

Factors influencing population trends of some abundant vertebrates in sardine-rich coastal ecosystems

R. J. M. Crawford

To cite this article: R. J. M. Crawford (1991) Factors influencing population trends of some abundant vertebrates in sardine-rich coastal ecosystems, South African Journal of Marine Science, 10:1, 365-381, DOI: [10.2989/02577619109504645](https://doi.org/10.2989/02577619109504645)

To link to this article: <http://dx.doi.org/10.2989/02577619109504645>



Published online: 08 Apr 2010.



Submit your article to this journal [↗](#)



Article views: 162



View related articles [↗](#)



Citing articles: 8 View citing articles [↗](#)

FACTORS INFLUENCING POPULATION TRENDS OF SOME ABUNDANT VERTEBRATES IN SARDINE-RICH COASTAL ECOSYSTEMS

R. J. M. CRAWFORD*

Many abundant populations of vertebrates in sardine-rich coastal ecosystems have experienced large changes in population sizes. This has led to wide fluctuations of some fish harvests and concern over the conservation status of some top predators. Research over the past 20 years into the causes of population changes of some abundant fish species, some southern pinnipeds and the most important guano-producing seabirds is briefly reviewed. Particular emphasis is given to populations off south-western Africa. Fish populations have been influenced in a complex manner by a variety of factors, including fishing, biological interactions and environmental change. Climate, operating at a basin scale, is probably an important cause of large and long-term changes in the abundance of some sardine populations. The impact of anticipated climate change on sardine-rich ecosystems is expected to receive emphasis in the future. The populations of some pinnipeds and seabirds were drastically reduced by former excessive harvests. Whereas pinnipeds have tended to recover under regimes of controlled exploitation, the numbers of some seabirds have continued to decrease even in the absence of exploitation. Various factors have contributed to the ongoing decreases, including competition with fisheries for prey resources and competition with pinnipeds for breeding space. The 1980s saw the introduction of legislation specifying conservation of marine ecosystems as a management objective in Antarctica and South Africa. Means of achieving this objective, given the biological interactions at the upper end of the trophic pathway, are expected to provide another focus for future research.

Etlike volop bevolkings van gewerweldes in sardynryk kus-ekostelsels het groot veranderinge in bevolkingsterkte ondervind. Dit het gelei tot wye skommelinge in sommige vissoeste en besorgdheid oor die bewaringstatus van sommige spitsroofoiere. Navorsing die afgelope 20 jaar oor die oorsake van bevolkingswisselinge van etlike volop visspesies, verskeie suidelike vinpotiges en die vernaamste ghwanolewende seevoëls word kortweg in oënskou geneem. Klem word veral gelê op bevolkings teenoor suidwestelike Afrika. Visbevolkings is op 'n ingewikkelde wyse deur 'n verskeidenheid faktore beïnvloed, visvangs, biologiese wisselwerking en omgewingsverandering ingesluit. Klimaat, werksaam op oseaankomskaal, is stellig 'n belangrike oorsaak van groot en langtermynse wisselinge in die talrykheid van sommige sardynbevolkings. Na verwagting sal daar in die toekoms klem gelê word op die uitwerking van die verwagte klimaatverandering op sardynryk ekostelsels. Die bevolkings van sommige vinpotiges en seevoëls is drasties verminder deur vorige oormatige oeste. Hoewel vinpotiges geneig was om te herstel onder regimes van beheerde benutting, het die getalle van sommige seevoëls steeds bly daal, selfs sonder benutting. Verskeie faktore het tot die aanhoudende daling bygedra, waaronder mededinging met visserye om prooiuipbronne en met vinpotiges om broeiruimte. In die 1980s is wetgewing deurgevoer wat bewaring van mariene ekostelsels in Antarktika en Suid-Afrika as doelwit vermeld. Middelste om hierdie doelwit te behaal, gegee die biologiese wisselwerkings aan die bopunt van die voedselleer, sal stellig 'n verdere fokuspunt vir toekomstige navorsing bied.

Sardines are abundant in six of the world's subtropical coastal regions (Fig. 1). Their taxonomy, biochemical genetics and zoogeography have recently been reviewed, and it now appears that just two species may be involved: *Sardina pilchardus* of the north-east Atlantic and the Mediterranean, and *Sardinops sagax* of the Californian and Humboldt systems in the eastern Pacific, the Japan region, Australasia and southern Africa (Parrish *et al.* 1989). In five of the six regions, the sardines have expanded their ranges over large areas at times when they have been particularly abundant (Lluch-Belda *et al.* 1989). There is little information for the sixth, the Australasian region. For example, the distribution of *S. pilchardus* off north-west Africa extended south to

28°N in 1966, but as far south as 15°N in the mid 1970s (Garcia 1982). Therefore, the distribution of sardines is not fixed but fluid. Areas that have an abundance of sardines at one time may not at another, and organisms that are coincidentally sympatric with sardines may vary with time.

There are, nevertheless, many similarities in the vertebrate fauna of the six regions where sardines are found (see Parrish *et al.* 1983). The fish assemblage is dominated by a small number of species that includes four types of small pelagic fish, sardines, anchovies *Engraulis* spp., horse (jack) mackerels *Trachurus* spp. and chub mackerels *Scomber* spp. (Parrish *et al.* 1989, Collette and Nauen 1983). The demersal hakes *Merluccius* spp. are plentiful in five of the systems, being

* Sea Fisheries Research Institute, Private Bag X2, Rogge Bay 8012, South Africa
Manuscript received: August 1990

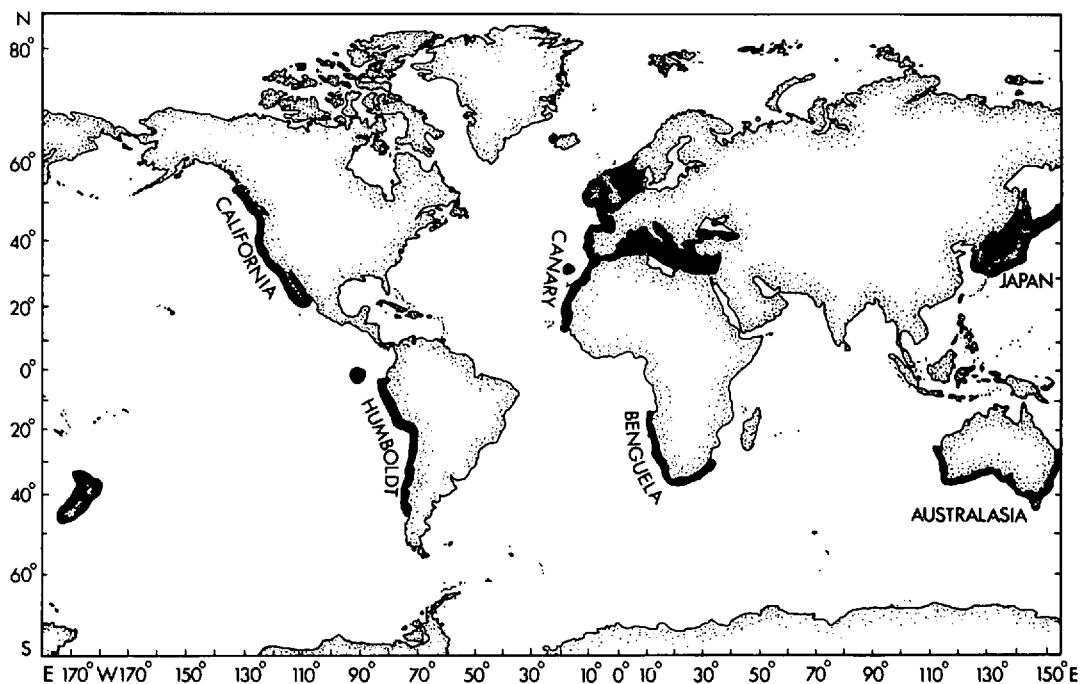


Fig. 1: The world distribution of sardines *Sardinops* and *Sardina* (from information in Lluch-Belda *et al.* 1989, Parrish *et al.* 1989)

absent only off Japan (Inada 1981).

Pinnipeds are well represented in all six regions inhabited by sardines (King 1983). Different species of sea lion are found off Japan, western America and Australasia. The northern fur seal *Callorhinus ursinus* breeds north of Japan and off California, and fur seals of the genus *Arctocephalus* in each of the three southern hemisphere systems. Grey seals *Halichoerus grypus* occur off western Europe, and harbour seals *Phoca* spp. in the three northern hemisphere systems. The Mediterranean monk seal *Monachus monachus* is found off western North Africa and in the Mediterranean, while northern elephant seals *Mirounga angustirostris* breed in the Californian system.

Seabirds are other conspicuous and well known predators in sardine-rich areas, perhaps especially so in the Benguela and Humboldt systems, the world's only two regions where seabird guano is collected commercially on an annual basis (Crawford and Shelton 1978, Duffy 1983). The guano harvests are sustained by large populations of piscivorous birds, notably Pelicaniformes of four genera — the similar gannets *Morus* sp. and boobies *Sula* spp., cormorants *Phalacrocorax* spp., and pelicans *Pelecanus* spp. Both the Benguela and Humboldt systems also support endemic penguins of the genus *Spheniscus* (Duffy *et al.* 1984, Randall 1989). Penguins are absent

in the three sardine-rich regions of the northern hemisphere, but various Alcidae (auks, guillemots, puffins) are often abundant (see Evans 1984, Hasegawa 1984, Jehl 1984).

Many of the more numerous vertebrates have undergone large-scale changes in abundance. Fluctuations in fish stocks have led to massive changes in catches, e.g. differences between the highest and the lowest annual catches of sardines and anchovies in five of the six regions add up to more than 29 million tons (Lluch-Belda *et al.* 1989). Some of the predators, especially the land-breeding seals and seabirds, have at times reached low levels of abundance. This has led to concern over their conservation status. For example, five species of seabird breeding in South Africa are listed in the most recent edition of that country's red data book (Brooke 1984).

For such commercial and conservation reasons, the large changes in population sizes have attracted widespread research attention. The similarities in the species assemblages in the various regions have led to considerable interest in comparative studies of factors influencing change (Parrish *et al.* 1983). To review all literature dealing with causes of change exhaustively would be an enormous undertaking, which is not the purpose of this paper. Rather, in keeping with the theme of the symposium at which this paper was pre-

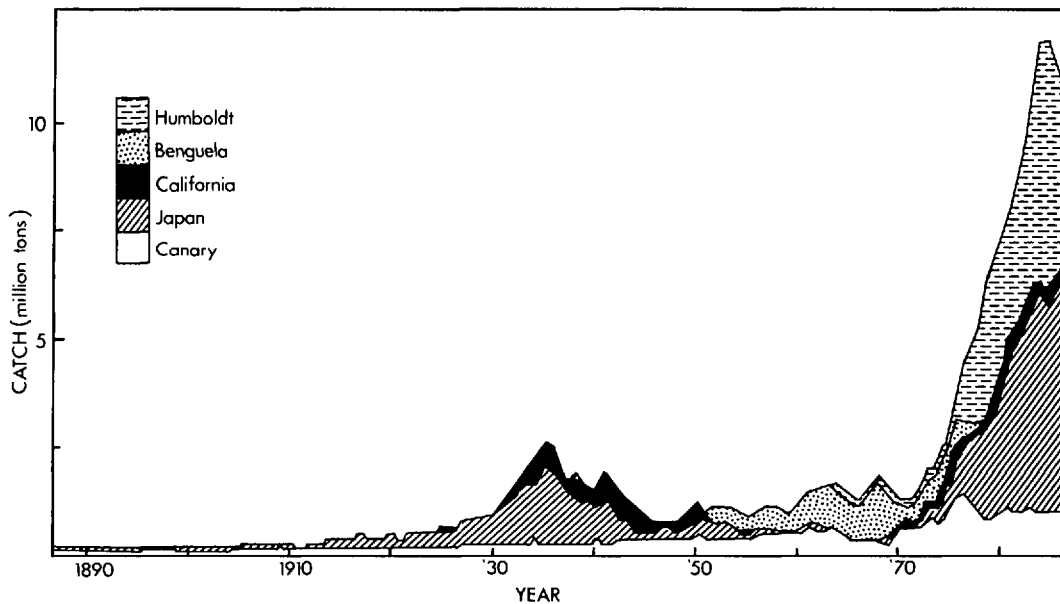


Fig. 2: Recorded catches of sardines *Sardinops* and *Sardina* from five regions of the world between the late 1800s and the 1980s

sented, it is intended to sketch development of thought over the past two decades and to speculate on directions that research may take in the next 20 years, particularly with regard to some of the more abundant vertebrates and in the context of the Benguela system (including the Agulhas Bank). Some of the abundant fish species will be considered first, followed by a few of the southern pinnipeds and then the guano-producing seabirds. Finally a few likely future research directions will be highlighted.

SOME ABUNDANT FISH SPECIES

Trends in the catches of sardines, anchovies and horse mackerels from five regions (excluding Australasia) are shown in Figures 2–4 respectively. Sources of information are the same as those listed in Lluch-Belda *et al.* (1989). Sardine catches peaked in the mid 1930s as a result of good catches off Japan and California, but decreased markedly after World War II. In the 1960s the bulk of the sardine catch came from the Benguela system (where the sardine is commonly known as pilchard), but catches there decreased in the 1970s whereas sardine catches in the Japanese, Californian, Humboldt and Canary systems increased. The result was that sardine catches attained a higher level in the 1980s than in any previous period,

with an annual take of more than 10 million tons.

Catches of anchovies were relatively low until the late 1950s. Then a large fishery developed off Peru, and a lesser one off Chile. As a result of these fisheries, the world catch of anchovies was well over 10 million tons in the late 1960s and early 1970s. However, the fisheries of the Humboldt system collapsed and catches of anchovies from the five regions fell to <2 million tons in the early 1980s.

Catches of horse mackerels were low until 1950, but then they increased off Japan and remained high until the early 1960s. From the 1970s, catches off Japan decreased, but they increased in the Benguela, Humboldt and Canary systems. In the early 1980s, catches of horse mackerel from the five regions were of the order of 3 million tons.

Combined catches of sardines, anchovies and horse mackerels from the five regions have shown a high degree of variability, particularly since 1950. However, because of a recent upswing in yields of sardines and horse mackerels, catches attained a maximum in the 1980s of some 20 million tons (Fig. 5) — about a quarter of the world's catch of marine fish.

Fishing

The collapses of the sardine fisheries off Japan and California after World War II stimulated much interest

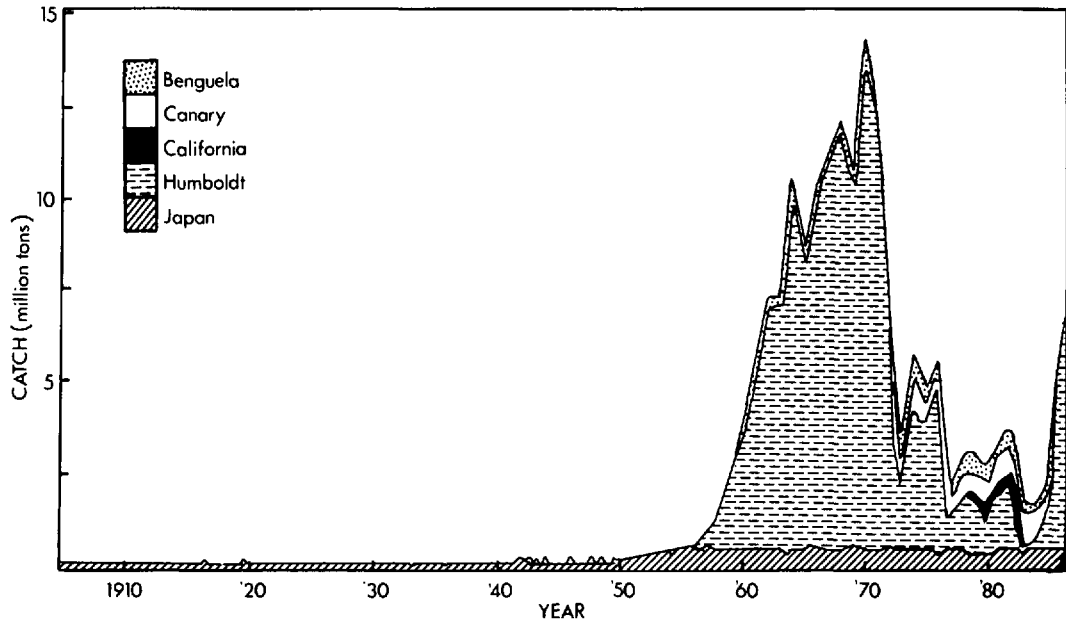


Fig. 3: Recorded catches of anchovies *Engraulis* spp. from five regions of the world in the 20th century

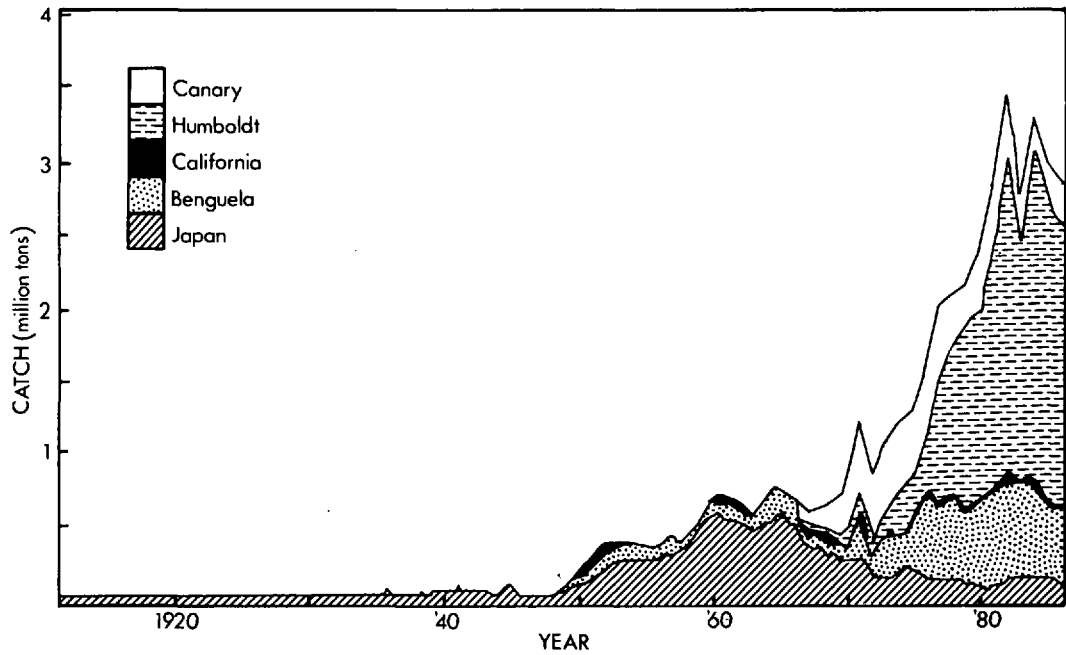


Fig. 4: Recorded catches of horse mackerels *Trachurus* spp. from five regions of the world in the 20th century

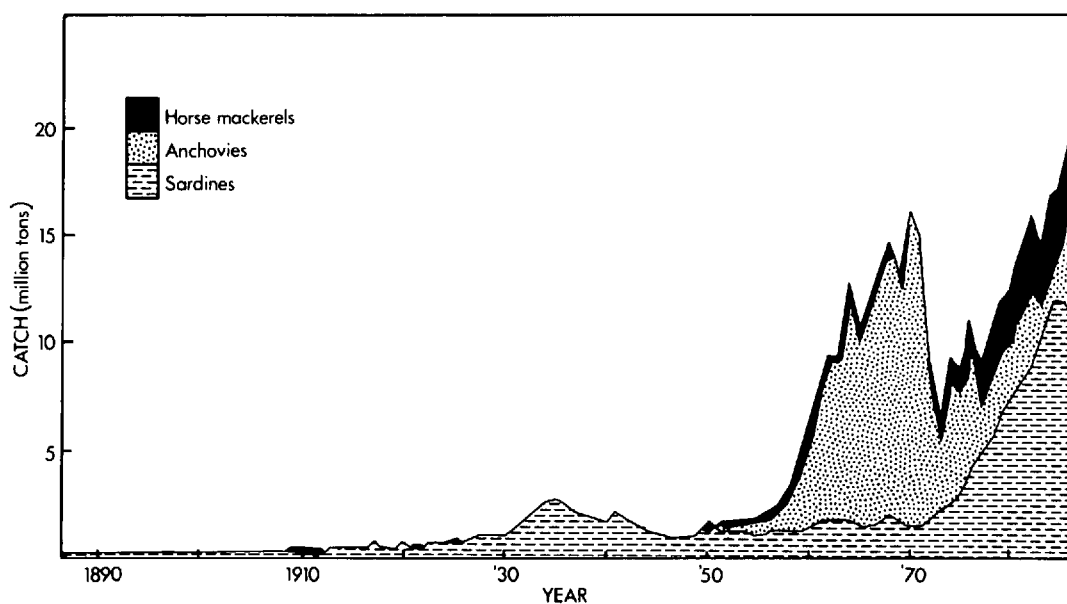


Fig. 5: Cumulative recorded catches of sardines *Sardinops* and *Sardina*, anchovies *Engraulis* spp. and horse mackerels *Trachurus* spp. from five regions of the world from the late 1800s to the 1980s

in the causes of population variability. Fishing pressure and environmental change were both invoked as possible reasons for the collapses (see Clark and Marr 1955). Murphy (1966), and later MacCall (1976), drew attention to the inverse relationship between sardine abundance and the catchability coefficient (the fishing mortality inflicted per unit of fishing effort) in the Californian fishery. Similar relationships have been demonstrated in the sardine fisheries of the Benguela system (Butterworth 1983, Shelton and Armstrong 1983). They have been attributed to the tight schooling behaviour of sardines (and some other pelagic species). They mean that modern fleets, with fish-finding aids and inter-ship communication, can rapidly locate what remains of a depleted stock and, for a period, take catches similar to harvests made when the stock was at a much higher level of abundance (Saville 1980). This forces the stock down even further.

In 1978, a symposium on the assessment and management of pelagic fish stocks, held at Aberdeen in Scotland, emphasized the impact of fishing on pelagic fish stocks. Saville (1980, p. 513) commented "Perhaps the most striking conclusion to be drawn from the papers which review the development of the pelagic fisheries is that there are few pelagic stocks

left in the world's oceans which have been subjected to modern fishing technology, whose current state does not give cause for alarm . . .". Saville continued "In some instances environmental changes may have played a part in the decline of the pelagic stocks . . . but generally their influence would appear to have been minor compared with the effects of fisheries."

Biological interactions

Sardines, anchovies and horse mackerels have not yet contributed high catches at the same time in any of the five regions where they co-occur and have been intensively fished. Although some fisheries developed later than others, e.g. the anchovy fisheries in the Benguela system started as the sardine fisheries there were collapsing (Crawford *et al.* 1987), in many instances there is sufficient information to indicate that the three species have not been simultaneously abundant. Few would assert that sardine was plentiful in the Humboldt system when very large catches of anchovy were being made there (Serra 1991). Indeed, surveys of fish larvae indicate otherwise (Loeb and Rojas 1988). Off Japan, sardine was scarce when high catches of anchovy and horse mackerel were being

made (Chikuni 1985). Overlapping distributions and similarities in diets of the three genera for much of their lifespan (see references in Crawford 1987) provide grounds for interpreting the changes in abundance as replacement of one or more of the species by others (Daan 1980).

It has proved possible to replicate observed changes in catches of the three species with a simple model that assumes the species compete with each other and that there is a lag in the response of fishing effort to altered levels of fish abundance (Silvert and Crawford 1988). Skud (1982) showed that changes in abundance of sardine and anchovy when they were dominant off California were correlated with environmental factors, such as upwelling, that apparently improved survival, but when either species was dominated by the other the signs of the correlations were reversed. In other words, abundance was negatively related to favourable conditions. He concluded that the abundance of the subordinate species depended on the density of the dominant one.

Other biological interactions that have attracted interest include predation of ichthyoplankton by the same species (i.e. cannibalism of eggs and larvae) or by one occupying a similar trophic position (e.g. consumption of anchovy eggs by sardine), and predation of planktivorous fish by species at a higher trophic level. Over the Agulhas Bank, cannibalism of eggs by adult anchovy has been estimated to account for 70 per cent of the total egg mortality and is related to the density of parents (Valdés *et al.* 1987). Cannibalism is also an important cause of mortality of anchovy eggs off Peru (Alheit 1987) and California (MacCall 1981). Other density-dependent responses have been observed for epipelagic fish in the Benguela system (Crawford *et al.* 1980b, Armstrong *et al.* 1989). Higher up the food chain, MacCall *et al.* (1985) considered an increased mortality rate of anchovy due to predation by chub mackerel a likely cause of a severe reduction in anchovy abundance off California. Predation by snoek *Thyrsites atun* may have had an impact on the anchovy resource of the southern Benguela system (Crawford and De Villiers 1985).

Environmental influences

The impetus for the change in dominance of fish species is of great interest. The reduction of one stock by heavy fishing may lead to its replacement by others (Crawford 1987). However, changes in the relative abundance of larvae of non-fished mesopelagic species in the Humboldt system in 1969/70, at a time when sardine was replacing anchovy as the dominant species, suggests that the environment may have been

exerting an influence on fish populations there (Loeb and Rojas 1988). In the southern Benguela system there was poor survival of sardine ichthyoplankton at a time when the anchovy was increasing, also pointing to environmental modulation of the populations (Crawford, Siegfried *et al.* 1990). Even in the absence of fishing, there has been considerable variability of fish resources in sardine areas (Soutar and Isaacs 1974, Crawford and Shelton 1978).

Two papers presented at the Aberdeen symposium of 1978 drew attention to the importance of the environment in influencing population trends of sardines and anchovies. Recovery of the Japanese sardine was attributed to the formation of a powerful year-class in 1972, as a result of a shift in the Kuroshio Current creating good foraging conditions for, and increasing the survival rate of, post-larvae (Kondo 1980). At about the same time that the Japanese sardine was initiating its recovery, the Peruvian anchovy collapsed. Csirke (1980) showed that there was a poor relationship between spawner biomass and recruitment when the density of spawners was ignored, but that predictions of recruitment improved when the density of spawners was taken into account. The density was affected not only by stock size, but also by environmental conditions. In years when El Niños occurred, the stock tended to be concentrated and recruitment depressed.

In 1983, an Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources was convened at San José, Costa Rica. In his paper, Kawasaki (1983) drew attention to the remarkable similarity in trends of catches of sardines in the three regions of the Pacific Ocean where they are found — in the Humboldt, Californian and Japanese systems. He suggested that the populations were being simultaneously influenced by climate operating at a basin scale. Subsequent application of Box-Jenkins statistics to the catch records has shown that the various series are significantly related to each other at the exact lags that would be expected from the various ages at which sardines recruit to the different fisheries (Crawford *et al.* 1991). This provides empirical support for Kawasaki's hypothesis. However, the way in which climate is influencing the sardines remains uncertain. There is some suggestion that changes in sea surface temperature may alter the extent of habitat available to sardines, thereby giving rise to the large changes in range which have been associated with changes in abundance (Lluch-Belda *et al.* 1989).

In the four major eastern boundary currents, sardines and anchovies tend not to spawn in areas of strong offshore surface transport, where ichthyoplankton would be removed from the coastal region, or in areas of intense turbulence, where food particles

would be dispersed (Parrish *et al.* 1983). In the Benguela system, empirical data suggest that the environment favours either epipelagic fish species, such as sardine and anchovy, or groundfish species such as hakes, but not both groups simultaneously (Shannon *et al.* 1988). Powerful year-classes of epipelagic fish have been associated with warm conditions, which perhaps facilitated either transport of ichthyoplankton between spawning and nursery grounds or larval retention. The strongest year-classes of Cape hakes *M. paradoxus* and *M. capensis* have been formed in cooler conditions. In warm periods the stocks may be compacted, leading to a greater degree of cannibalism of young hake by adults. Off California, retention of larvae is important for formation of good year-classes of Pacific hake *M. productus* (Bailey 1981). Again in this system, half the pelagic biomass appears to be sensitive to cool conditions and the remaining half to warm conditions. Hake and chub mackerel do well in warm years, whereas anchovy do better in cool years (Ware and McFarlane 1989), so the response is somewhat different from that in the Benguela system. In the Humboldt system, the area of distribution of the Peruvian hake *M. gayi* increases markedly during El Niños, i.e. warm conditions, and this is thought to decrease cannibalism of young by adults (Espino and Wosnitza-Mendo 1988).

SOME SOUTHERN PINNIPEDS

In the Benguela system the number of South African (Cape) fur seals *A. pusillus pusillus* has increased during the 20th century, a trend attributed to recovery of the population after it had been reduced to a low level by uncontrolled exploitation during the 17th-19th centuries (David 1989). By early in the 20th century, seals had been extirpated at 23 islands where they had formerly bred (Shaughnessy 1984). Four of these islands have since been recolonized (Crawford *et al.* 1989). Seals have also initiated breeding at six mainland localities where they did not breed formerly, probably because of the presence of terrestrial predators, including man. Establishment of diamond security areas and the removal of predators has now created disturbance-free zones suitable for colonization by seals (Best and Shaughnessy 1979, David *op. cit.*). High mortality of pups has resulted from excessive disturbance of breeding animals by man (Kruger 1949).

The establishment of mainland colonies may represent relocation of some of the herds from islands where breeding no longer takes place (Best and Shaughnessy 1979). However, the large mainland

colonies at Wolf and Atlas bays are opposite Long Islands (Fig. 6), for which Kruger (1949, p. 603) comments "Sealing expeditions were undertaken during the winter and summer months of 1948 but, in both cases with less success than during the previous year. . . . seals had to a large extent left the principal seal preserve at Long Island for the mainland, which is inaccessible." Therefore, the colonies at Wolf and Atlas bays may have been formed as a result of disturbance at Long Islands caused by sealing. Later, sealing disturbance at Wolf and Atlas bays may in turn have triggered recolonization of Mercury Island (Crawford *et al.* 1989). The ability of South African fur seals to colonize new areas, and in particular to breed successfully at mainland sites with restricted access by humans, has doubtlessly facilitated the recovery of overall population numbers.

South African fur seals eat many fish species targeted for by large commercial fisheries (David 1987). They have adapted to reduced stocks of some of these species by concentrating on alternative prey, and also feed prolifically at commercial fishing boats on fish trapped in or spilt from nets (Shaughnessy 1984, Crawford and Payne 1989).

Off Peru, the southern sea lion *Otaria byronia* and South American fur seal *A. australis* had been greatly reduced by exploitation by the early 1950s. Rough estimates of total numbers of both species were between 400 000 and 500 000 individuals in 1940, but the combined populations were only about 12 500 in 1961. Populations have since increased and there were about 49 200 animals in 1984. Except for the period 1971-75, harvesting of the fur seal has been prohibited since 1950, and of the sea lion since 1956. During the 1982-83 El Niño event, there was high mortality of fur-seal pups, with near zero survival of those born between October 1982 and March 1983. It is thought that the pups starved as a result of reduced availability of food for females, which were therefore unable to provide the pups with enough milk. Juvenile and adult mortalities were also higher in 1982-83 than in normal years. There was a decrease in the fur-seal population between 1968 and 1971, possibly because of a greatly reduced biomass of anchovy during this period. In the period of low abundance of anchovy after 1971, both the fur-seal and sea-lion populations expanded rapidly, making use of alternative food resources (Muck and Fuentes 1987). These alternative resources may have expanded to fill the niche formerly utilized by anchovy.

The population trends of pinnipeds in two of the southern hemisphere areas where sardines are plentiful (the Humboldt and Benguela systems) both appear to have been primarily influenced by exploitation. It is likely that food shortage

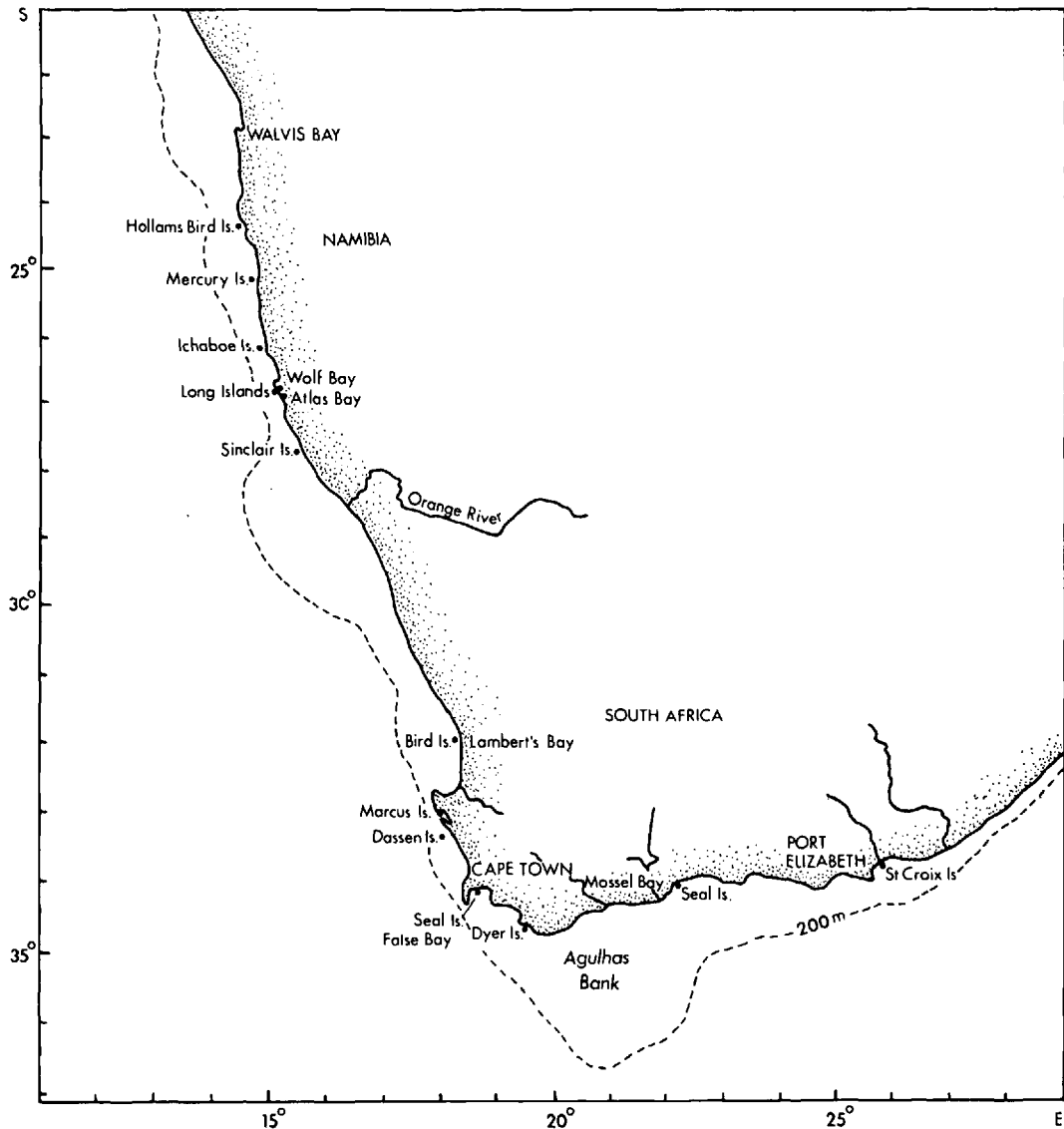


Fig. 6: The locations of some southern African places referred to in the text

has also had an important impact in some cases.

Thus:

$$N_t = N_o + B - D \quad (1)$$

GUANO-PRODUCING SEABIRDS

In a closed population, the number of seabirds at some time t (N_t) can be represented as the number at some earlier time (N_o) augmented by subsequent births (B) and reduced by subsequent deaths (D).

In monogamous seabirds, the number of births (taken as equivalent to the number of eggs produced) will be a function of the mean number of breeding pairs (P), the mean clutch size (C) and the mean number of layings (L) by each breeding pair. The number of breeding pairs will usually be a variable proportion

of the number of adults in the population. The number of deaths will be the sum of the deaths occurring during the different stages of development. Four major stages can be identified: eggs, chicks at nest, immature birds and adults. If deaths in these categories are represented by D_e , D_c , D_i and D_a respectively, the population equation can be rewritten as:

$$N_t = N_o + (P.C.L) - (D_e + D_c + D_i + D_a) \quad (2)$$

The population will respond to changes in any of the parameters affecting the number of births or deaths, which may in turn be influenced by a variety of factors. Those that have been identified include the supply of food (Crawford 1987), the availability of suitable breeding sites (Crawford *et al.* 1989), predation, including human exploitation (Berruti 1986, Randall 1989), disease (Crawford *et al.* 1980a), disturbance (Hockey and Hallinan 1981) and environmental factors, including pollution (Crawford *et al.* 1986, Randall and Randall 1986).

Availability of food as a limiting factor

For seabirds in tropical systems, and some species at higher latitudes, Ashmole (1963) considered that supply of food was the factor most likely to be regulating population numbers. In sardine-rich systems, the importance of food in influencing trends of seabird populations has also often been emphasized (Jordán 1967, Crawford and Shelton 1978, 1981, Anderson *et al.* 1980).

Ashmole (1963) believed that the major influence of food was on the output of young, through affecting breeding success (i.e. D_e and/or D_c), or the rate of recruitment of adults to the breeding population (i.e. P), or both. He thought it less likely that food affected the mortality of adults (D_a) or fledged young (D_i). In agreement with this perspective, adult mortality in the Benguela system has usually been regarded as low. For example, Furness and Cooper (1982) assumed annual adult mortalities for African penguins *S. demersus*, Cape gannets *M. capensis* and Cape cormorants *P. capensis* to be 13, 10 and 20 per cent respectively. Over a six-year period, Randall (1989) estimated annual mortality of adult African penguins at St Croix Island to be 7 per cent. At Dyer Island, a maximum value of 31 per cent has been reported (La Cock and Hänel 1987). At Marcus Island, between 1979 and 1985, estimates of the mortality of adult African penguins were much higher — between 30 and 67 per cent per annum (La Cock *et al.* 1987). However, this seems to have been an exceptional case, and mortality may well have been overestimated if birds were dis-

placed elsewhere, or if they did not return to Marcus Island to breed. For some longlived seabirds there may be interannual variation in the proportion of adults breeding (Coulson 1984).

In the Humboldt system, a shortage of food brought about by El Niños has often been thought to reduce seabird populations rapidly (Tovar and Galarza 1983, Hays 1986), but again it is likely that the observed reductions can be partially explained by birds failing to return to nesting colonies to breed. For example, the measured increase in the Chilean population of Humboldt penguins *S. humboldti* after the 1982–83 El Niño was too great to be attributed to reproduction alone, and mortality of adult penguins during that El Niño is now considered less than was originally envisaged (Araya and Todd 1988). Adult mortality will probably only occur during periods of extreme food shortage (Cairns 1987), but it may still be higher in the variable Benguela and, especially, Humboldt systems than in some other coastal environments.

Cairns (1987) has postulated that, when food is slightly more plentiful, but still scarce, many birds may not breed and, for those that do, the breeding success may be low, i.e. P , D_e and D_c may be influenced. Off Peru, Humboldt penguins did not breed during the El Niño conditions of 1983 (Hays 1986). Off western South Africa, a weak anchovy year-class was formed in 1989 (I. Hampton, Sea Fisheries Research Institute, pers. comm.). During the 1989/90 seabird breeding season, many fewer Cape cormorants than normal attempted to breed (Fig. 7). The species preys extensively on anchovy off western South Africa (Duffy *et al.* 1987). In the same region Cape gannets were seemingly less affected (pers. obs.), although anchovy was also one of their major prey items in the 1980s (Berruti 1987). Off Peru, El Niños decrease the availability of anchovy to seabirds and cause a 35 per cent desertion of nesting areas by the main guano-producing seabirds at intervals of about five years (Duffy 1983).

For Cape gannets and African penguins, there is little evidence that breeding success (i.e. D_e and D_c) is influenced by food availability, except in conditions of extreme food shortage. High mortality of Cape gannet chicks is seldom reported, although in 1970 there was widespread starvation of chicks at all three ganneries off Namibia following a massive decrease in the size of the Namibian sardine resource (Crawford *et al.* 1983). At that time sardine dominated the diet of Cape gannets off Namibia (Matthews 1961, Matthews and Berruti 1983). Indices of the breeding success of African penguins at islands where food has been scarce have been little different from those at other localities (La Cock *et al.* 1987, Crawford *et al.* in prep.). However, the severe El Niño of 1982/83 led to

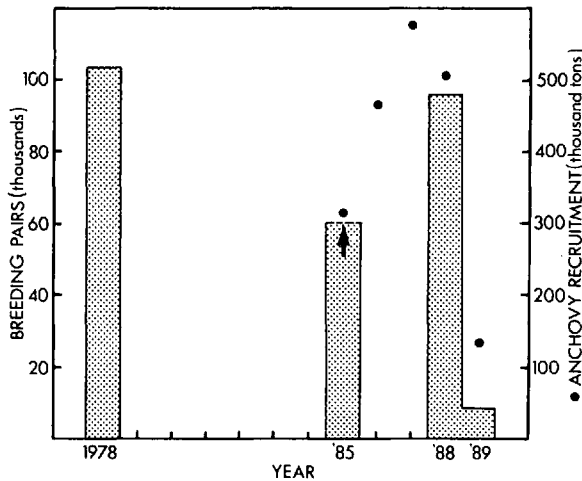


Fig. 7: Estimates of the number of pairs of Cape cormorants breeding off western South Africa in four recent censuses, and of the year-class strength of anchovy in the same region 1985–1989 (from I. Hampton, pers. comm.), showing the much reduced breeding by cormorants in 1989 when the anchovy year-class was poor. The cormorant census of 1985 was incomplete and therefore the estimate is a minimum one

many Humboldt penguins deserting their chicks (Hays 1986). Food may have a much greater impact on the breeding success of Cape cormorants, which are known to desert eggs or chicks frequently (Crawford *et al.* 1986).

Less is known about the influence of food availability on the mortality of immature birds, but especially in the early stages of independence this could be great (Jarvis 1974). The impact of food on clutch size in sardine-rich systems has been little studied, but the smaller the clutch size the less likely it is to vary (Ashmole 1963).

Therefore, the stage at which food will impact guano-producing seabirds will depend on the severity of the food depletion and on the species of seabird involved. In catastrophic instances adults may die, but more often breeding success, the proportion of adults breeding and the closely related breeding frequency will be affected. For gannets and other seabirds that are generally successful at raising chicks, food may have its greatest impact on the mortality of immature birds.

Availability of breeding sites as a limiting factor

It has been suggested that availability of suitable breeding sites may have been important in limiting

numbers of seabirds prior to the settling of Europeans in southern Africa (Burger and Cooper 1984), i.e. that regulation of seabird populations was through the control of P in Equation 2. Competition between different seabirds (e.g. between Cape gannets and African penguins) for breeding space may still be locally important in the Benguela system, but it is not thought to limit the overall number of seabirds there (Duffy and La Cock 1985).

At Ichaboe Island, Cape and bank cormorants now occupy some areas where Cape gannets bred in the 1950s (Fig. 8), and at Bird Island (Lambert's Bay), gannets have replaced African penguins as the dominant species (Crawford 1987). These changes may have resulted from independent decreases and increases in populations. For example, the decrease in the number of gannets and the increase in the number of cormorants at Ichaboe Island may have been caused by the partial replacement of the Namibian sardine, after its collapse, by the bearded goby (Crawford *et al.* 1985). Surface-shoaling sardines are readily available to gannets, but gobies, which live at greater depths, are less so. Bank cormorants, which dive deeper than gannets, may be better able to exploit the gobies. Gobies were also the main prey of Cape cormorants at Ichaboe Island in the period 1978–1980 (Crawford *et al.* op. cit.).

During the 20th century, expanding herds of South African fur seals have been excluding seabirds from a number of localities where they formerly bred, e.g. portions of Hollams Bird, Mercury, Sinclair, Seal (False Bay) and Seal (Mossel Bay) islands (Shaughnessy 1980, Crawford *et al.* 1989). Off Peru, the numbers of seabirds rose in the 1950s to levels higher than previously recorded, probably because increased nesting space had been made available through the walling off of coastal headlands with predator-proof concrete fences (Duffy and Siegfried 1987).

Therefore, in both the Benguela and Humboldt systems, nesting space has been limiting in certain regions. In areas of plentiful food, populations may remain small if breeding space is limiting. The African penguin provides an example (Crawford, Williams *et al.* 1990).

Some other limiting factors

Predation on seabirds may increase the mortality of any one of the four stages identified above (i.e. D_e , D_c , D_i and D_a). Adults and immature birds are susceptible to predation at sea, for example by seals or

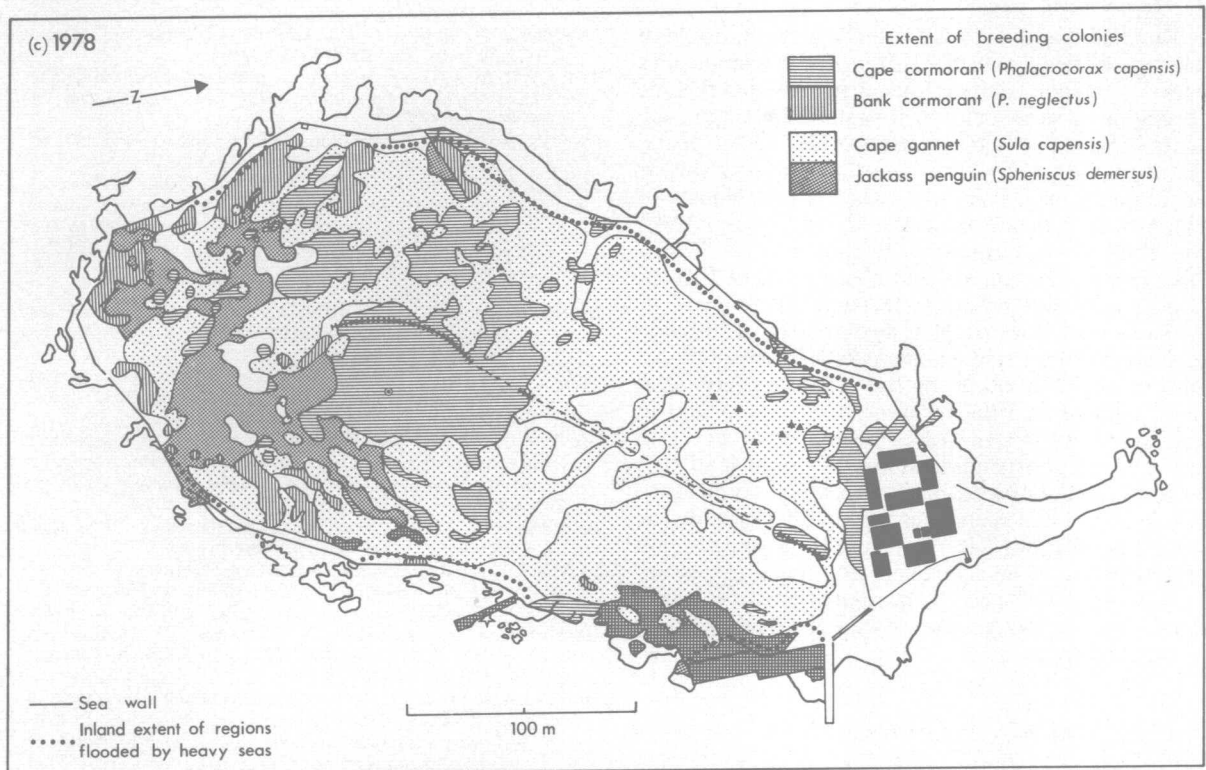


Fig. 8a: The distribution of four species of seabird breeding at Ichaboe Island in 1978 determined from aerial photographs at the Sea Fisheries Research Institute, Cape Town. Ground truth information was obtained from Rand (1963) and collected during 1978 (Shelton *et al.* 1982). Note the interpretation of the aerial photographs differs substantially from that in Duffy and La Cock (1985), who did not use the ground-truth information of 1978

sharks (Cooper 1974, Randall *et al.* 1988). At islands, predation will tend to be highest on chicks and eggs, although man has inflicted mortality on older birds (Rand 1949, Duffy *et al.* 1984). There are both natural (usually avian) predators and introduced predators, the latter being a cause for concern. Berruti (1986) found that 9 per cent of the chicks of African penguins produced at Dassen Island were killed by feral cats *Felis catus*. High mortality of eggs of the African penguin and guanay cormorant *P. bougainvillii* has been inflicted by man's commercial harvests of eggs (Cott 1953). In the case of the African penguin, the egg harvests brought about a very large decrease in population numbers. They were terminated in 1967 (Shelton *et al.* 1984).

Since this cessation of commercial exploitation of eggs, the numbers of African penguins have continued to decrease, a trend attributed to various factors, includ-

ing competition with fisheries for food, and with seals for breeding space, and mortality caused by oil spills (Crawford, Williams *et al.* 1990). As most oiling is at sea, the stages affected would be the adults and immatures. Disturbance to seabirds at islands may affect both the size of the breeding population (Jarvis and Cram 1971) and breeding success (Crawford and Cochrane 1990).

Mortality may result directly from several natural environmental factors, for example the flooding of nests by rain or deserting of nests as a result of excessive heat (Randall 1989). The impact of such events has sometimes been increased by man's activities: collection of guano has formed depressions in breeding areas increasing the susceptibility of nests to flooding (Randall and Ross 1979). At some localities there is now insufficient guano for penguins to construct burrows, and they may therefore be more susceptible to factors

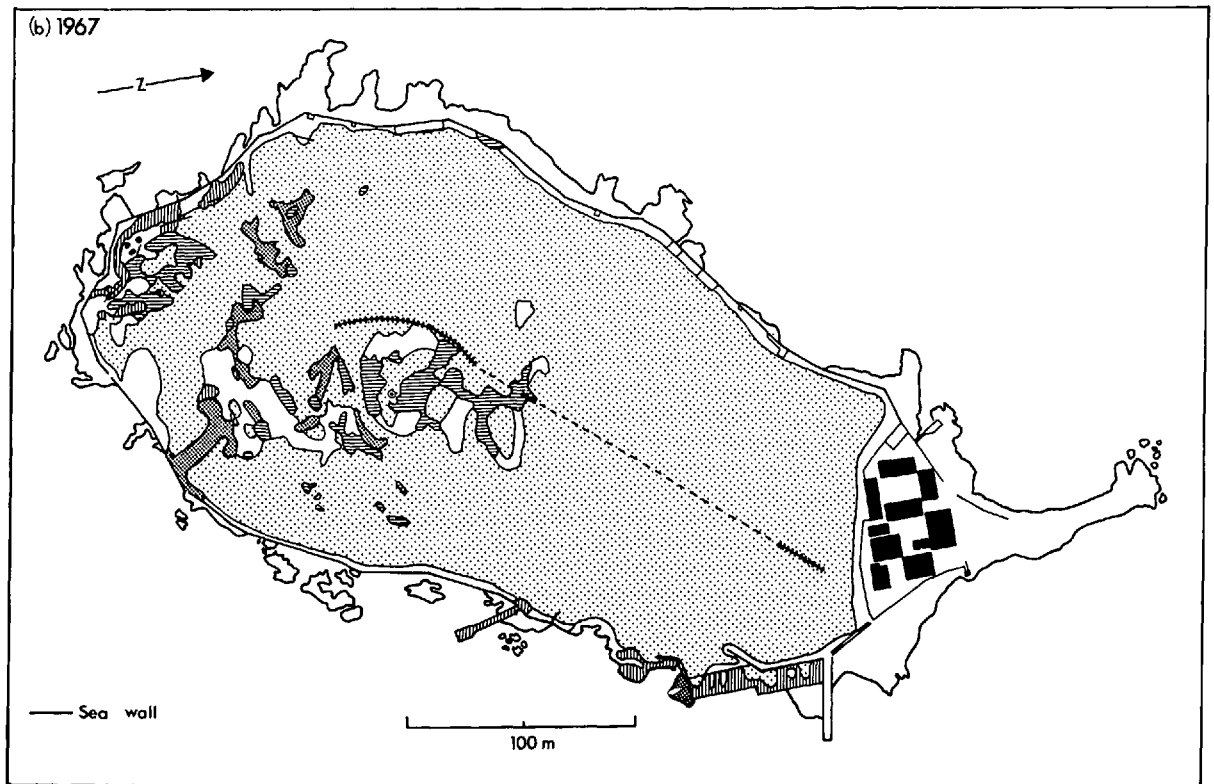


Fig. 8b: The distribution of four species of seabird breeding at Ichaboe Island in 1967 determined from aerial photographs at the Sea Fisheries Research Institute, Cape Town. Ground truth information was obtained from Rand (1963) and collected during 1978 (Shelton *et al.* 1982). Note the interpretation of the aerial photographs differs substantially from that in Duffy and La Cock (1985), who did not use the ground-truth information of 1978

such as heat stress (Randall 1983).

SOME LIKELY FUTURE RESEARCH DIRECTIONS

Climate change and marine resources

From the foregoing, it is apparent that the fluctuations of many fish populations in sardine-rich systems are influenced by a variety of factors, including exploitation, biological interactions and the environment. These factors have probably acted in a complex manner to produce past observed changes in the fish resources, and probably will continue to do so in future. The interaction of different factors complicates diagnosis of past change, and makes the prediction of future change difficult. For this reason, short-term

management of fisheries is increasingly being based on survey assessments of abundance conducted just prior to, or during, fishing seasons, the more so as techniques for rapid assessments become available (Hampton 1987).

However, longer-term decisions, such as those relating to the replacement of fishing fleets or the construction of processing plants, would benefit from the ability to forecast realistic scenarios (Lluch-Belda *et al.* 1989). The likely influence of climate on long-term and large-scale changes in fish stocks, and the possibility that future climate may change, has led to considerable interest in how an altered climate may influence marine ecosystems in areas where sardines are abundant (I.G.B.P. 1989, Crawford, Siegfried *et al.* 1990, Crawford *et al.* 1991). The impacts are potentially dramatic (Bakun 1990). It seems probable that, during the next few decades, considerable research effort will be directed at addressing this issue.

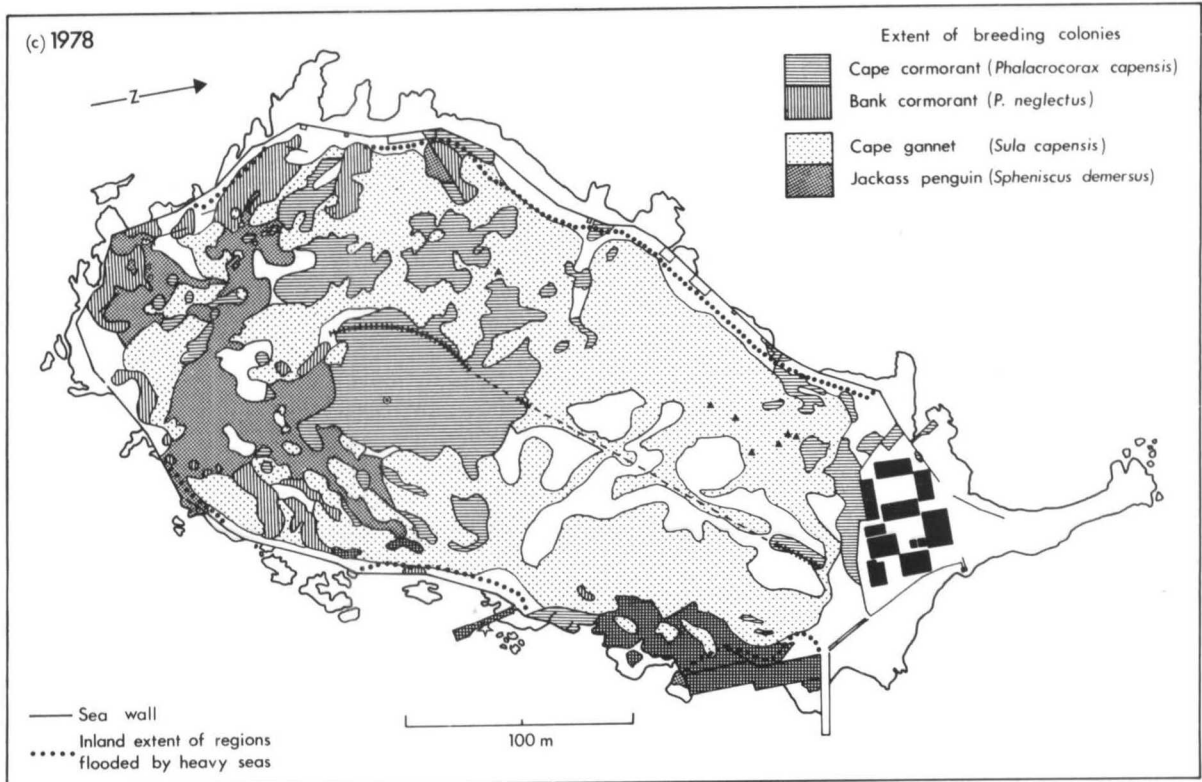


Fig. 8c: The distribution of four species of seabird breeding at Ichaboe Island in 1978 determined from aerial photographs at the Sea Fisheries Research Institute, Cape Town. Ground truth information was obtained from Rand (1963) and collected during 1978 (Shelton *et al.* 1982). Note the interpretation of the aerial photographs differs substantially from that in Duffy and La Cock (1985), who did not use the ground-truth information of 1978

Conservation of marine ecosystems

The 1980s witnessed concern that exploitation of marine resources should not adversely affect the functioning of the ecosystems of which they formed a part. In 1980, Article II of the Convention for the Conservation of Antarctic Marine Living Resources recorded the convention's objective as "the conservation of Antarctic marine living resources" and that any harvesting of resources should be conducted in such a manner as to ensure *inter alia* "maintenance of the ecological relationships between harvested, dependent and related populations" (Miller 1991). In 1983, a Scientific Committee of Enquiry into the Exploitation of Pelagic Fish Resources of South Africa and South West Africa advised that exploitation of fish resources should be conducted without "unacceptably disrupting the functioning of the ecosystem" (Alant 1983). South Africa's Sea Fishery Act No. 12 of 1988 has the

conservation of marine ecosystems as an objective in its long title, and it stresses the same objective in a section dealing with policy (Anon. 1988).

It is clear that organisms at the upper end of the trophic chain are often influenced by perturbations of food resources, and sometimes also interact with each other. In the past, however, the conservation objective for marine ecosystems has usually been accounted for only in the management objectives set for single resources, e.g. an anchovy population. Such an objective may be to obtain maximum yield from a resource with a certain acceptable risk of collapse (Bergh and Butterworth 1987). It is necessary to define collapse, i.e. the level of resource depletion, and both this level and the specified risk are generally adopted with little consideration of inter-relationships between organisms. *De facto*, the assumption is made that what is acceptable to man will also ensure the conservation of other organisms within the ecosystem.

There are valid reasons for this approach, not least that it is difficult to establish functional relationships between exploited and dependent species, and that the generation of sufficient data for establishment of such relationships in any event takes a number of years. However, the track record is not always satisfactory. For example, the conservation status of both Humboldt and African penguins continues to deteriorate (Araya and Todd 1988, Crawford, Williams *et al.* 1990). Strengths of year-classes and abundances of fish resources are often serially correlated (Shannon *et al.* 1988) so that, if an adopted level of risk of resource depletion is 20 per cent, in other words there is a probability of depletion occurring four years in every 20, it could well be that the resource may be depleted in four successive years. The effect of such an event on predators is poorly understood. It could lead to a breeding failure of a seabird species, e.g. cormorants, in four successive years, thereby rapidly depleting the seabird population. Clearly, if legislated conservation objectives are to be adequately accounted for, issues such as these will need to be addressed with greater rigour, and this too promises to be a challenging future research direction.

ACKNOWLEDGEMENTS

I thank three anonymous reviewers for constructive comments on the original manuscript, and colleagues with whom I have had the opportunity to discuss various of the ideas presented in this paper.

LITERATURE CITED

- ALANT, T. G. (Chairman) 1983 — Final report of the scientific committee of enquiry into the exploitation of pelagic fish resources of South Africa and South West Africa. Cape Town; Department of Environment Affairs and Fisheries: 171 pp. (mimeo).
- ALHEIT, J. 1987 — Egg cannibalism versus egg predation: their significance in anchovies. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 467–470.
- ANDERSON, D. W., GRESS, F., MAIS, K. F. and P. R. KELLY 1980 — Brown pelicans as anchovy stock indicators and their relationships to commercial fishing. *Rep. Calif. coop. oceanic Fish. Invest.* 21: 54–61.
- ANON. 1988 — Sea Fishery Act, 1988. *Government Gazette S. Afr.* 273(11201): 61 pp.
- ARAYA M., B. and F. S. TODD 1988 — Status of the Humboldt penguin in Chile following the 1982–83 El Niño. *Spheniscid Penguin Newsl.* 1(1): 8–10.
- ARMSTRONG, M. J., ROEL, B. A. and R. M. PROSCH 1989 — Long-term trends in patterns of maturity in the southern Benguela pilchard population: evidence for density-dependence? *S. Afr. J. mar. Sci.* 8: 91–101.
- ASHMOLE, N. P. 1963 — The regulation of numbers of tropical oceanic birds. *Ibis* 103B: 458–473.
- BAILEY, K. M. 1981 — Larval transport and recruitment of Pacific hake *Merluccius productus*. *Mar. Ecol. Prog. Ser.* 6(1): 1–9.
- BAKUN, A. 1990 — Global climate change and intensification of coastal ocean upwelling. *Science, N.Y.* 247: 198–201.
- BERGH, M. O. and D. S. BUTTERWORTH 1987 — Towards rational harvesting of the South African anchovy considering survey imprecision and recruitment variability. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 937–951.
- BERRUPI, A. 1986 — The predatory impact of feral cats *Felis catus* and their control on Dassen Island. *S. Afr. J. Antarct. Res.* 16(3): 123–127.
- BERRUPI, A. 1987 — The use of Cape gannets in management of the purse-seine fishery of the Western Cape. Ph.D. thesis, University of Natal (Pietermaritzburg): 304 pp.
- BEST, P. B. and P. D. SHAUGHNESSY 1979 — An independent account of Captain Benjamin Morrell's sealing voyage to the south-west coast of Africa in the *Antarctic*, 1828/29. *Fish. Bull. S. Afr.* 12: 1–19.
- BROOKE, R. K. 1984 — South African red data book – birds. *Rep. S. Afr. natn. scient. Progrms* 97: vii + 213 pp.
- BURGER, A. E. and J. COOPER 1984 — The effects of fisheries on seabirds in South Africa and Namibia. In *Marine Birds: their Feeding Ecology and Commercial Fisheries Relationships*. Nettleship, D. N., Sanger, G. A. and P. F. Springer (Eds). Ottawa; Canadian Wildlife Service: 150–160.
- BUTTERWORTH, D. S. 1983 — Assessment and management of pelagic stocks in the southern Benguela region. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* 291(2): 329–405.
- CAIRNS, D. K. 1987 — Seabirds as indicators of marine food supplies. *Biol. Oceanogr.* 5: 261–271.
- CHIKUNI, S. 1985 — The fish resources of the North-West Pacific. *F.A.O. Fish. tech. Pap.* 266: 180 pp.
- CLARK, F. N. and J. C. MARR 1955 — Population dynamics of the Pacific sardine. *Prog. Rep. Calif. coop. oceanic Fish. Invest.* 1 July 1953 to 31 March 1955: 11–48.
- COLLETTE, B. B. and C. E. NAUEN 1983 — F.A.O. species catalogue. 2. Scombrids of the world. An annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date. *F.A.O. Fish. Synop.* 125: 137 pp.
- COOPER, J. 1974 — The predators of the jackass penguin *Spheniscus demersus*. *Bull. Brit. orn. Club* 94: 21–24.
- COTT, H. B. 1953 — The exploitation of the wild birds for their eggs. *Ibis* 95(3): 409–449.
- COULSON, J. C. 1984 — The population dynamics of the eider duck *Somateria mollissima* and evidence of extensive non-breeding by adult ducks. *Ibis* 126: 525–543.
- CRAWFORD, R. J. M. 1987 — Food and population variability in five regions supporting large stocks of anchovy, sardine and horse mackerel. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 735–757.
- CRAWFORD, R. J. M. and K. L. COCHRANE 1990 — Onset of breeding by Cape gannets *Morus capensis* influenced by availability of nesting material. *Ostrich* 61: 147–149.
- CRAWFORD, R. J. M., CRUICKSHANK, R. A., SHELTON, P. A. and I. KRUGER 1985 — Partitioning of a goby resource amongst four avian predators and evidence for altered trophic flow in the pelagic community of an intense, perennial upwelling system. *S. Afr. J. mar. Sci.* 3: 215–228.
- CRAWFORD, R. J. M., DAVID, J. H. M., WILLIAMS, A. J. and

- B. M. DYER 1989 — Competition for space: recolonising seals displace endangered, endemic seabirds off Namibia. *Biol. Conserv.* **48**: 59–72.
- CRAWFORD, R. J. M. and G. DE VILLIERS 1985 — Snoek and their prey — interrelationships in the Benguela upwelling system. *S. Afr. J. Sci.* **81**(2): 91–97.
- CRAWFORD, R. J. M. and A. I. L. PAYNE 1989 — Southern Africa's ocean ecosystems. In *Oceans of Life off Southern Africa*. Payne, A. I. L. and R. J. M. Crawford (Eds). Cape Town; Vlaeberg: 347–359.
- CRAWFORD, R. J. M., SHANNON, L. V. and D. E. POLLOCK 1987 — The Benguela ecosystem. 4. The major fish and invertebrate resources. In *Oceanography and Marine Biology. An Annual Review* **25**. Barnes, M. (Ed.). Aberdeen; University Press: 353–505.
- CRAWFORD, R. J. M. and P. A. SHELTON 1978 — Pelagic fish and seabird interrelationships off the coasts of South West and South Africa. *Biol. Conserv.* **14**(2): 85–109.
- CRAWFORD, R. J. M. and P. A. SHELTON 1981 — Population trends for some southern African seabirds related to fish availability. In *Proceedings of the Symposium on Birds of the Sea and Shore, 1979*. Cooper, J. (Ed.). Cape Town; African Seabird Group: 15–41.
- CRAWFORD, R. J. M., SHELTON, P. A., BATCHELOR, A. L. and C. F. CLINNING 1980a — Observations on the mortality of juvenile Cape cormorants *Phalacrocorax capensis* during 1975 and 1979. *Fish. Bull. S. Afr.* **13**: 69–75.
- CRAWFORD, R. J. M., SHELTON, P. A. and A. BERRUTI 1983 — Cape cormorants as potential indicators of pelagic fish stocks off southern Africa. *S. Afr. J. Sci.* **79**(11): 466–468.
- CRAWFORD, R. J. M., SHELTON, P. A. and L. HUTCHINGS 1980b — Implications of availability, distribution and movements of pilchard (*Sardinops ocellata*) and anchovy (*Engraulis capensis*) for assessment and management of the South African purse-seine fishery. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* **177**: 355–373.
- CRAWFORD, R. J. M., SIEGFRIED, W. R., SHANNON, L. V., VILLACASTIN-HERRERO, C. A. and L. G. UNDERHILL 1990 — Environmental influences on marine biota off southern Africa. *S. Afr. J. Sci.* **86**: 330–339.
- CRAWFORD, R. J. M., UNDERHILL, L. G., SHANNON, L. V., LLUCH-BELDA, D., SIEGFRIED, W. R. and C. A. VILLACASTIN-HERRERO 1991 — An empirical investigation of trans-oceanic linkages between areas of high abundance of sardine. In *Long-term Variability of Pelagic Fish Populations and their Environment*. Kawasaki, T., Tanaka, S., Toba, Y. and A. Taniguchi (Eds). Oxford; Pergamon: 319–332 (Proceedings of an International Symposium in Sendai, Japan, November 1989).
- CRAWFORD, R. J. M., WILLIAMS, A. J. and P. B. CRAWFORD 1986 — A note on mortality of seabirds off western southern Africa, October 1985 – February 1986. *S. Afr. J. mar. Sci.* **4**: 119–123.
- CRAWFORD, R. J. M., WILLIAMS, A. J. and B. M. DYER (in preparation) — Solitary versus colonial breeding – African penguins at Possession Island.
- CRAWFORD, R. J. M., WILLIAMS, A. J., RANDALL, R. M., RANDALL, B. M., BERRUTI, A. and G. J. B. ROSS 1990 — Recent population trends of jackass penguins *Spheniscus demersus* off southern Africa. *Biol. Conserv.* **52**(3): 229–243.
- CSIRKE, J. 1980 — Recruitment in the Peruvian anchovy and its dependence on the adult population. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* **177**: 307–313.
- DAAN, N. 1980 — A review of replacement of depleted stocks by other species and the mechanisms underlying such replacement. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* **177**: 405–421.
- DAVID, J. H. M. 1987 — Diet of the South African fur seal (1974–1985) and an assessment of competition with fisheries in southern Africa. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 693–713.
- DAVID, J. H. M. 1989 — Seals. In *Oceans of Life off Southern Africa*. Payne, A. I. L. and R. J. M. Crawford (Eds). Cape Town; Vlaeberg: 288–302.
- DUFFY, D. C. 1983 — Environmental uncertainty and commercial fishing: effects on Peruvian guano birds. *Biol. Conserv.* **26**: 227–238.
- DUFFY, D. C., HAYS, C. and M. A. PLENGE 1984 — The conservation status of Peruvian seabirds. In *Status and Conservation of the World's Seabirds*. Croxall, J. P., Evans, P. G. H. and R. W. Schreiber (Eds). *Tech. Publ. int. Coun. Bird Preserv.* **2**: 245–259 (Proceedings of the ICBP Seabird Symposium, Cambridge, U.K., August 1982).
- DUFFY, D. C. and G. D. LA COCK 1985 — Partitioning of nesting space among seabirds of the Benguela upwelling region. *Ostrich* **56**: 186–201.
- DUFFY, D. C. and W. R. SIEGFRIED 1987 — Historical variations in food consumption by breeding seabirds of the Humboldt and Benguela upwelling regions. In *Seabirds Feeding Ecology and Role in Marine Ecosystems*. Croxall, J. P. (Ed.). Cambridge; University Press: 327–346.
- DUFFY, D. C., WILSON, R. P. and M. P. WILSON 1987 — Spatial and temporal patterns of diet in the Cape cormorant off southern Africa. *Condor* **89**: 830–834.
- ESPINO, M. and C. WOSNITZA-MENDO 1988 — Efecto de la concentración en la mortalidad natural y su aplicación en el análisis de cohortes. In *Long Term Changes in Marine Fish Populations*. Wyatt, T. and M. G. Larrañeta (Eds). Vigo; Instituto de Investigaciones Marinas de Vigo: 235–252 (Proceedings of a symposium held in Vigo, November 1986).
- EVANS, P. G. H. 1984 — Status and conservation of seabirds in northwest Europe (excluding Norway and the USSR). In *Status and Conservation of the World's Seabirds*. Croxall, J. P., Evans, P. G. H. and R. W. Schreiber (Eds). *Tech. Publ. int. Coun. Bird Preserv.* **2**: 293–321 (Proceedings of the ICBP Seabird Symposium, Cambridge, U.K., August 1982).
- FURNESS, R. W. and J. COOPER 1982 — Interactions between breeding seabird and pelagic fish populations in the southern Benguela region. *Mar. Ecol. Prog. Ser.* **8**(3): 243–250.
- GARCIA, S. 1982 — Distribution, migration and spawning of the main fish resources in the northern CECAF area. *F.A.O. UNDPCECAF/IECAF series* **82/25**: 9 pp.
- HAMPTON, I. 1987 — Acoustic study on the abundance and distribution of anchovy spawners and recruits in South African waters. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 901–917.
- HASEGAWA, H. 1984 — Status and conservation of seabirds in Japan, with special attention to the short-tailed albatross. In *Status and Conservation of the World's Seabirds*. Croxall, J. P., Evans, P. G. H. and R. W. Schreiber (Eds). *Tech. Publ. int. Coun. Bird Preserv.* **2**: 487–500 (Proceedings of the ICBP Seabird Symposium, Cambridge, U.K., August 1982).
- HAYS, C. 1986 — Effects of the 1982–83 El Niño on Humboldt penguin colonies in Peru. *Biol. Conserv.* **36**: 169–180.
- HOCKEY, P. A. R. and J. HALLINAN 1981 — Effect of human disturbance on the breeding behaviour of jackass penguins *Spheniscus demersus*. *S. Afr. J. Wildl. Res.* **11**(2): 59–62.
- I.G.B.P. 1989 — Southern hemisphere perspectives of global change: scientific issues, research needs and proposed activities. *Rep. int. Geosphere-Biosphere Program*. **9**: 55 pp.
- INADA, T. 1981 — Studies on the merlucciid fishes. *Bull. Far Seas Fish. Res. Lab.* **18**: 172 pp.
- JARVIS, M. J. F. 1974 — The ecological significance of clutch size in the South African gannet (*Sula capensis* (Lichténstein)).

- J. Anim. Ecol.* **43**(1): 1–17.
- JARVIS, M. J. F. and D. L. CRAM 1971 — Bird Island, Lambert's Bay, South Africa: an attempt at conservation. *Biol. Conserv.* **4**: 269–272.
- JEHL, J. R. 1984 — Conservation problems of seabirds in Baja California and the Pacific northwest. In *Status and Conservation of the World's Seabirds*. Croxall, J. P., Evans, P. G. H. and R. W. Schreiber (Eds). *Tech. Publ. int. Coun. Bird Preserv.* **2**: 41–48 (Proceedings of the ICBP Seabird Symposium, Cambridge, U.K., August 1982).
- JORDAN, R. 1967 — The predation of guano birds on the Peruvian anchovy (*Engraulis ringens* Jenyns). *Rep. Calif. coop. oceanic Fish. Invest.* **11**: 105–109.
- KAWASAKI, T. 1983 — Why do some fishes have wide fluctuations in their numbers? — Biological basis of fluctuation from the viewpoint of evolutionary ecology. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(3): 1065–1080.
- KING, J. E. 1983 — *Seals of the World*. Oxford; University Press: 207 pp.
- KONDO, K. 1980 — The recovery of the Japanese sardine — the biological basis of stock-size fluctuations. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* **177**: 332–354.
- KRUGER, T. L. 1949 — The Government Guano Islands. *Fmg S. Afr.* **24**: 602–603.
- LA COCK, G. D., DUFFY, D. C. and J. COOPER 1987 — Population dynamics of the African penguin *Spheniscus demersus* at Marcus Island in the Benguela upwelling ecosystem: 1979–85. *Biol. Conserv.* **40**: 117–126.
- LA COCK, G. D. and C. HANEL 1987 — Survival of African penguins *Spheniscus demersus* at Dyer Island, southern Cape, South Africa. *J. Fld. Ornithol.* **58**(3): 284–287.
- LLUCH-BELDA, D., CRAWFORD, R. J. M., KAWASAKI, T., MACCALL, A. D., PARRISH, R. H., SCHWARTZLOSE, R. A. and P. E. SMITH 1989 — World-wide fluctuations of sardine and anchovy stocks: the regime problem. *S. Afr. J. mar. Sci.* **8**: 195–205.
- LOEB, V. J. and O. ROJAS 1988 — Interannual variation of ichthyoplankton composition and abundance relations off northern Chile, 1964–83. *Fishery Bull., Wash.* **86**(1): 1–24.
- MACCALL, A. D. 1976 — Density dependence of catchability coefficient in the California Pacific sardine, *Sardinops sagax caerulea*, purse seine fishery. *Rep. Calif. coop. oceanic Fish. Invest.* **18**: 136–148.
- MACCALL, A. D. 1981 — The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as *Engraulis*. In *Report and Supporting Documentation of the Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, 1980*. Sharp, G. D. (Conv. Ed.). Paris: Unesco: 201–220 (*I.O.C. Workshop Rep.* **28**).
- MACCALL, A. D., KLINGBEIL, R. A. and R. D. METHOT 1985 — Recent increased abundance and potential productivity of Pacific mackerel (*Scomber japonicus*). *Rep. Calif. coop. oceanic Fish. Invest.* **26**: 119–129.
- MATTHEWS, J. P. 1961 — The pilchard of South West Africa *Sardinops ocellata* and the marsbanker *Trachurus trachurus*. Bird predators, 1957–1958. *Invest. Rep. mar. Res. Lab. S.W. Afr.* **3**: 35 pp.
- MATTHEWS, J. P. and A. BERRUTI 1983 — Diet of Cape gannet and Cape cormorant off Walvis Bay, 1958–1959. *S. Afr. J. mar. Sci.* **1**: 61–63.
- MILLER, D. G. M. 1991 — Exploitation of Antarctic marine living resources: a brief history and a possible approach to managing the krill fishery. *S. Afr. J. mar. Sci.* **10**: 321–339.
- MUCK, P. and H. FUENTES 1987 — Sea lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982. In *The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change*. Pauly, D. and I. Tsukayama (Eds). *ICLARM Stud. Rev.* **15**: 234–247.
- MURPHY, G. I. 1966 — Population biology of the Pacific sardine (*Sardinops caerulea*). *Proc. Calif. Acad. Sci., Ser. 4* **34**(1): 1–84.
- PARRISH, R. H., BAKUN, A., HUSBY, D. M. and C. S. NELSON 1983 — Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(3): 731–777.
- PARRISH, R. H., SERRA, R. and W. S. GRANT 1989 — The monotypic sardines, *Sardina* and *Sardinops*: their taxonomy, distribution, stock structure, and zoogeography. *Can. J. Fish. aquat. Sci.* **46**(11): 2019–2036.
- RAND, R. W. 1949 — Some early references to the Cape penguin. *Ostrich* **20**(1): 2–5.
- RAND, R. W. 1963 — The biology of guano-producing seabirds. 5. Composition of colonies on the South West African islands. *Invest. Rep. Div. Sea Fish. S. Afr.* **46**: 26 pp.
- RANDALL, B. M., RANDALL, R. M. and L. J. V. COMPAGNO 1988 — Injuries to jackass penguins (*Spheniscus demersus*): evidence for shark involvement. *J. Zool., Lond.* **214**: 589–599.
- RANDALL, R. M. 1983 — Biology of the jackass penguin *Spheniscus demersus* (L.) at St Croix Island, South Africa. Ph.D. thesis, University of Port Elizabeth: 262 pp.
- RANDALL, R. M. 1989 — Jackass penguins. In *Oceans of Life off Southern Africa*. Payne, A. I. L. and R. J. M. Crawford (Eds). Cape Town; Vlaeberg: 244–256.
- RANDALL, R. [M.] and B. [M.] RANDALL 1986 — The Kapodistrias affair — another oiling incident affecting seabirds. *Bokmakierie* **38**(2): 37–40.
- RANDALL, R. [M.] and G. J. B. ROSS 1979 — Increasing population of Cape gannets on Bird Island, Algoa Bay, and observations on breeding success. *Ostrich* **50**(3): 168–175.
- SAVILLE, A. 1980 — Discussion and conclusions of the symposium on the biological basis of pelagic fish stock management. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* **177**: 513–517.
- SERRA, R. 1991 — Long-term variability of the Chilean sardine. In *Long-term Variability of Pelagic Fish Populations and their Environment*. Kawasaki, T., Tanaka, S., Toba, Y. and A. Taniguchi (Eds). Oxford; Pergamon: 165–172 (Proceedings of an International Symposium in Sendai, Japan, November 1989).
- SHANNON, L. V., CRAWFORD, R. J. M., BRUNDRIT, G. B. and L. G. UNDERHILL 1988 — Responses of fish populations in the Benguela ecosystem to environmental change. *J. Cons. perm. int. Explor. Mer* **45**(1): 5–12.
- SHAUGHNESSY, P. D. 1980 — Influence of Cape fur seals on jackass penguin numbers at Sinclair Island. *S. Afr. J. Wildl. Res.* **10**(1): 18–21.
- SHAUGHNESSY, P. D. 1984 — Historical population levels of seals and seabirds on islands off southern Africa, with special reference to Seal Island, False Bay. *Invest. Rep. Sea Fish. Res. Inst. S. Afr.* **127**: 61 pp.
- SHELTON, P. A. and M. J. ARMSTRONG 1983 — Variations in parent stock and recruitment of pilchard and anchovy populations in the southern Benguela system. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke

- (Eds). *F.A.O. Fish. Rep.* **291**(3): 1113-1132.
- SHELTON, P. A., CRAWFORD, R. J. M., COOPER, J. and R. K. BROOKE 1984 — Distribution, population size and conservation of the jackass penguin *Spheniscus demersus*. *S. Afr. J. mar. Sci.* **2**: 217-257.
- SHELTON, P. A., CRAWFORD, R. J. M., KRIEL, F. and J. COOPER 1982 — Methods used to census three species of southern African seabirds, 1978-1981. *Fish. Bull. S. Afr.* **16**: 115-120.
- SILVERT, W. and R. J. M. CRAWFORD 1988 — The periodic replacement of one fish stock by another. In *Long Term Changes in Marine Fish Populations*. Wyatt, T. and M. G. Larrañeta (Eds). Vigo; Instituto de Investigaciones Marinas de Vigo: 161-180 (Proceedings of a symposium held in Vigo, November 1986).
- SKUD, B. E. 1982 — Dominance in fishes: the relation between environment and abundance. *Science, N.Y.* **216**(4542): 144-149.
- SOUTAR, A. and J. D. ISAACS 1974 — Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. *Fishery Bull., Wash.* **72**(2): 257-273.
- TOVAR S., H and N. GALARZA M. 1983 — Fluctuaciones mensuales de las poblaciones de aves guaneras durante "El Niño" de 1972. *Infmes Inst. Mar Perú* **83**: 38 pp.
- VALDÉS, E. S., SHELTON, P. A., ARMSTRONG, M. J. and J. G. FIELD 1987 — Cannibalism in South African anchovy: egg mortality and egg consumption rates. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 613-622.
- WARE, D. M. and G. A. McFARLANE 1989 — Fisheries production domains in the northeast Pacific Ocean. In *Effects of Ocean Variability on Recruitment and an Evaluation of Parameters used in Stock Assessment Models*. Beamish, R. J. and G. A. MacFarlane (Eds). *Can. Spec. Publ. Fish. aquat. Sci.* **108**: 359-379.