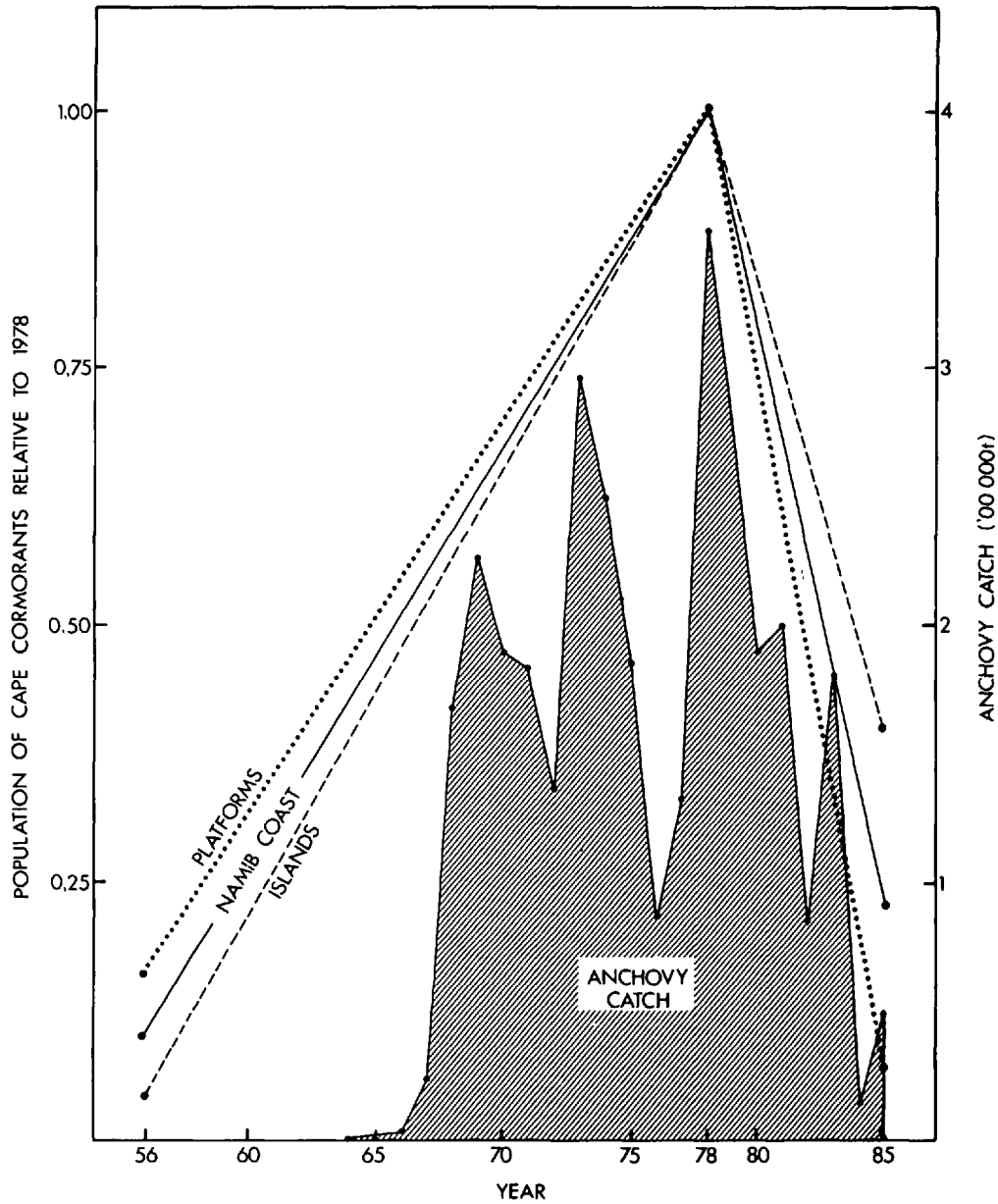
Fig. 13: Trends in the catch of anchovy and in the breeding population of Cape cormorants at islands, platforms and overall along the Namib coast, 1956–1985 (after Crawford et al. 1987)

of the prey species remains more or less constant. Off the southern African coast, the bulk of the Cape cormorant population (99,85 per cent in the period 1977–1981) breeds west of Cape Agulhas (Cooper et al. 1982), where trends in the numbers of breeders are often closely related to availability of anchovy (Fig. 13). Cape cormorants forage in flocks and are probably dependent on large, dense shoals of fish (Duffy et al. 1984a). Although large shoals of anchovy occur east of Cape Agulhas, the major shoals are

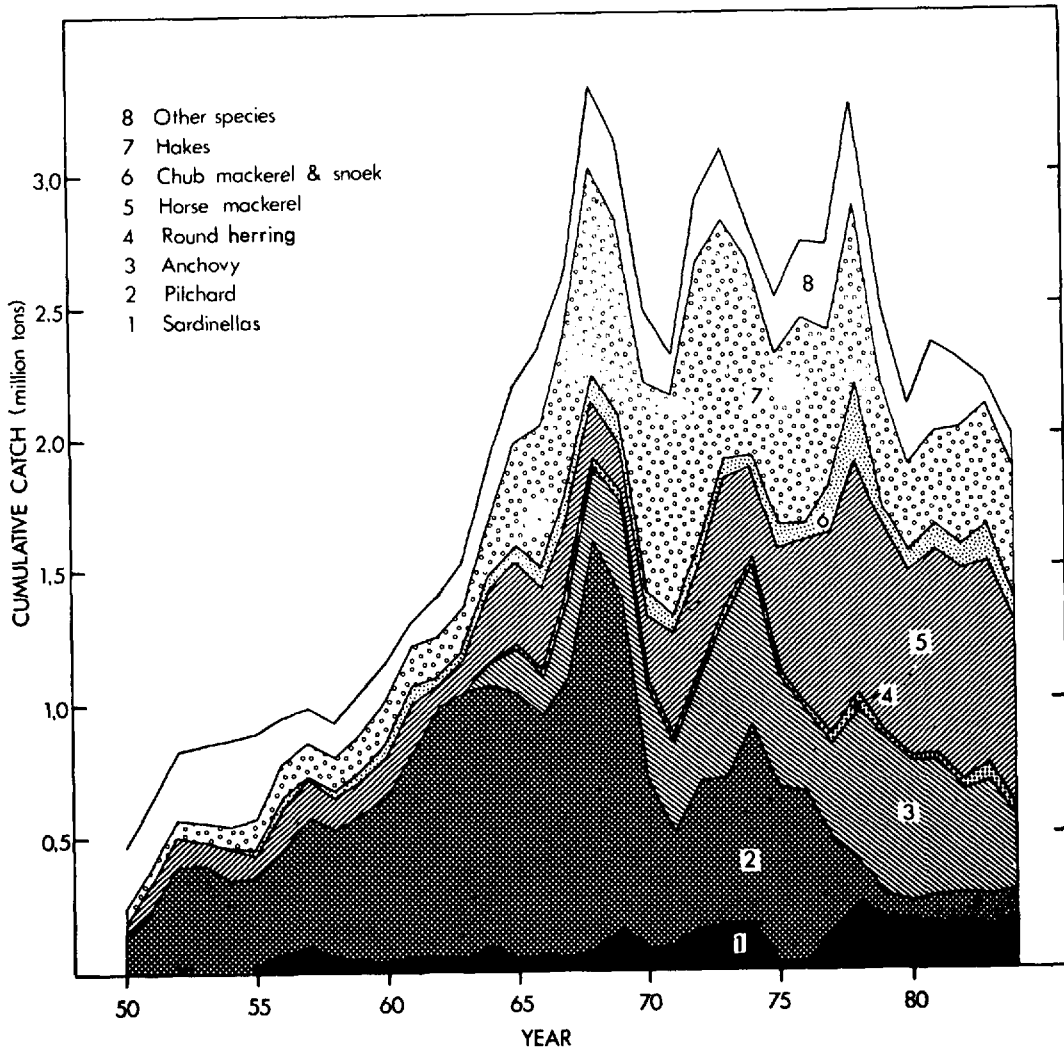Fig. 14: Cumulative catches of major species groups from the Benguela system, 1950-1984 (after Crawford. *et al.* 1987)

frequently at some distance from the coast (Hampton *et al.* 1985) and probably often below the upper surface waters (Crawford 1980). Therefore, east of Cape Agulhas the behaviour of the anchovy places it beyond the foraging range of Cape cormorants, whereas along the west coast of southern Africa it is readily available to these birds.

Seabirds are generally opportunistic predators, eating whatever prey species are readily available (Ainley 1980), but limitations in their foraging range and depth may make them more susceptible than most other predators to system perturbations. The

jackass penguin is flightless, has a limited foraging range when breeding (Frost *et al.* 1976) and, in the Benguela system, has been more severely affected than other seabirds by the collapses of the pilchard resources (Crawford and Shelton 1981).

CATCHES

In all five of the regions shown in Figure 1 there have been large fluctuations in the harvests of
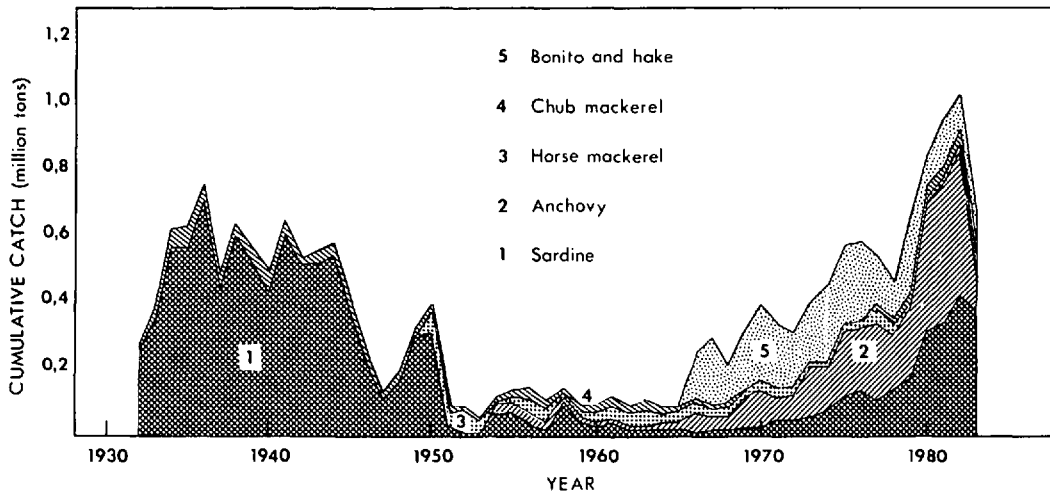
Fig. 15: Cumulative catches of major species from the California system, 1932-1983. Data used for recent years are those provided by F.A.O., although catches for *Scomber* have been taken from MacCall *et al.* (1985). Other sources include Collins *et al.* (1980), Troadec *et al.* (1980) and Francis *et al.* (1984)

individual species. In no region have sardine, anchovy and horse mackerel been simultaneously abundant in catches. Combined catches of all species have generally been considerably more stable than those of any one species, although there has been a tendency for overall yields to be depressed during periods in which species dominance in the catches of epipelagic fish has changed (Silvert and Crawford in press). Shifts in the dominance of individual species have often been sustained over a number of years (e.g. Skud 1982).

In the Benguela system, the combined annual catch of all species has been between some 2,0 and 3,3 million tons since the mid 1960s (Fig. 14). However, catches of individual species have shown large fluctuations. Yields of pilchard fell from 1,5 million tons in 1968 to about 60 000 tons in 1980. Those of anchovy were negligible prior to 1964 but were over 600 000 tons in 1973. Harvests of horse mackerel *Trachurus* spp. rose from just over 100 000 tons in 1963 to almost a million tons in 1978. Catches of Cape hakes were about 200 000 tons in 1964, more than one million tons in 1972, but only some 300 000 tons in 1980.

Harvests of sardine were high off California from the mid 1930s through the mid 1940s (Fig. 15), but by 1952 had fallen disastrously. The collapse was followed by rapid growth of the anchovy population in the 1950s and early 1960s (MacCall 1980), although catches of anchovy remained low until the 1970s. More recently there have been indications of a lower

biomass of anchovy, but of increased abundance of sardine, especially off Mexico (cf. Kawasaki 1983, Lasker and MacCall 1983, MacCall 1984). Catches of chub mackerel were high in the mid 1930s but had decreased to low levels by the late 1960s and early 1970s. There was a subsequent recovery (MacCall *et al.* 1985). The combined catch of the different species has varied considerably, there being reduced fishing after the collapse of the sardine until the mid 1960s, when the fishery for Pacific hake developed. In this interim period, the greatly reduced catches probably resulted from stringent regulatory measures rather than from greatly decreased overall abundance of fish.

Off Peru and Chile the fishery for anchovy collapsed from a harvest of over 13 million tons in 1970 to less than 2 million tons in 1973 (Fig. 16). There was a partial recovery to a catch of over 4 million tons in 1976, but subsequently catches fell to the order of 100 000 tons by 1983. Catches of sardine and horse mackerel in the Humboldt system have increased markedly, and the total annual catch of major species in the early 1980s was 6-7 million tons, similar to levels in the mid 1960s.

In the eastern central Atlantic, catches of sardine halved following peak harvests in the mid 1970s (Fig. 17). The combined catch of sardinellas *Sardinella* spp., sardine, horse mackerel, chub mackerel and hake has fluctuated between 1,3 and 2,2 million tons since 1970. In the catches of Morrocan purse-seiners, there is suggestion of alternation between
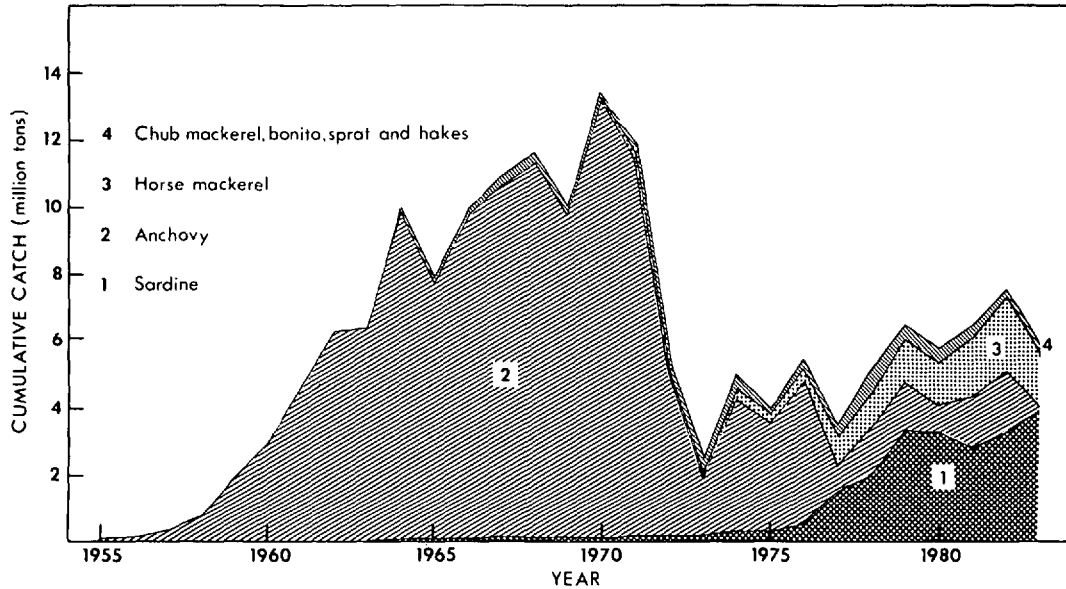
Fig. 16: Cumulative catches of major species from the Humboldt system, 1955-1983 (data from F.A.O. records and Jordán 1983)

species (Belvèze and Erzini 1983, Silvert and Crawford in press).

Large catches of sardine were made off Japan in the 1930s and again from the late 1970s. In the intervening period yields of this species were low, but catches of anchovy, horse mackerel and chub mackerel were much higher than before (Fig. 18, Hayasi 1983). Combined catches were relatively stable throughout the 1950s and 1960s and similar in magnitude to catches of sardine and anchovy in the mid 1930s. The resurgence of the sardine resource, which has been attributed to the outstanding success of the 1972 year-class (Kondo 1980), led to an increase in total yield thereafter.

FOOD AND POPULATION VARIABILITY

Saville (1980) pointed out that there must have been drastic changes in ecology in areas where major pelagic stocks had been reduced to very low levels, and that it would be of considerable importance to know how the food formerly eaten by collapsed stocks was later utilized. In systems with high densities of sardine, anchovy and horse mackerel, there is frequently a close relationship between predator populations and the abundance of their prey, at least for populations such as seabirds for which information is readily available. It may not be unreasonable to assume that populations of consumers lower down the food chain could also be influenced by changes in the availability of forage, possibly being advantaged by an increased food supply (cf. Jones 1983).

A basis for such possible changes in energy flow is provided by the opportunistic feeding of important species, whose distributions frequently overlap (e.g. Crawford 1980). In certain instances there is evidence to suggest that changes in the energy flow have taken place. For example, in the intense perennial upwelling region between Walvis Bay and Lüderitz in the northern Benguela system, it seems likely that pelagic goby replaced large pilchard in the 1970s (Crawford *et al.* 1985). Walsh (1981) commented that, off Peru, the collapse of the anchovy *E. ringens* had apparently led to increases in plankton biomass and in stocks of sardine *S. sagax* and hake *M. gayi*.

Skud (1982) assumed that long-term trends in landings of Atlantic herring *Clupea harengus* and Atlantic mackerel *Scomber scombrus* between the Gulfs of Maine and St Lawrence represented major fluctuations in abundance of the populations, and he found supporting evidence in the form of close agreement between catches and some estimates of abundance. He further demonstrated that, for both
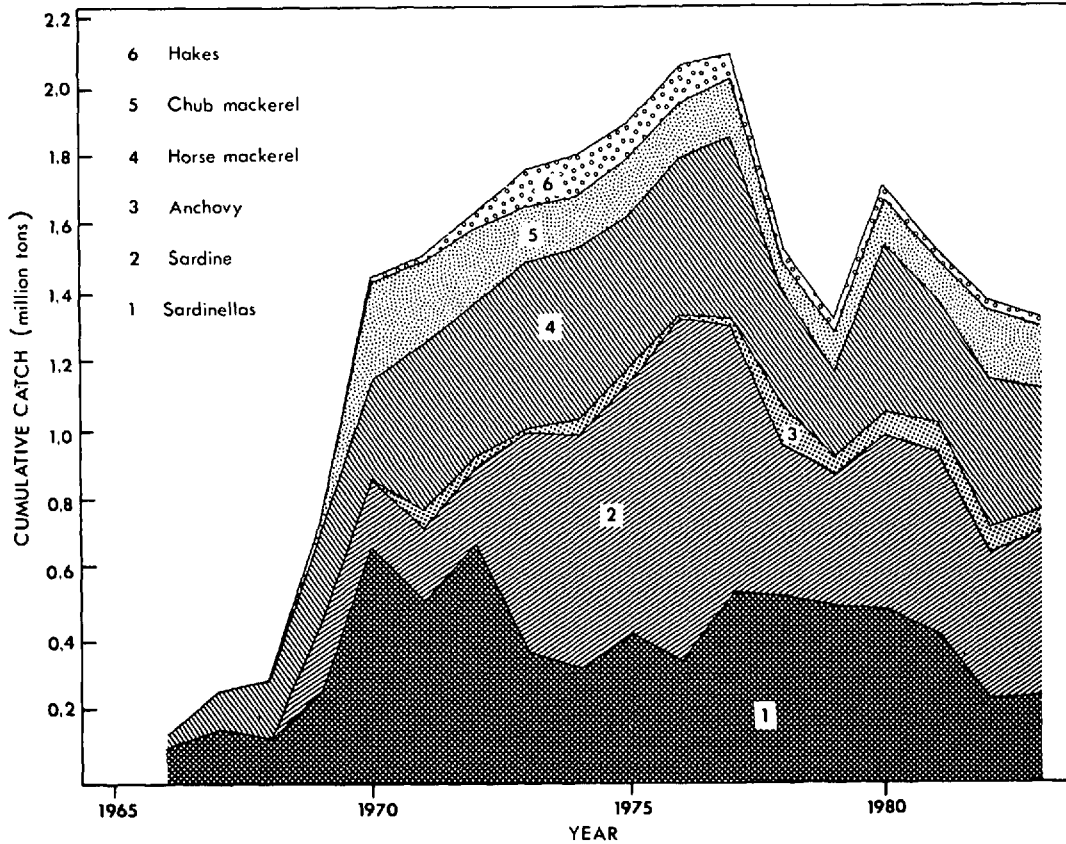
Fig. 17: Cumulative catches of major species from the Canary system, 1966-1983 (data from F.A.O. records)

the herring-mackerel pairing and sardine and anchovy off California, changes in abundance of the dominant species were positively correlated with environmental factors that improved survival, and that abundance of the subordinate species was negatively correlated with the same factors. When dominance changed, the responses of both the formerly dominant and subordinate species also changed. Skud (op. cit.) concluded that the abundance of the subordinate species depended on the density of the dominant species.

Daan (1980) stated that approximately compensatory replacement of sardine by anchovy could not be rejected as a plausible explanation of observed changes off California. Lasker and MacCall (1983) showed that anchovy scales from anaerobic sediments were significantly smaller when the rate of deposition of sardine scales was high, but observed that, although such a relationship was consistent with a hypothesis of competition, there could be other explanations.

Species replacements in catches have been reported for the Canary system and may in some instances have been related to changes in the availability of food, as for example the discarding of huge quantities of fish providing a plentiful food source for cephalopods (Gulland and Garcia 1984).

Modelling has shown that the alternation of species in catches in the five regions considered in this report is not inconsistent with species replacements that might be expected in systems in which production is relatively constant and in which there is a lagged response of fishing effort to changes in fish abundance (Silvert and Crawford in press). However, this need not be the only valid explanation for cyclic changes in fish abundance. MacCall (1980), for example, suggested that weak upwelling from 1947 to 1952 may have resulted in poor year-classes of a number of fish species in the California Current, including anchovy, sardine, chub mackerel and
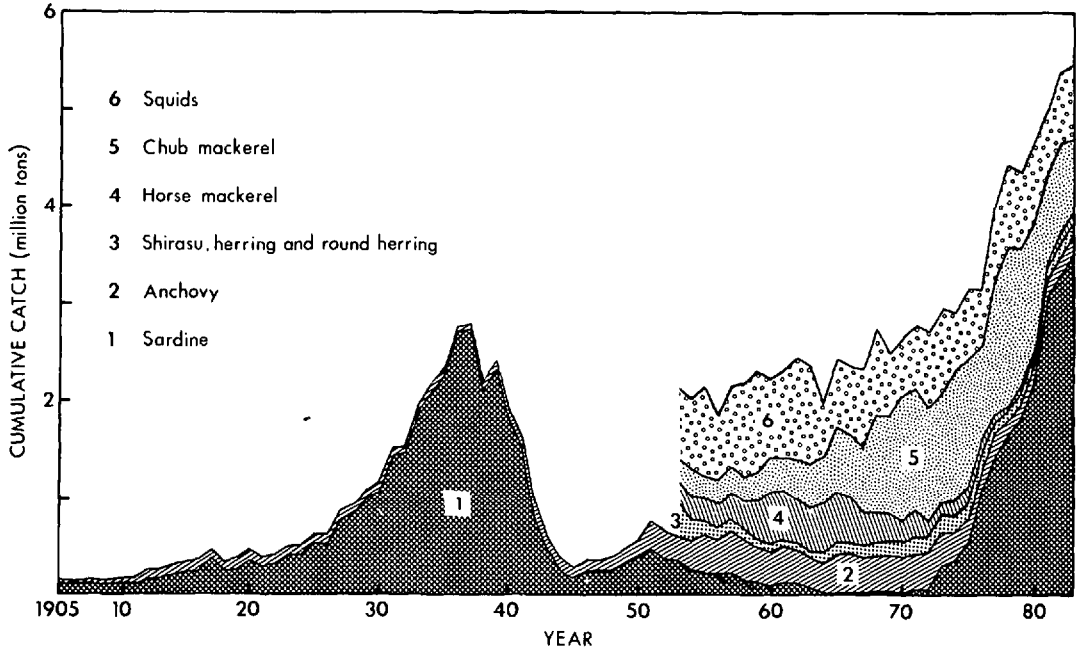
Fig. 18: Cumulative catches of major species from the coastal waters of Japan, 1905-1983 (data from F.A.O. records and Hayasi 1967, 1983)
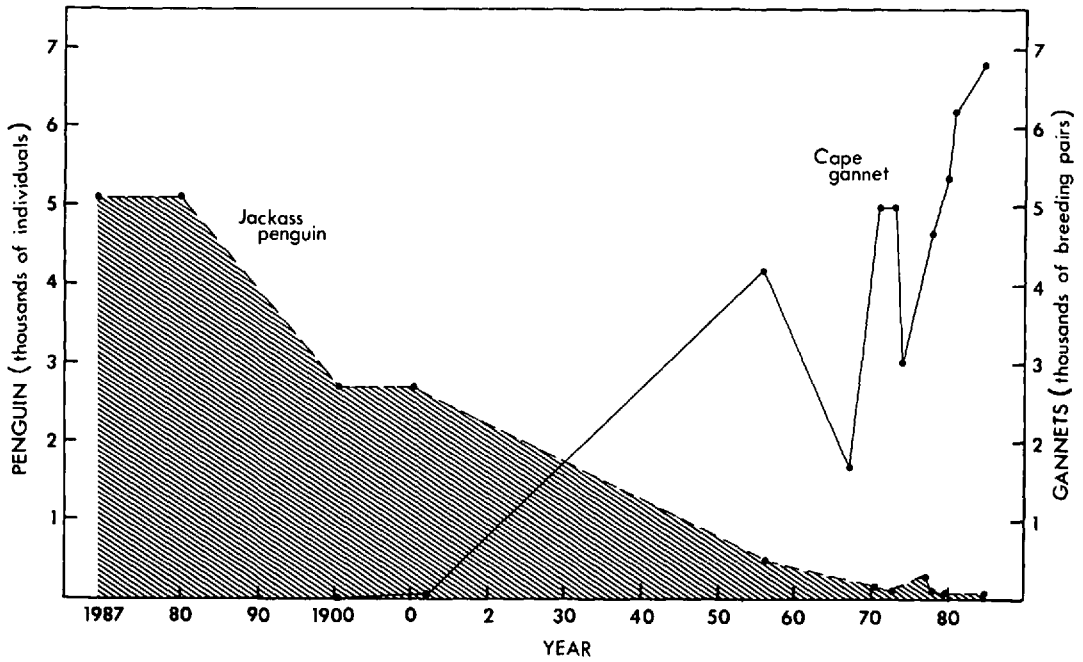

Fig. 19: Trends in numbers of jackass penguins and Cape gannets at Bird Island, Lambert's Bay, 1870-1985 (updated from information in Crawford *et al.* 1983 and Shelton *et al.* 1984)

bonito, and that growth of the anchovy resource through the 1950s and 1960s was simply a recovery of the resource to more usual levels of abundance. Similarly, resource changes in the Canary system may have been environmentally induced (Gulland and Garcia 1984).

Frequently, dogmatism as to whether or not replacement has taken place is precluded by the fact that some species, such as anchovy in the Benguela system, only became important commercial targets after other resources had been severely depleted. However, in this specific instance it is of interest that, at the time of the collapses of the pilchard resources off the southern African coast, both scientists and fishermen regarded anchovy as scarce (Newman 1970, Crawford and Kriel 1985). Anchovy were also scarce in research catches of juvenile fish at inshore stations off the Western Cape during the 1950s, when the pilchard biomass was high (Crawford *et al.* 1987).

Estimates of numbers of two seabird species breeding at Bird Island, Lambert's Bay, in the southern Benguela are available at intermittent intervals since 1870 (Crawford *et al.* 1983, Shelton *et al.* 1984). They show that, at Lambert's Bay, Cape gannets have largely replaced jackass penguins (Fig. 19). The decrease in abundance of penguins was probably initiated by excessive harvests of eggs (Shelton *et al.* op. cit.) and illustrates that human impact on a population can lead to its replacement by another species. In this instance, breeding space was presumably created for gannets, but a plentiful food supply was also available in the vicinity (Crawford and Shelton 1978). Daan (1980) considered that the impetus for replacement in sardine-anchovy complexes could be of oceanographic origin, but that exploitation might also influence replacements.

The prevalence of opportunistic feeding in some of the systems examined suggests that, if the flow of energy was diverted following the collapse of a major resource, it need not be only one species that would benefit from increased availability of food. As an example, it need not necessarily be anchovy that would replace a depleted sardine resource. A number of species could expand following the collapse of a particularly abundant resource. It is likely that, off the Namib coast, the formerly abundant pilchard was replaced by horse mackerel to the north and pelagic goby farther south, with stocks of anchovy and jellyfish, particularly *Chrysaora* sp., probably also increasing (Crawford *et al.* 1985, 1987, Thomas 1985). Off Japan, and in the Humboldt and Benguela systems, the catches of more than one species have increased following the collapses of a particularly abundant resource, in each instance suggesting replacements by more than one species if the increased catches can be assumed to represent trends in
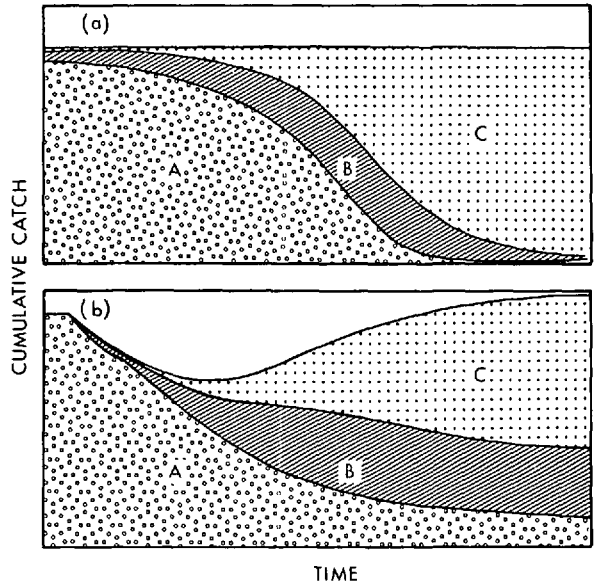

Fig. 20: Simulated changes in the catches of three species subject to different catchability coefficients. Species A was initially dominant, but had the highest catchability. The two subordinate species, B and C, were initially equally abundant, but B was subject to a higher catchability than C. (a) assumes a constant production and an equivalent constant loss from the combined resources. (b) is an extension of the model of Silvert and Crawford (in press) to include three species. In both instances, Species C became the main replacing species

abundance.

If the collapse of a species can lead to its replacement by more than one species, it is of interest to know what factors could influence the likelihood of a particular species replacing the once-dominant resource. Intuitively one might expect that a subordinate species subject to heavy mortality through predation or fishing would be less likely to be the main replacing species than one utilized less intensively.

In a simple simulation of three competing species, assuming a constant overall production and an equivalent constant overall loss to predators and fisheries, a dominant species was forced to decrease. The two subordinate species were initially at the same level of abundance, but they were subject to different rates of utilization, and it was the species initially utilized least intensively that gained eventual dominance (Fig. 20a). A similar result was obtained with the model of Silvert and Crawford (in press), expanded to allow for three species (Fig. 20b). This model is also based on constant production, but
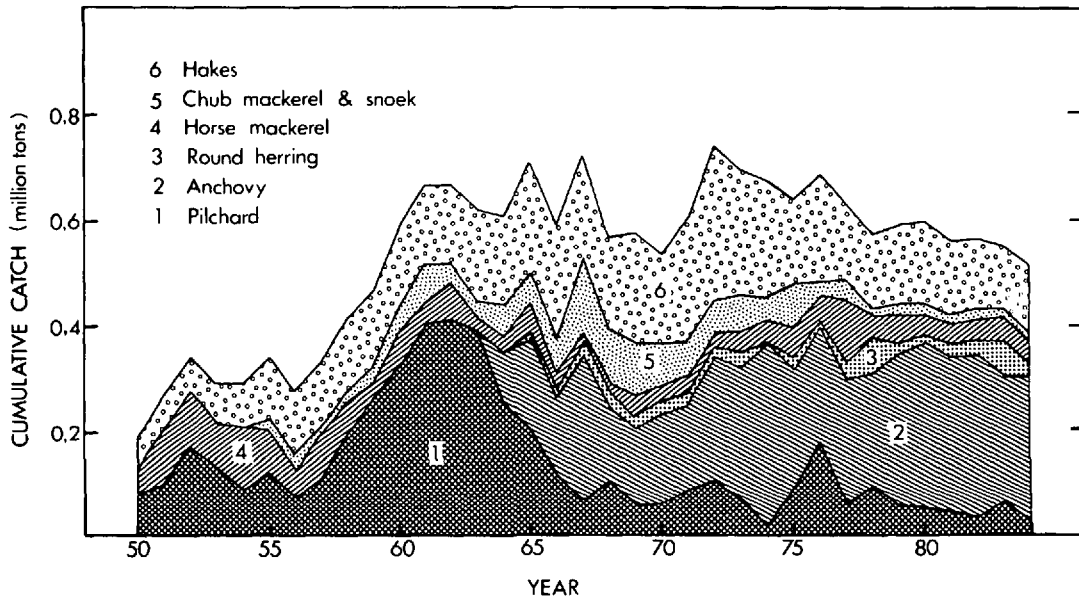
Fig. 21: Cumulative catches of major species groups in the southern Benguela, 1950-1984, illustrating the replacement of pilchard by anchovy (after Crawford et al. 1987)

changes in effort (fishing and predation) directed at any particular species are computed as a function of both stock size and effort, it being assumed that the level of effort at any one time will depend on the previous level of effort and on the size of the resource.

Cool, highly turbulent, weakly stratified water at the centre of the Benguela system forms a major environmental barrier that effectively divides the system in two (Shannon 1985) and, for many species, stocks in the northern and southern regions may be regarded as relatively independent (Crawford et al. 1987). At different times, collapses of pilchard have occurred in both regions, with replacement in the catches being mainly by anchovy in the south (Fig. 21) and horse mackerel in the north (Fig. 22). In the north, anchovy was exploited as heavily as possible when catches of pilchard were decreasing in order to minimize competition (Butterworth 1983), whereas in the south, introduction of a small-mesh net and the close proximity of processing plants to nursery grounds led to heavy exploitation of young horse mackerel and early depletion of strong year-classes of this species (Crawford et al. op. cit.). Therefore, in both regions species initially exploited intensively were not the main replacing species.

CONCLUSIONS

The prevalence of opportunistic feeding in the five systems examined in this report suggests that changes in the flow of energy may well occur when the systems are subject to large perturbations. Populations may respond to changes in the availability of food and it may not be unreasonable to interpret species replacements in catches as reflecting shifts in the dominance of species. Generalized feeding creates the possibility that more than one species may benefit from energy made available by the collapse of an abundant resource, and the likelihood of a particular organism becoming the main replacing species will probably be influenced by the degree to which it is utilized both by man and natural predators during and after the collapse of the originally dominant resource.

The greater the degree of catholicism in the diet of a species, the better buffered it is likely to be against large changes in the composition of species within a system. In this respect, there appear to be advantages in being able to forage over a wide range both vertically and horizontally. Seabirds are generally unable to feed at great depths and, when breeding.
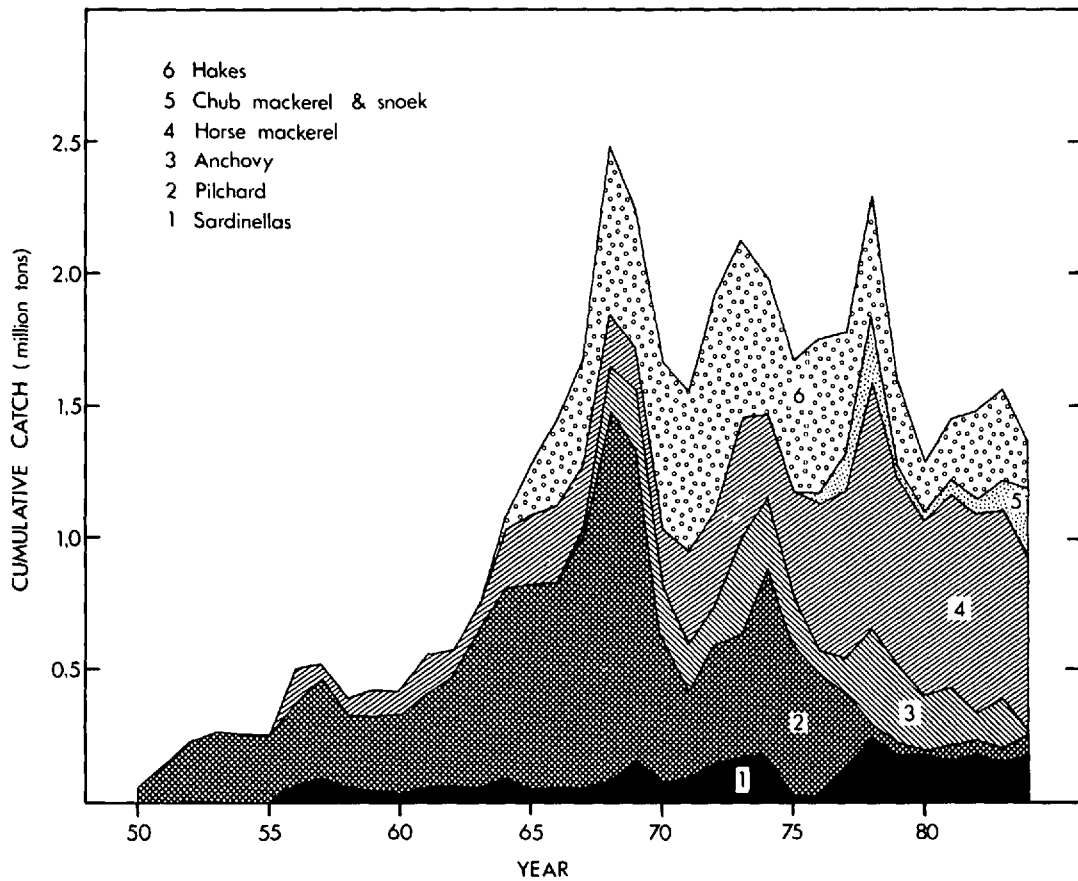
Fig. 22: Cumulative catches of major species groups in the northern Benguela, 1950-1984, illustrating the replacement of pilchard by horse mackerel (after Crawford *et al.* 1987)

may also have a limited horizontal foraging range (e.g. Frost *et al.* 1976). Although, in some instances, seabirds have been able, to a certain extent, to adapt the size of prey ingested (e.g. Crawford *et al.* 1985), they provide some of the best examples of populations being limited by the availability of food.

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