The effects of fisheries on seabirds in South Africa and Namibia

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1. Abstract

Seabirds have been affected by two major fisheries in South Africa and Namibia (South-West Africa). Demersal trawlers operating at the continental shelf edge provide large amounts of food to seabirds, mainly non-breeding migrant procellariiforms. The effects of this fishery on seabird populations are not yet known. The purse-seine fishery removes the same pelagic fish species as Jackass Penguins (Spheniscus demersus), Cape Gannets (Sula capensis). and Cape Cormorants (Phalacrocorax capensis), and operates within the same areas as these birds. Intensive purse-seining in the 1960s and 1970s caused significant decreases in several fish stocks, notably those of the pilchard (Sardinops ocellata) and horse mackerel (Trachurus trachurus), and a decrease in the average size of fish available. These changes had major effects on certain seabirds. Census data, supplemented by records of guano harvests, indicated substantial changes in the populations of the Jackass Penguin. Cape Gannet, and Cape Cormorant, which may be attributable to changes in prey availability. The diets of these three species also changed markedly between the mid 1950s and 1978-80. Some seabird species were more resilient to the chauges than others. Jackass Penguins probably have been most severely affected by the purse-seine fishery. Many seabird species do not eat commercially important organisms and have not been affected by the fisheries. We discuss possible limiting factors of seabird populations, and emphasize a need for investigation into limiting factors in order to plan meaningful conservation measures for seabirds.

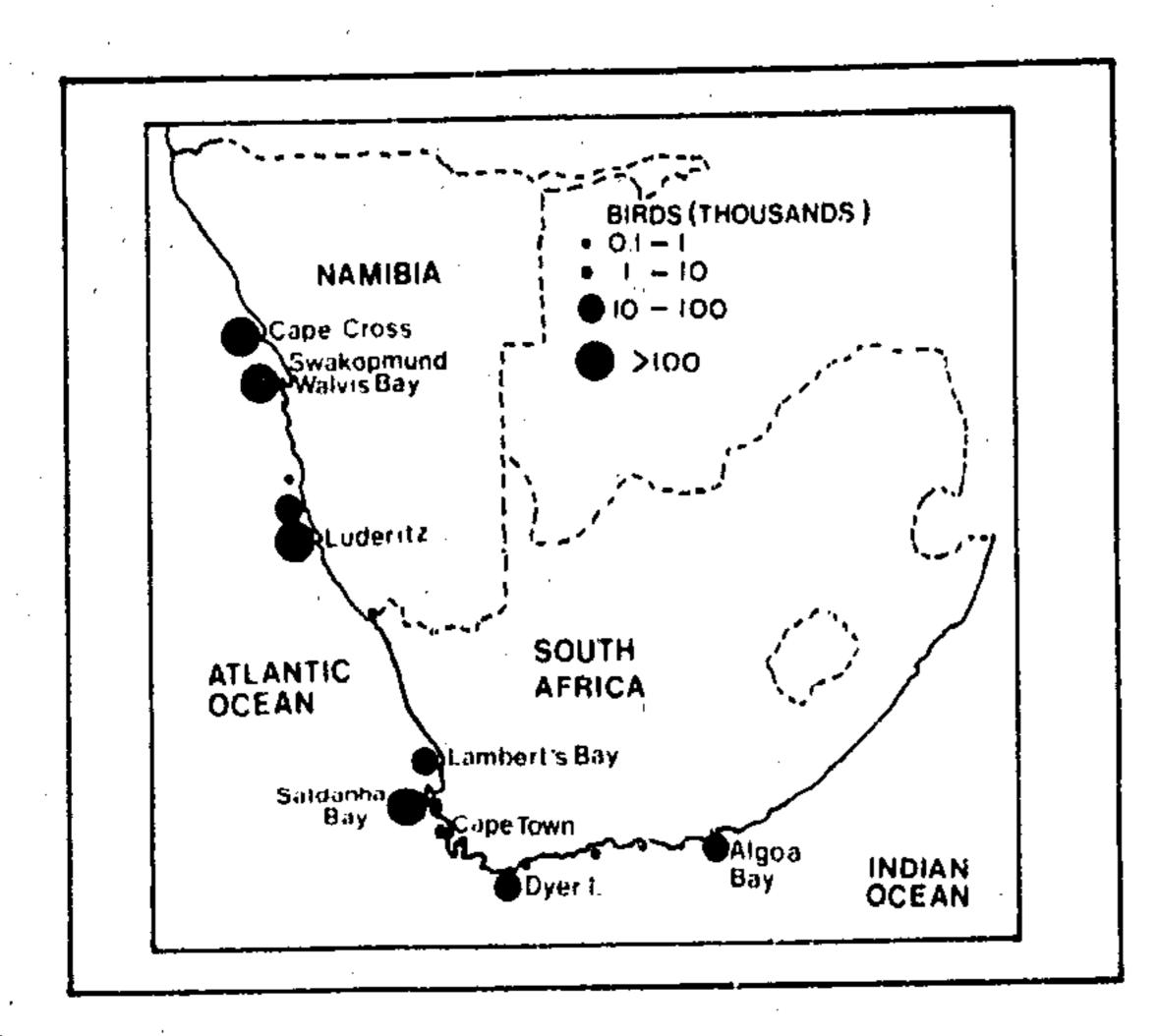
2. Résumé

Deux types de pêche importants ont influé sur les populations d'oiseaux de mer en Afrique du Sud et en Namibie (sud-ouest de l'Afrique). Les chaluts de fond qui opèrent au bord du plateau continental fournissent de grandes quantités de nourriture aux oiseaux de mer. principalement aux procellariiformes migrateurs qui ne nichent pas dans la région. Les effets de cette pêche sur les populations d'oiseaux de mer restent encore inconnus. La pêche à la senne coulissante prélève les mêmes espèces de poissons pélagiques que le Manchot (Speniscus demersus), le Fou du Cap (Sula capensis) et le Cormoran du Cap (Phalacrocorax capensis) et se déroule dans les mêmes régions fréquentées par ces oiseaux. La pêche intensive à la senne coulissante dans les années 1960 et 1970 a réduit considérablement les stocks de poissons, notamment ceux du pilchard (Sardinops ocellata) et du chinchard (Trachurus trachurus), et a entraîné une diminution de la taille moyenne des poissons disponibles. Ces changements ont eu des effets dramatiques. sur certains oiseaux de mer. Les données du recensement, complétées par des relevés de récolte du guano, révèlent l'existence de profondes modifications dans les populations du Manchot, du Fou du Cap et du Cormoran du Cap, qui doivent être attribuables à des variations de la disponibilité : des proies. Les régimes alimentaires de cès trois espèces ont également changé de façon spectaculaire entre la moitié des années 1950 et 1978–1980. Certaines espèces ont mieux résisté aux changements que d'autres. C'est le Manchot qui a probablement souffert le plus de la pêche à la senne coulissante. De nombreuses espèces d'oiseaux de mei ne consomment pas d'organismes d'importance commerciale de sorte qu'elles n'ont pas été touchées par la pêché. Nous examinons certains facteurs limitatifs possibles de la population d'oiseaux de mer et soulignons le besoin d'études sur cés facteurs pour pouvoir planifier des mesures de conservation mieux articulées en faveur des oiseaux de mer.

3. Introduction

Scabirds and people compete for fish off the coast of southern Africa. The upwelling of the Benguela Current and inshore upwelling and mixing produce areas of high productivity (Cushing 1971, Crawford 1980) which support very large numbers of seabirds (Fig. 1) and a large commercial fishery. The first intensive research into scabitels was undertaken in this region in the 1950s, mainly to estimate the effects of seabird predation on the commercial fish stocks (Davies 1955, 1956; Rand 1959, 1960a, 1960b, 1963a, 1963b; Matthews 1961). These studies suggested that certain seabirds did eat commercially important fish species. Some form of control of seabird populations was recommended (Davies 1958) but never implemented. During the past decade, however, biologists have been increasingly concerned about the consequences of intensive fishing on the populations of seabirds (Frost et al. 1976; Crawlord and Shelton 1978, 1981; Cooper et al. 1982; Cooper, 1984; Furness and Cooper 1982). In addition, fisheries biologists: have become interested in the analysis of seabird population trends, breeding success, and dietary changes as possible indicators of available fish stocks (Crawford and Shelton 1978, 1981; Newman and Crawford 1979). As a result. seabird research has become increasingly popular at South African universities and research institutes. Understanding of the seabirds in the region has increased considerably. although the feeding behaviour of many species is still poorly known. This paper reviews the recent studies of the population sizes and diets of selected species of scabirds in

Figure 1
Distribution of the major seabird colonies in South Africa and Namibia. (South-West Africa). The greatest number of seabirds breed within the Benguela Current system of the Atlantic Ocean. Census data from references quoted in the text



South Africa and Namibia (South-West Africa) and the effects of commercial fishing on these seabirds.

People and seabirds have a long history of interaction in southern Africa. The hunter-gatherers who frequented the Cape coast for many thousands of years relied quite extensively on beached seabird carcasses for food in certain seasons (Avery 1977). Settlers from Europe began exploiting seabirds over 300 years ago. Eggs and guano were the principal products harvested. Disturbance and over-exploitation led to the extinction of some colonies of Jackass Penguins (*Spheniscus demersus*) (Westphal and Rowan 1971, Shaughnessy and Shaugnessy 1978) and the drastic reduction in size of others (Frost *et al.* 1976). Egg-collecting has now been halted. Harvesting of adults and chicks has not been common in the past century, although sporadic killing of adult seabirds at sea for human food still occurs (Cooper 1977).

The collection of guano has also affected the seabirds. The huge accumulated deposits of guano capping the offshore islands were removed by 1845 (Jarvis 1970) thereby changing the characteristics of the seabird colonies. Jackass Penguins, which dug burrows into the guano, lost optimal nesting sites (Berry et al. 1974, Frost et al. 1976). Harvesting of the annual deposits continues to the present, with mixed consequences for seabirds. The harvest destroys many of the eggs, chicks, and nests of late breeders, but the protected status of the guano islands might have reduced other human disturbances. At several sites in Namibia, large wooden platforms have been built to collect guano deposited by breeding and roosting seabirds. The platforms, with a total area of 10 ha, have been very effective and over 100 000 Cape Cormorants (Phalacrocorax capensis) now breed regularly in areas with no suitable islands (Berry 1976a, Crawford and Shelton 1981). Guano-harvesting has become less profitable recently and has ceased on a number of islands. Penguin guano is no longer collected.

African seabirds are affected by other human actions. Pollution of the sea by petroleum has led to high seabird mortality on several occasions, and is a potential threat to the population of Jackass Penguins (Westphal and Rowan 1971, Frost et al. 1976, Morant et al. 1981). Fish-oil pollution (Anon. 1974, Berry 1976b) and harbour development (Jarvis 1970, Anon. 1973, Brooke et al. 1982, Crawford et al. 1982a) have also affected seabirds.

Intensive commercial fishing now appears to be the greatest single threat to the populations of some seabird species in southern Africa. Evidence reviewed below shows that the overall abundance of certain populations of prey has been reduced by fishing in several areas, while the proportions of prey species and the size of fish available have been altered in most areas. This has coincided with noticeable changes in the population sizes and diets of some species of seabirds.

4. Seabird species in southern Africa

Approximately 65 species of seabirds have been recorded within territorial waters off South Africa and Namibia (Brooke 1981). These include 14 species that breed on these shores and about 20 species that commonly occur as non-breeding visitors.

Estimates of the populations of the locally breeding species vary (Crawford and Shelton 1978, 1981; Cooper 1984) but at least 700 000 individuals breed annually within the region. Over 95% of these birds are Jackass Penguins, Cape Cormorants, and Cape Gannets (Sula capensis) (Crawford and Shelton 1978). These three species all prey predominantly on fish, particularly the pelagic shoaling species which are of commercial importance (Crawford and Shelton 1981, Batchelor 1982, Cooper 1984). Since they are the most common species and eat commercially important fish, these birds have been studied most intensively and they are the main focus of this review.

The fishing industry appears to have little impact on the feeding of Bank Cormorants (Phalacrocorax neglectus), Whitebreasted Cormorants (P. carbo lucidus), Crowned Cormorants (P. coronatus), and the four species of resident terns. These birds tend to prey on marine organisms that are of little or no commercial interest to people (Rand 1960b, Randall and Randall 1978, Cooper 1981, Brooke et al. 1982. Crawford et al. 1982b). More intensive research might reveal that the diets of some of these species might be affected by the fishery now or in the future. The Great White Pelican (Pelicanus onocrotalus) breeds in small numbers on islands and platforms on the coast but it does not always feed at sea. The gulls that breed on the coast may have benefited from the fishery (Crawford et al. 1982a). Kelp Gulls (Larus dominicanus) and Hartlaub's Gulls (L. hartlaubi) are common scavengers at fish-processing factories and Kelp Gulls at fishing vessels.

The sea off southern Africa also supports large numbers of non-breeding migrants from the northern hemisphere and the southern ocean. The greatest numbers are terns from the northern hemisphere and albatrosses, shearwaters, and petrels (Order Procellariiformes) from the south. These birds are beginning to get serious attention from biologists in southern Africa, with attempts being made to obtain quantitative data on their densities, distributions, and feeding behaviour (Summerhayes et al. 1974, Cooper and Dowle 1976, Abrams and Griffiths 1981, Griffiths 1981, Abrams 1983).

Changes in the fish populations

Two major fishing methods have affected seabirds: purse-seining in inshore waters and demersal trawling at the

continental shelf edge.

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Purse-seining is used to catch pelagic shoaling lish. including pilchard (Sardinops ocellata), anchovy (Engraulis capenis), horse mackerel (Trachurus trachurus), mackerel (Scomber japonicus), round-herring (Etrumeus teres), and other species. Intensive purse-seining began in the mid 1940s and rapidly developed into one of the larger industries of this kind in the world. In South Africa and Namibia this intensive fishing produced changes in the population size and age-structure of certain fish stocks. Most of these fish species are migratory, and various age-classes of a species often have different distributions (Crawford 1980). Certain species also have two or more independent populations. For example, the population of pilchards off South Africa is apparently independent of the Namibian population (Crawford 1981a).

Off South Africa the purse-seiners concentrated initially on pilchard and horse mackerel but later developed a multi-species fishery. To a certain extent the annual fluctuations in the catches of the different species were out of phase, so that the total annual catch remained fairly stable, although by the 1960s and 1970s there was good evidence of overexploitation of certain populations (Newman and Crawford 1979). Pilchard landings reached a peak in the years 1960-63 (Fig. 2) following exceptionally strong recruitment between 1956 and 1959 (Newman and Crawford 1980, Crawford 1981a), but decreased dramatically from 1964 to 1967. Catches of horse mackerel decreased 100-fold in 20 years and have not recovered (Fig. 2). Much of the increased fishing effort was diverted to anchovies (Fig. 2), with a reduction in the net mesh diameters from 32 to 12.7 mm in 1963-65 (Crawford 1981a). Currently, anchovies are the most commonly caught shoaling fish off South Africa. Over half the catch comprises fish of one year old or less and Crawford 1981b suggested that older anchovies were infrequently accessible to seabirds due to their migratory movements and the effects of the fisheries. Smallpilchards, 2-4 years old, are still seasonally abundant on the south and east coasts of South Africa, but the older pilchards which were once abundant on the west coast have been "virtually eliminated" (Crawford 1981a, 1981b).

Similar trends occurred off Namibia (Fig. 3). The intensive exploitation of pilchards in the late 1960s led to a collapse of the stocks in 1971. The stocks recovered partially in 1973--74, but decreased again in 1976 (Cram 1978). The pilchard catch exceeded 1.3 million metric tons in 1968. which was well in excess of the 0.8 million metric tons estimated to be the sustainable yield (Newman 1970). Intense exploitation of anchovy, which partially replaced pilchard in catches, was followed by a decrease in catches in 1977, when several processing factories were forced to close. Populations of the pelagic goby (Sufflogobius bibarbatus) may have increased off Namibia north of Lüderitz in the 1970s (Cruickshank et al. 1980). This small shoaling species is of little commercial importance but is now important in the

diets of some seabirds (see below).

Coinciding with the changes in fish populations were changes in the size and age structure of some species (Fig. 4) and reductions in egg production (Cram and Visser 1973, Cram 1978, Newman and Crawford 1979, Crawford 1980). These changes appear to be related to overfishing. CurrentFigure 2 Annual catches of pilchard, anchovy, and horse mackerel off South Africa. 1950-78, plotted on a logarithmic scale. From Frost et al. (1976) with additional data from Newman and Crawford (1979).

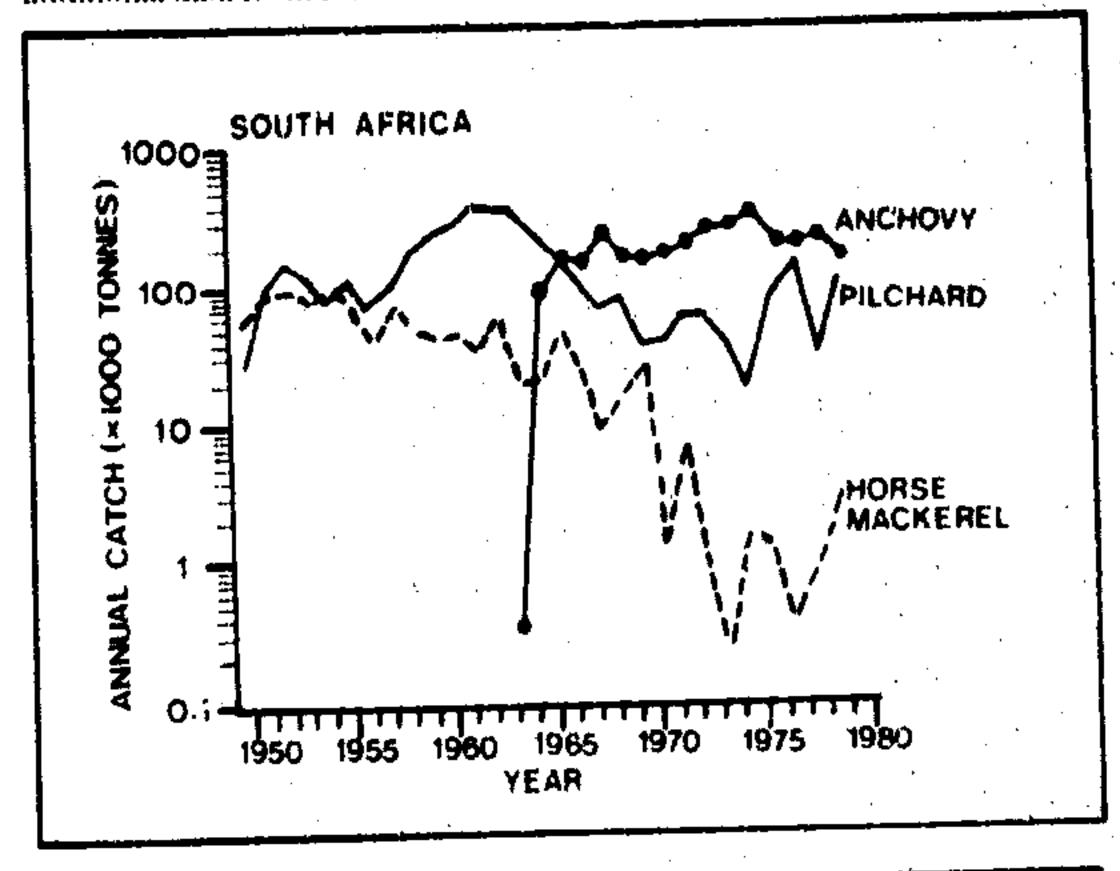
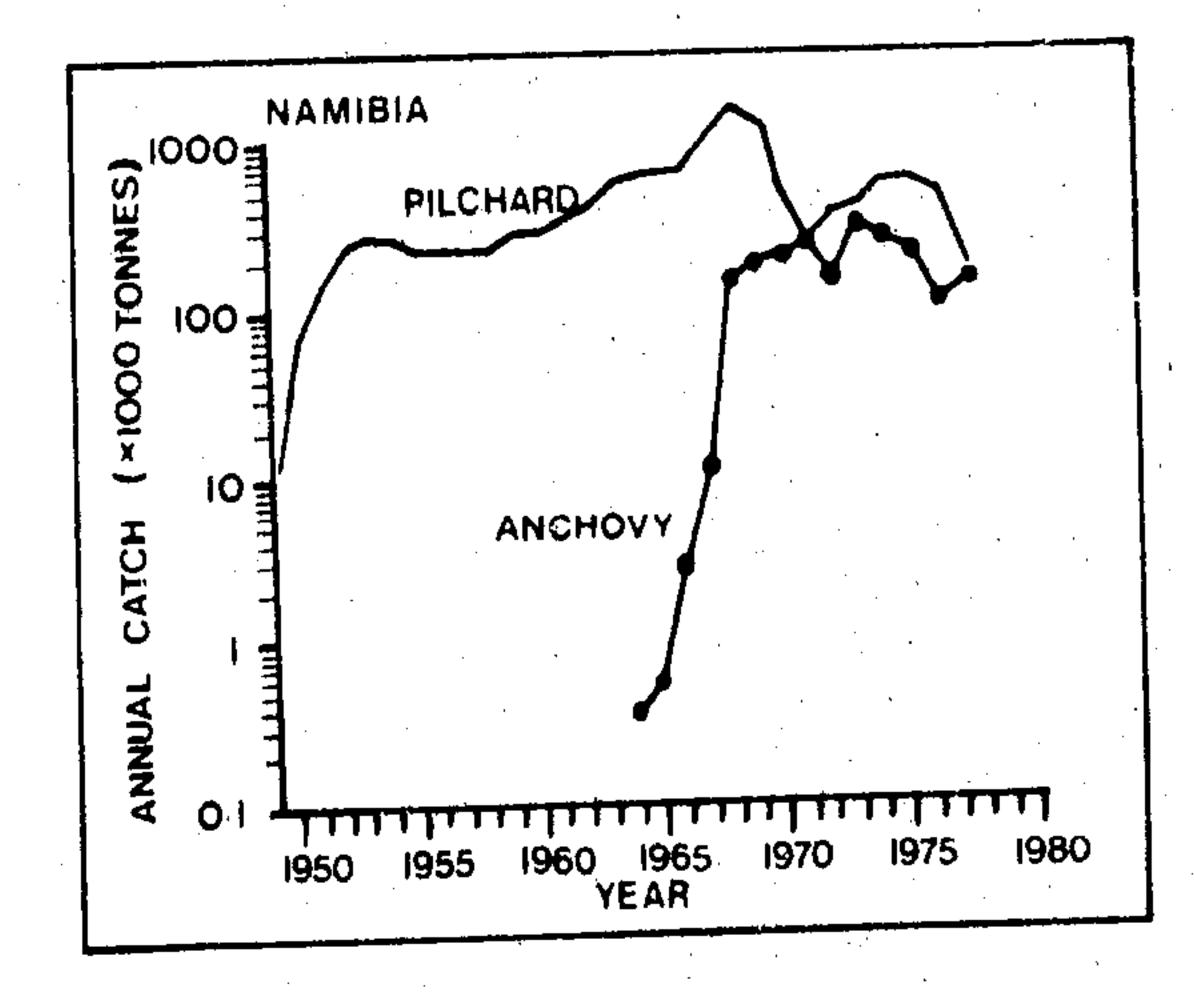


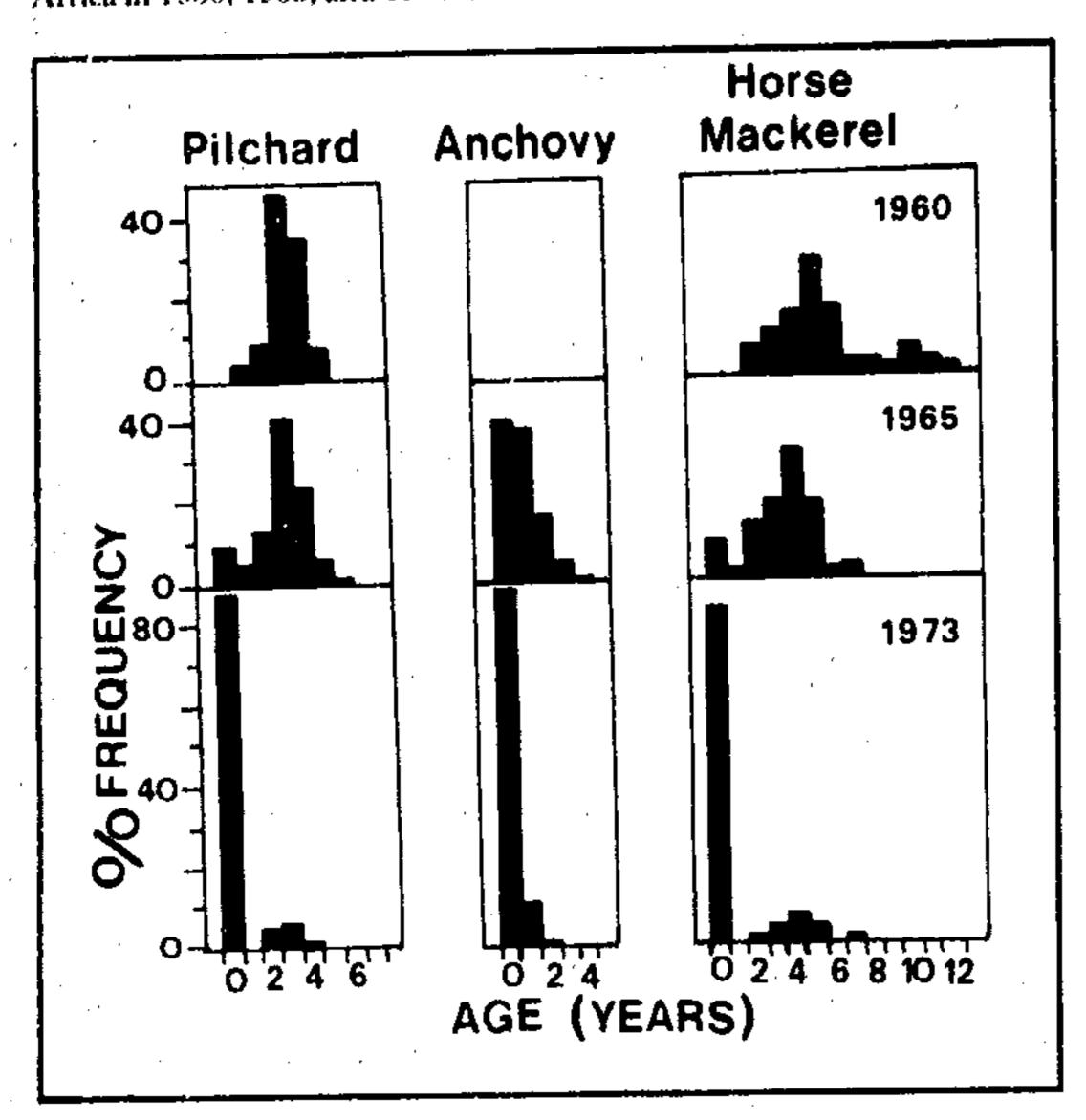
Figure 3 Annual catches of pilchard and auchovy off Namibia, 1950-77, pionest ona logarithmic scale. From Frosc*et al.* (1976) with additional data from Cram (1978).



ly efforts are being made to diversity the industry, to shift the emphasis of production to more fish for direct human consumption and less fish meal, and to reduce the overall fishing effort (Cram 1978, Newman and Crawford 1979).

Most of the seabirds that breed in southern Abrica feed fairly close inshore. For example 85, 95, and 70% of the Jackass Penguins, Cape Cormorants, and Cape Gannets, respectively, feed within 50 km of the coast (Cooper 1984). Since the purse-seine industry operates within the same area, and removes the same suite of fish species as do these scabirds, this fishery is potentially a major competitor of these scabirds (Frost et al. 1976; Crawford and Shelton 1978, 1981). The pelagic shoaling fish are also caten by large populations of Cape fur scals (Arctocephalus pusillus) and several species of predatory fish (see references in Crawford 1980).

Figure 4
Age composition of pilchard, anchovy, and horse mackerel off South
Africa in 1960, 1965, and 1973. From Newman and Crawford (1979)



A second major fishery in southern Africa involves mid- and deep-water stern trawling, usually at the edge of the continental shelf, 90–150 km offshore. Hake (Merluccius spp.) are the most common catch. The demersal fish taken by trawlers are not normally freely available to seabirds, but the recent development of this industry has attracted very large numbers of seabirds which eat the netted fish and discarded offal (Sinclair 1978, Abrams 1983, Cooper 1984). The only locally breeding seabirds that regularly visit trawlers are Cape Gannets and Kelp Gulls, but they are greatly outnumbered by albatrosses, shearwaters, and petrels. Jackass Penguins, Cape Cormorants, and other local breeders appear to be precluded from this new food resource by their restricted feeding ranges and inappropriate feeding methods.

Quantitative estimates of the food taken by seabirds from demersal trawlers, and the proportions of this food eaten by each seabird species are not yet available. These trawlers provide a great quantity of food to certain migrant seabirds (Sinclair 1978, Abrams 1983), but it is not known whether this has affected their survival or population sizes.

6. Changes in breeding seabird populations

6.1. Changes detected from colony surveys

Censuses of the major seabird colonies in southern Africa have been sporadic until recently (Crawford and Shelton 1981). Fairly complete censuses were made in 1956 (Rand 1960b, 1963a, 1963b) prior to the intensive exploitation of pelagic shoaling fish. Incomplete censuses were made in 1967–69 and complete censuses in 1978–81 (Crawford and Shelton 1978, 1981). Comparisons of these data show some of the effects of changing fish stocks. Although the population trends are clear, the actual numbers need to be interpreted with caution. Many counts apply to only one

Table I
Population estimates for Cape Gannets, Jackass Penguins, and Cape
Cormorants, 1956–78, in South Africa and Namibia. From Crawford and
Shelton (1981)

	Year				
Locality	1956	1967 or 73*	1978		
Cape Gannet			_		
(number of individuals)	ganto	44.054	0500		
All islands off South Africa	50913	44 954	97 045		
All islands off Namibia	169 656	131 818	88 706		
Total population	220 569	176 772	185 751		
Jackass Penguin (summer breeding population)					
All islands off South Africa	148 154	Incomplete data	-80160		
All islands off Namibia	88 367	48 039	-24484		
Total population	236521	Incomplete data	104 344		
Cape Cormorant (number of individuals)					
All islands off South Africa	90 403	No data	177520		
All guano platforms in Namibia	19 984	521 000	112 181		
	6161	No data	82 277		
All islands off Namibia			371 978		
Total population	116548	Incomplete data	371378		

^{*}Data is for 1967 for Cape Gannet and Jackass Penguin and 1973 for Cape Cormorant

time of year but some of the seabirds have extended or variable breeding seasons. Aerial photography was extensively used and this method does not always give reliable estimates of total breeding populations of all species (Frost et al. 1976, Crawford and Shelton 1981).

There were fewer Gape Gannets breeding in 1978 than in 1956, but slightly more than in 1967 (Table 1). Breeding populations at all three gannetries in Namibia decreased, coinciding with a decrease in the biomass of pilchards in that region (Crawford and Shelton 1981). The population counted in Namibia in 1978 was only 52% of that of 1956 (Table 1). Populations at the two gannetries on the west coast of South Africa decreased from 1956 to 1967 but subsequently increased and in 1978 exceeded the 1956 size (Crawford and Shelton 1981). The initial declines followed decreases in the pilchard biomass, whereas recent increases might have been due to increased availability of anchovy to the gannets (Crawford and Shelton 1981). Gannet numbers at the colony on Bird Island, Algoa Bay on the east coast doubled between 1956 (40 156 breeding adults) and 1977–79 (average over three seasons = 85 838 breeding adults) (Randall and Ross 1979, Batchelor 1982).

Censuses of the summer breeding population of Jackass Penguins indicate a large decrease in the total population (Table 1). The changes were not uniform throughout the bird's range. There were severe decreases at all five colonies south of Lüderitz, Namibia (Fig. 1) which were attributed to the collapse of the local pilchard stocks (Crawford and Shelton 1981) and, at one island, to interference from Cape fur seals (Shaughnessy 1980). By contrast, numbers of Jackass Penguins increased at Mercury and Ichaboe islands, north of Lüderitz (Crawford and Shelton 1981), where the birds appear to be exploiting. locally abundant pelagic gobies (see below). In South Africa, the large decrease (Table 1) was entirely due to a 50% or greater decrease in the sizes of colonies on the west coast, attributed to low pilchard biomass and apparent failures of the penguins to respond to increased anchovy biomass (Crawford and Shelton 1981). At Dyer Island on the south coast (Fig. 1) the population increased five-fold from 1956 to 1978, and Crawford and Shelton (1981) speculated that this might be due to movements of penguins away from the

west coast to a region where pilchard were still available. Penguin numbers at islands in Algoa Bay (Fig. 1) also increased (Crawford and Shelton 1981), perhaps indicating that food availability was not a serious problem there.

The serious decrease in the population of Jackass Penguins is also evident in the decline in numbers of eggs harvested from islands off South Africa. At Dassen Island, the largest colony off South Africa, over 450 000 eggs were harvested annually between 1900 and 1930, indicating a minimal breeding population of 300 000 adults (Frost et al. 1976). In 1978 the population was only 22 440 adults (Crawford and Shelton 1981). Frost et al. (1976) concluded that "the decline in the Jackass Penguin population was initiated by prolonged over-exploitation of eggs, together with excessive disruption of breeding birds." Since egg-collecting and guano-harvesting at penguin colonies has now officially ceased, competition with purse seiners is possibly the greatest human threat to the Jackass Penguin (see Section 8: Discussion).

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Accurate estimates of the total breeding populations of Cape Cormorants are difficult to obtain (Crawford and Shelton 1981), but the available data indicate an overall increase in the total population since 1956 (Table 1). The increase of Cape Cormorants at guano platforms between 1956 and 1973 (Table 1) was attributed to the construction of a large platform at Swakopmund in the early 1960s (Crawford and Shelton 1981). The subsequent decrease in numbers between 1973 and 1978 was related to the decline in pilchard biomass over this period (Crawford and Shelton 1981). Cape Cormorant populations off South Africa increased after 1956 (Table 1). The numbers at colonies on the west coast increased by 50% or more, while the population at Dryer Island, the only major colony east of Cape Point, increased from 3186 in 1956 to 46 393 birds in 1978 (Crawford and Shelton 1981).

The population of Bank Cormorants appears to have doubled between 1956 and 1978 to a total of 18 000 birds (Cooper 1981, 1984). The increase occurred in Namibia where the Bank Cormorants appear to have benefited from the decrease in Cape Gannet numbers at nesting colonies and the availability of a large population of the pelagic goby (Cooper 1984).

The small population of White Pelicans breeding in coastal Namibia has apparently declined during the late 1960s and 1970s and Crawford et al. (1981) have related this to declining local populations of the Cape Cormorants whose eggs and chicks are preyed on by the pelicans.

The populations of Crowned and Whitebreasted cormorants and Kelp Gulls have shown local fluctuations in size historically but no clear overall trends are discernible (Crawford et al. 1981, Brooke et al. 1982, Crawford et al. 1982a). The Roseate Tern (Sterna dougallii) has decreased in numbers, but this is not attributed to changes in prevavailability (Randall and Randall 1980). Little or nothing is known about overall changes in the population sizes of other breeding species: Hartlaub's Gulls, Greyheaded Gulls (Larus cirrocephalus), Swift Terns (Sterna bergii), Damara Terns (S. balaenarum), and Caspian Terns (S. caspia). Reasonably accurate estimates of present population sizes do exist for these last five species (J. Cooper, unpubl. data).

6.2. Changes estimated from guano harvests

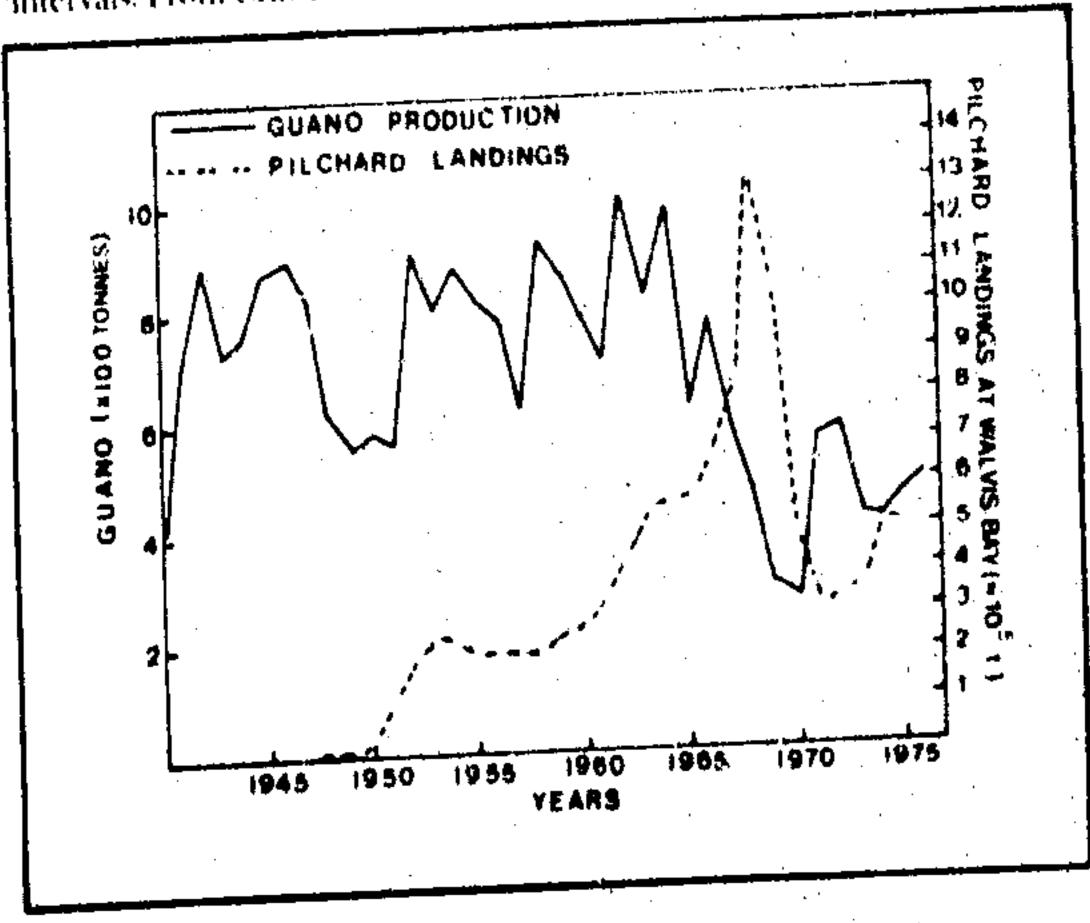
In the absence of a long series of censuses of seabird populations, Crawford and Shelton (1978) and Siegfried

and Crawford (1978) used the records of the annual guano harvests to monitor population changes of seabirds. Guano records are available from many islands since before 1900. Virtually all of the guano was produced by Cape Cormorants, Cape Gannets, and Jackass Penguins. These records illustrate some of the effects of intensive fishing on seabird populations.

The guano records from the colony of Cape Cormorants at the Bird Rock platform showed the effects of intensive fishing for pilchard on the Namibian coast, near Walvis Bay (Fig. 5). Guano harvests fluctuated widely prior to 1965, then decreased significantly. The decrease coincided with an exponential increase in the landings of pilchards by purse seiners and a corresponding decrease in the catch per unit effort (Crawford and Shelton 1978). Guano harvests correlated significantly with available fish stocks at some other locations too (Fig. 6). Cyclic fluctuations of guano harvests also indicate the possibility of periodic oscillations in the factors affecting seabirds at some colonies (Crawford and Shelton 1978, Siegfried and Crawford 1978).

Crawford and Shelton (1978) found that guano harvests correlated well with known population changes of seabirds at several localities, although this is not always the case. For example, Randall and Ross (1979) showed that the population of Cape Gannets at Bird Island, Algoa Bay. doubled between 1956 and 1978, but the guano harvests actually decreased during this period. Guano harvests were affected by many variables including labour problems and periodic heavy rainfall which washed away guano (Craw-) ford and Shelton 1978, Randall and Ross 1979). Also, non-breeding birds which roosted, and thus defecated, on islands, often greatly outnumbered the breeding birds (Frost et al. 1976, Furness and Cooper 1982) and thus guanoharvests did not only reflect the breeding populations. The proximity of profitable fish shoals to the breeding colonies would affect the amount of time the birds spera on the islands and thus the amount of guano deposited. Crawford and Shelton (1978) also suggested that variable guano-

Figure 5
Cuano production from Bird Rock platform near Walvis Bay, Nambia and total catch of pikhard off Walvis Bay, 1940–75. The annual totals of guano have been smoothed by calculating moving averages of 3-year intervals. From Crawford and Shelton (1978)



harvests might reflect changes in breeding success of the birds, and that the effects of food shortages on adult populations might be deferred. Despite some reservations, guano harvests are useful indicators of the effects of intensive fishing on seabird populations.

Guano harvests from all the South African islands combined, showed wide fluctuations prior to 1950, reduced fluctuations from 1950-62, and a significant decrease since 1962 (Fig. 7). These changes coincided with the onset of intensive purse-seining in the 1950s and the severe reductions in certain fish stocks, notably pilchards, in the 1960s and 1970s (Crawford and Shelton 1978). Guano harvests from Namibia likewise showed reduced fluctuations since the 1950s, but there was little overall decrease in the average harvest (Fig. 7).

Figure 6
Annual guano production from Bird Island, Lamberts Bay off the west coast of South Africa (smoothed by threes) and the biomass of 0-year-old South African pilchard, 1950-76. From Crawford and Shelton (1978)

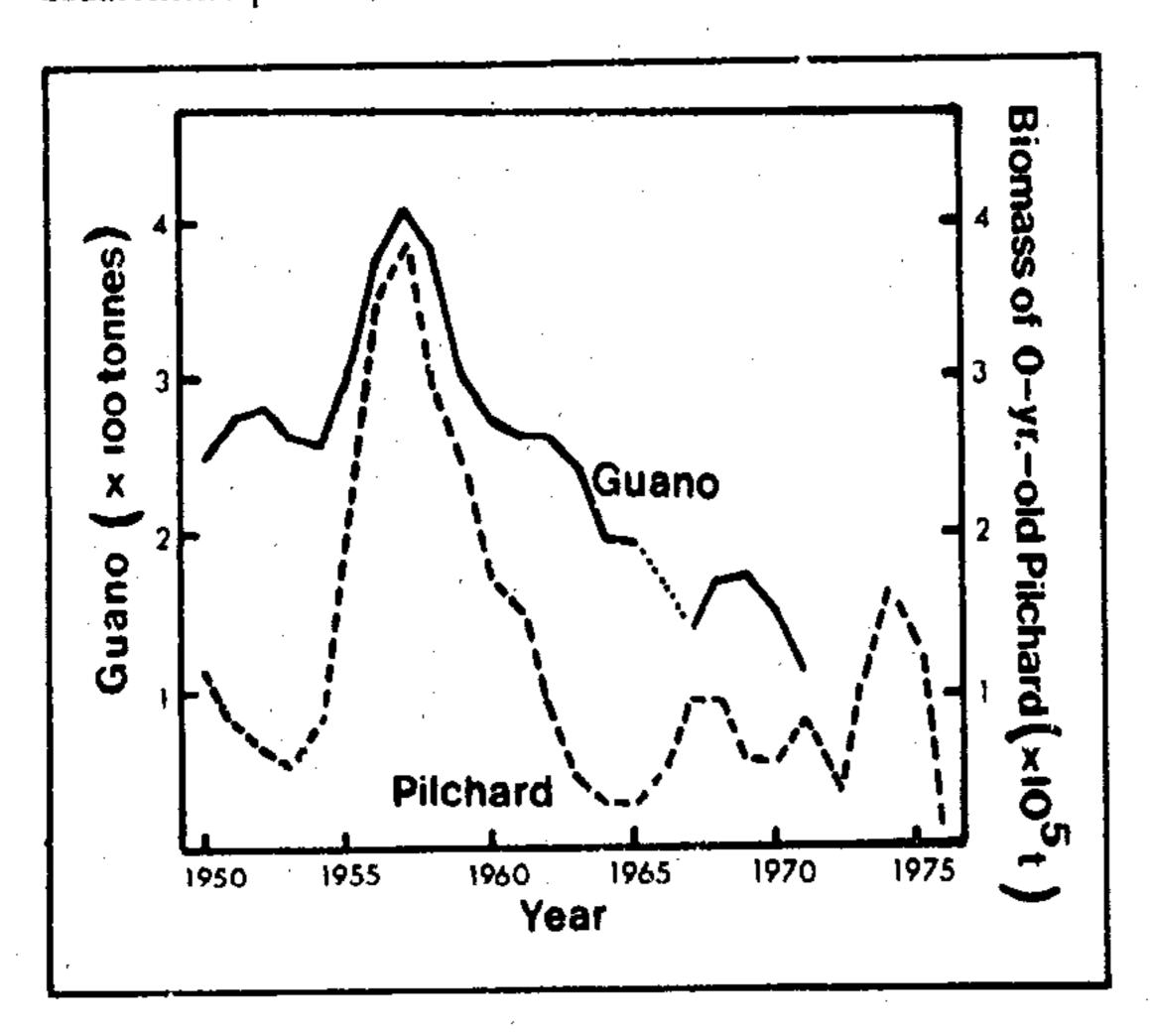
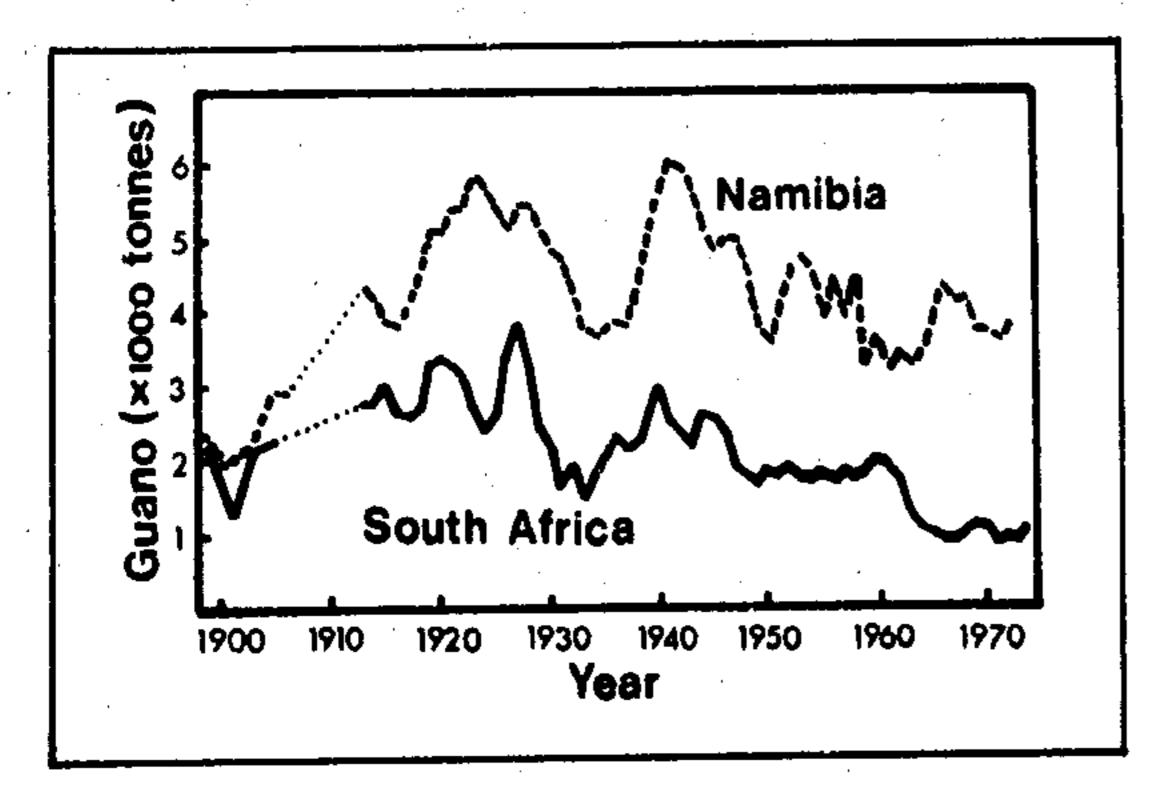


Figure 7
Guano production on all islands situated off South Africa and Namibia, excluding the guano platforms (smoothed by threes). From Crawford and Shelton (1978) with additional data from Newman and Crawford (1979)



7. Dietary changes in the seabirds

Analyses of the diets of Cape Gannets, Jackass Penguins, and Cape Cormorants on the west coast of South Africa and in Namibia are shown in Tables 2 and 3. These data show the percentage relative abundance of items in the stomach contents. Analyses of the percentage mass of prey items in stomach contents show the same trends (Crawford and Shelton 1978, 1981; Cooper 1984; Furness and Cooper 1982). Dietary changes between the mid 1950s and 1977–80 show the effects of the very intensive purse-seine fishing

between these periods.

The larger-sized shoaling fish, notably pilchards and horse mackerel, which were very important prey for all three seabird species in the 1950s, became absent or much reduced in the diets of the birds (Tables 2 and 3). This trend correlated with the decrease in landings of pilchards and horse mackerel by purse seiners (Figs. 2 and 3). In 1977-80, anchovies were the main food resource for all three seabird species on the west coast of South Africa, and for Cape Gannets in Namibia. Round-herring increased in importance in the diets of the penguin and the Cape Cormorant. The increase of pelagic gobies in the diets of Jackass Penguins and Cape Cormorants breeding north of Lüderitz, Namibia possibly indicates an increase in the stocks of this fish in a localized area (Cruickshank et al. 1980). The penguins breeding on the islands just south of Lüderitz did not eat gobies to the same extent in 1980 (Table 3).

Despite changes in the species composition of their diets, between the 1950s and 1977–80, the Jackass Penguin and Cape Cormorant continued to feed predominantly on the pelagic shoaling fish. These birds possess anatomical and behavioural adaptations for exploiting this type of prey (Siegfried et al. 1975a, 1975b; Burger 1978). The Cape Gannets on the west coast of South Africa have shown a shift in their diet to include more non-shoaling fish species, and to include demersal hake scavenged from the deep-sea

trawlers (Cooper 1984).

Batchelor (1982) made an intensive study from 1978 to 1981 of the diet of Cape Gannets breeding on Bird Island, Algoa Bay on the east coast of South Africa. He found that pilchards were the most common prey, comprising 44.4% of the numerical frequency of items in regurgitations, with anchovy (34.0%) and sauries (Scomberesox saurus) (14.0%) also common. Scavenging of demersal fish from trawlers was also evident but was apparently not as frequent as found by Cooper (1984) for gannets on the west coast. There are no data from Algoa Bay from earlier years with which to compare Batchelor's (1982) data. Batchelor found during the 4 years of study that pilchards became less important, and anchovies and sauries more important in the gannets' diet.

8. Discussion

There have been major changes in the populations of pelagic fish species off southern Africa during the past three decades. Fisheries biologists have attributed these changes to overexploitation of certain stocks by purseseiners (Crawford and Shelton 1978, Newman and Crawford 1979), although this might have accentuated naturally occurring population fluctuations (Crawford and Shelton 1978). Although the fisheries have had reduced harvests, it is difficult to assess whether there has been an overall

decrease in the quantities of fish available to seabirds in southern Africa. The available evidence is inadequate and contradictory.

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Analyses of catch statistics indicated that the combined abundance of all commercially important pelagic fish species in South Africa declined by 60-70% since 1960 (Newman and Crawford 1979). The guano data have been interpreted as indicating a 50% reduction in availability of fish to seabirds in the same interval (Newman and Crawford 1979). By contrast, censuses of breeding birds indicate an increase in abundance of seabirds between 1956 and 1978 in South Africa (Table 2). In Namibia, despite declining landings by fishermen, the guano harvests did not decrease significantly. Populations of Cape Cormorants in Namibia were greater in 1978 than they were in 1956, although this was probably due to the increased availability of nest sites on guano platforms. Clearly the factors affecting seabirds are not identical to factors affecting fishing harvests, and continued monitoring of the populations and diets of scabirds in specific regions is needed.

The cause for concern is perhaps not that there might be fewer pelagic fish, of all species, now available to seabirds but that certain important changes have occurred which have affected seabirds: there are now fewer pilchards and horse mackerel available; there are fewer large fish available, of any pelagic shoaling species. Pilchards were the most frequent prey of Cape Gannets, Cape Cormorants,

and Jackass Penguins in 1956 and the depletion of the stocks of adult pilchards on the west coast of South Africa and off Namibia has had major consequences for these birds. It is significant that Crawford and Shelton (1978) found correlations between local pilchard abundance and guano harvests at several localities in these regions. Horse mackerel were important in the diets of these seabirds oft South Africa in 1956, but following the drastic reduction of this fish in purse-seine catches, were negligible in their diets in 1977–79. Cape Gannets, Jackass Penguins, and Cape Cormorants have all shown capability of switching prev species, when pilchards and horse mackerel were apparently less available, but they have not been equally successful at adapting to the changes.

The decrease in the population of Cape Gamets off Namibia seems to be associated with the reduced availability of pilchards. The decrease was perhaps mediated by the availability of anchovies, although the greatest concentrations of anchovies are not close to the gannetries (Crawford and Shelton 1981). The gannet populations on the west coast of South Africa have remained fairly stable and pilchards and horse mackerel have been replaced in their diers by anchovies, non-shoaling pelagic fish and hake taken from demersal trawlers (Cooper 1984). The gannet has a greater foraging range and a larger gape than the penguin and the Cape Cornorant, and appears better suited to scavenging the large fish available at the offshore

Table 2
Changes in the diets of Cape Gannets, Jackass Penguins, and Cape Cornorants in the southwestern Cape coast, South África. The species composition of the birds' diets is expressed as percentage relative abundance of items in the stomach contents

abundance of items in the siomach contents					Jackass Penguin		Cape Cormorant					
Sample period: Source of data:	1953-54 Davies	1954-55 Davies (1956)	Rand			1953-54 Davies (1955)			1953-54 Davies (1955)	1954-55 Davies (1956)	1954-56 Rand (1960b)	1977–78 Cooper (1984)
Pilchard Anchovy Horse mackerel Round herring	(1955) 44 30 18 0	62 26 11 0	19 25 30 1	2 78 1 3 0	13 39 1 1	37 2 23 -0 20	19 44 2 0	1 81 0 14 0	36 32 21 	11 19 11 0	15 12 16 3	50)
Mackerei Other fish, crustac and cephalopod		ì	21	ļti	45	18		-		1 h	<u></u>	<u>ju</u>
No. of birds examined	98	191	257	1224	203	16	112	(90)	17	1.6	204	119

Table 5
Changes in the diets of Cape Gannets, Jackass Penguins, and Cape Cormorants in Namibia. The species composition of the birds' diets is expressed as relative abundance of items in stomach contents

		To the Books of the			Cape Cormorant		
ance of items in stomach contents Cape Gannet		Jackass Penguin			1957-58	1978-79	
1957-58 Matthews	1978-79 Crawford and	Matthews	Crawford and	Crawford and	Matthews (1961)	Crawford and Shelton (1981)	
(1961)	Shelton (1901)		(1	(1	76	()	
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	1957-58 Matthews (1961)	1957-58 1978-79 Matthews Crawford and (1961) Shelton (1981) 85 1 85 1 95 95 95 95 95 95 95 95 95 95 95 95 95	1957-58 1978-79 1957-58 Matthews Crawford and (1981) Matthews (1961) (1961) Shelton (1981) (1961) 85 1 83 10 0 6 10 5 0 5 8 11	1957-58 1978-79 1957-58 1980* Matthews (1961) Crawford and (1961) Matthews (1961) Crawford and Shelton (1981) 85 1 83 0 0 85 0 0 10 0 6 0 0 5 0 92 5 8 11 9	1957-58	1957-58 1978-79 1957-58 1980* 1980* 1980* Matthews Crawford and (1981) Matthews (1981) Crawford and Shelton (1981) Crawford and Shelton (1981) Matthews (1961) 85 1 83 0 0 76 0 85 0 0 21 0 10 0 6 0 18 18 10 0 5 0 02 17 0 5 8 11 9 61 5 10 121 83 210	

^{*}From Mercury and Ichaboe islands, north of Lüderitz. †From Halifax and Possession islands, south of Lüderitz.

trawlers. The increase in the gannet colony at Algoa Bay was perhaps due to the availability of pilchards there. Pilchards were the most important prey of these gannets in 1978–81 (Batchelor 1982) and Crawford (1981a) has shown that there might still be seasonally abundant stocks of pilchard on the south and east coasts. Pilchards were very common in the stomach contents of hake caught near Algoa Bay but not in hake off the west coast (Crawford 1981a).

Jackass Penguins have almost certainly been adversely affected by the purse-seine fishery. The greatest concentrations of the penguins are on the west coast of South Africa and Namibia, where there has been the most intensive fishing and where stocks of the penguins' preferred prey have been depleted. The population of penguins has decreased alarmingly, despite the abundance of anchovies in some areas (Crawford 1981b). By contrast, penguin populations have increased on the south and east coasts, where there are stocks of 2-4-year-old pilchards (Crawford , 1981a). Jackass Penguins are thought to require predictable shoals of prey close to their breeding colonies, because of their restricted foraging range (Frost et al. 1976). Pilchards have a predictable temporal and spatial distribution, and are therefore probably better suited to the penguins than the less predictable anchovies (Crawford 1981a, 1981b). Jackass Penguins at two islands off Namibia appear to be successfully exploiting pelagic gobies, but further investigation is needed to determine whether this fish will continue to support the penguin population.

Crawford and Shelton (1978) speculated that the increase in the population of Jackass Penguins at Dyer Island might be due to immigration from the west coast. This requires confirmation. Such movements to favourable feeding areas could be an important adaptation for overcoming variability of the food resource. The Jackass Penguin is regarded as a threatened species (Frost et al. 1976). Its population and diet are being monitored at a few colonies. These activities need to continue and expand and several of the research priorities outlined by Frost et al.

(1976) still require attention.

The recent changes in the pelagic fish populations have apparently affected the Cape Cormorant less than the gannet and the penguin (Crawford and Shelton 1981, Cooper et al. 1982). These cormorants are the smallest of these species, and perhaps better adapted to feeding profitably on the smaller shoaling fish. Crawford and Shelton (1981) showed that aspects of the breeding biology of the Cape Cormorant are well adapted to exploiting variable food resources and moving into colonies near available food supplies. Off South Africa these cormorants have successfully exploited the available anchovies and round herring, and their numbers have increased. The very large increase of the Dyer Island colony might be related to the availability of pilchard there. Off Namibia, the censuses and records of guano harvests at the platforms show that the population of Cape Cormorants increased when additional breeding space became available in the 1960s, but that the population decline that followed coincided with reductions in the pilchard biomass (Crawford and Shelton 1981, Cooper et al. 1982).

Although there has been no apparent adverse effect of the fishing industry on the overall population of Cape Cormorants, Cooper *et al.* (1982) have warned that over-exploitation of anchovies and other pelagic fish could lead to drastic decreases in Cape Cormorant numbers.

Reductions of pilchard populations probably meant a reduction in the quality of fish available to seabirds off southern Africa. Batchelor (1982) showed that the energy content and concentrations of protein and fat were higher in pilchards than in anchovies, sauries, horse mackerel, hake (Merluccius capensis), and squid. Batchelor (1982) found that Cape Gannet chicks experimentally fed on pilchards had higher assimilation efficiencies, growth rates, and maximum weights than chicks fed on hake. Further experiments are required to test the effects of fish quality on breeding success in South African seabirds.

begun to monitor population changes and breeding success in selected seabird species, to assess their use as indicators of available fish stocks (Newman and Crawford 1979; P.A. Shelton, pers. comm.). The underlying assumption is that food availability is the ultimate limiting factor for these populations. This might not always have been the case and we present a series of graphical models, showing how human interference might have altered seabird populations.

and the factors limiting them (Fig. 8).

We suggest that, prior to the arrival of European settlers, 330 years ago, the overall population of all seabirds in southern Africa was limited by the availability of nest sites. All major seabird colonies were on small offshore islands. The breeding success and densities of birds on each island might have been restricted by the availability of food within the foraging range of the breeding adults, and hence fluctuations in local fish populations might have caused fluctuations in guano deposits, as seen recently on some islands. But the lack of suitable islands near some of the richest foraging areas, particularly off Namibia, probably limited overall numbers. An analogous situation is found off the coast of Senegal, where despite high marine productivity there are few seabirds. This is possibly a consequence of a lack of suitable nesting habitat (Brown 1979). Under these conditions, fluctuations of fish populations in time and space might seldom have had major effects on total seabird numbers (Fig. 8a).

Human disturbance reduced the availability of suitable nesting habitat. The exploitation of eggs and guano led to the extinction of some seabird colonies and the reduction of others (Westphal and Rowan 1971, Frost *et al.* 1976, Shaughnessy and Shaughnessy 1978). These disturbances might have reduced overall numbers of seabirds (Fig. 8b).

The construction of the huge guano platforms in the 1930s and 1960s at Walvis Bay, Cape Cross, and Swakopmund (Berry 1975; Crawford and Shelton 1981) increased the availability of nesting habitat in the proximity of the very productive sea off Namibia. There have been over 500 000 Cape Cormorants breeding or roosting on these platforms (Berry 1976a), where previously there had been no natural offshore islands. Some Cape Cormorants and Great White Pelicans had previously been using a few temporary sandy islands in coastal lagoons (Crawford et al. 1981, Cooper et al. 1982). The overall population of seabirds probably increased at this time (Fig. 8c).

Following the reduction of certain populations of pelagic shoaling fish by purse seiners, it now seems probable that food is limiting seabird populations in many areas of southern Africa (Fig. 8d). Direct censuses plus analysis of guano harvests have shown that numbers at some seabird colonies seem to be correlated with the abundance of certain local fish stocks, notably those of pilchards (Crawford and Shelton 1978, 1981; Cooper 1984). This trend is not always

apparent because some seabird species have shown greater resilience to change than others. Reductions in large populations of seabirds have been found in ecologically similar coastal areas of Peru. California, and elsewhere, following intensive commercial fishing of shoaling fish (Jordan 1967, Idyll 1973, Ainley and Lewis 1974, and these proceedings).

There have been few attempts to relate apparent reductions of fish to poor breeding success in seabirds in southern Africa. High chick mortality, nest-desertion, and reduced breeding success of Cape Cormorants at several colonies have been attributed to low food availability (Berry 1976a, Crawford et al. 1980), but Rand (1960b) noted similar events in years before there was evidence of overfishing.

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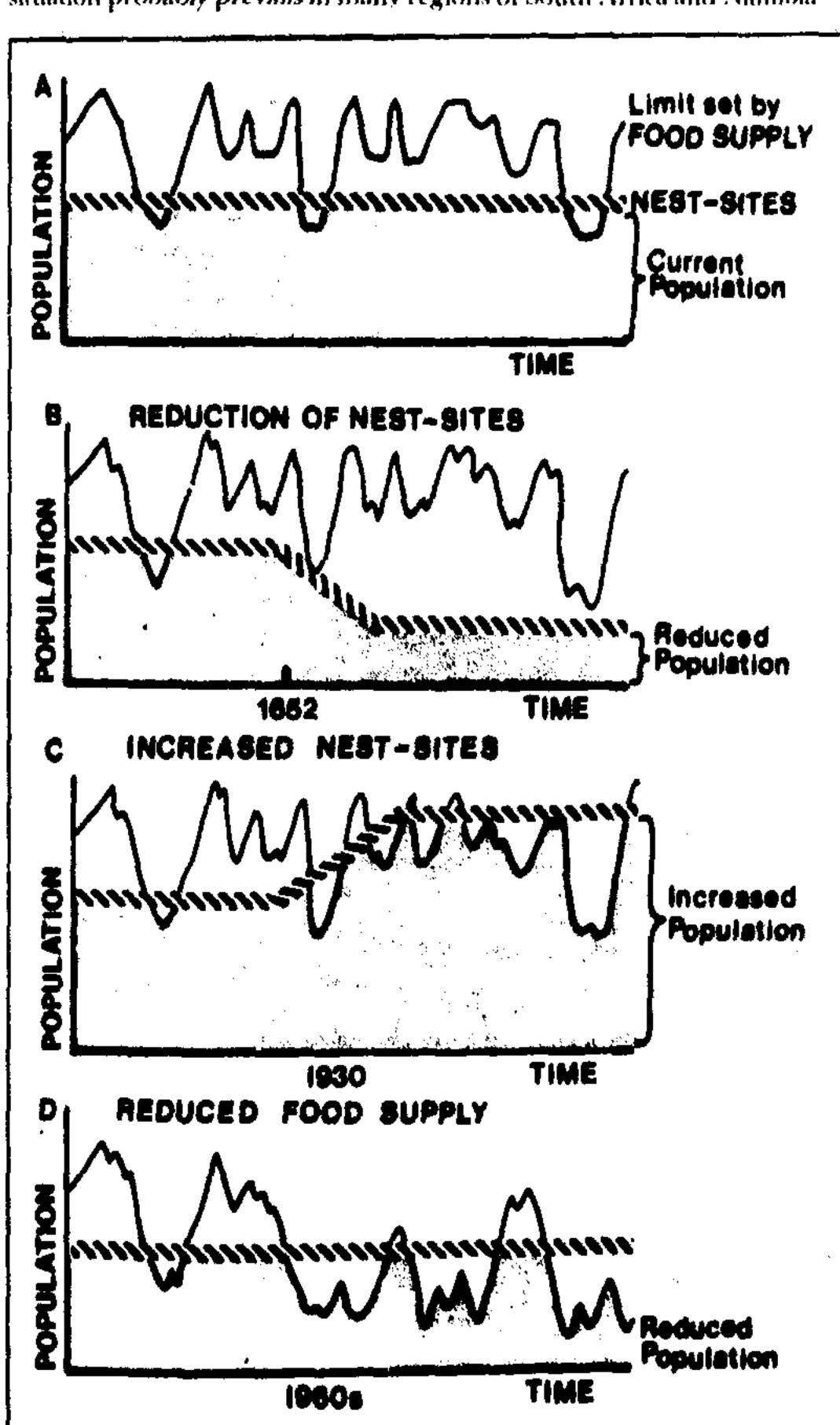
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Factors possibly limiting populations of seabirds in southern Africa. A — Populations limited by the availability of suitable nesting sites. This situation might have occurred prior to the settling of Europeans in South Africa and Namibia, and might still apply to certain regions. B — Since the arrival of Europeans in the 17th century, exploitation and disturbance reduced the availability of undisturbed nest sites, possibly resulting in a population decline. C — The availability of nest sites increased with construction of guano platforms and the population of Cape Cormorants and some other species probably increased and might have become limited by food. D — Following a reduction in food availability related to intensive fishing, seabird populations were limited by food, not nest sites; the overall population size decreased and fluctuated with changing fish stocks. This situation probably prevails in many regions of South Africa and Namibia



It is a healthy sign that fisheries biologists have begun to include seabirds in their management plans. A greater knowledge of the responses by scabirds to changes in the availability of their prey is essential for seabird conservation and in the use of seabirds to monitor fish stocks. In particular it is essential to determine the factors limiting seabird populations at specific colonies, and the adaptability of each species for using alternative food resources. The effects on seabirds of changing fishing activities, such as the possible development of a pelagic goby harvest, would need to be monitored. Clearly seabird conservation and fisheries management are interlinked, and it is a welcome sign that the South African Government's Sea Fisheries Institute has recently appointed its first permanent seabird ornithologist.

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