Benguela Dynamics
Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington (Eds). *S. Afr. J. mar. Sci. 19: 355–364*
1998

RESPONSES OF AFRICAN PENGUINS TO REGIME CHANGES OF SARDINE AND ANCHOVY IN THE BENGUELA SYSTEM

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Regional trends in numbers of African penguins *Spheniscus demersus* conform with an altered distribution of sardine *Sardinops sagax* and anchovy *Engraulis capensis* prey. In the 1950s, sardine dominated the pelagic fish component of the Benguela system. Abundance of this fish decreased in the 1960s and early 1970s and it was replaced by anchovy. Beginning in the early 1980s, sardine started to increase and anchovy to decrease in abundance. The decrease of the sardine resulted in collapses of colonies of African penguins between Lüderitz and Table Bay. Although colonies east of Table Bay increased, the overall population of African penguins fell by 25%. As the Benguela system started to revert to one dominated by sardine, penguin colonies between Lüderitz and Table Bay stabilized. Three new colonies were established in the vicinity of Table Bay, but the large colony at Dyer Island underwent a massive decrease. As a result, overall numbers of African penguins decreased by a further 19%. During shifts between regimes dominated by sardine and anchovy, African penguins that are breeding for the first time immigrate to colonies where food is plentiful. Inability of African penguins to cope with recent shifts between regimes may have resulted from increased competition for food with fishermen and seals during the 20th century.

Worldwide, where anchovies *Engraulis* spp. and sardine *Sardinops sagax* co-occur, the two species alternate in relative abundance (Skud 1982). Long-term, large-scale shifts in relative abundance are termed regimes (Lluch-Belda *et al.* 1989, 1992). Off the west coasts of South America and southern Africa, large changes in populations of several seabird species that feed on anchovy and sardine are considered to be responses to the regime changes (Crawford 1987). In the Benguela system, relatively discrete stocks of both sardine and anchovy *E. capensis* are found to the north and south of an area of intense upwelling near Lüderitz, Namibia (Crawford *et al.* 1987, 1989).

The African penguin *Spheniscus demersus*, endemic to southern Africa, now breeds at 27 localities between Hollams Bird Island, Namibia, and Bird Island in Algoa Bay, South Africa (Fig. 1, Crawford *et al.* 1995a). A large decrease in numbers of African penguins during the 20th century, from about 1.5 million adults (Shannon and Crawford in press) to <0.2 million (Crawford *et al.* 1995a), has led to its classification as "vulnerable" (Brooke 1984). This term is applied to a taxon that is not immediately endangered, but is facing a high risk of extinction in the wild within 100 years (Croxall *et al.* 1996).

This paper describes the responses of African penguins to regimes of sardine and anchovy that have occurred in the Benguela system since 1950, by which date purse-seine fisheries had been established off Namibia and South Africa (Crawford *et al.* 1987).

REGIMES OF SARDINE AND ANCHOVY OFF SOUTHERN AFRICA

Abundance

When sardine was abundant in the 1950s and the 1960s, a total of 13.5 million tons was harvested by purse-seine fisheries, 3.7 million off South Africa and 9.8 million off Namibia. The South African sardine fishery collapsed in the mid 1960s, ahead of that off Namibia, which decreased in the early 1970s (Crawford *et al.* 1987). In the following two decades, from 1970 to 1989, the sardine catch totalled 5.7 million tons, of which 1.2 million tons were taken from South Africa and 4.5 million tons from Namibia. The annual South African catch peaked at 0.41 million tons in 1962; the lowest catch (16 000 tons) was recorded in 1974 (Fig. 2a). Off Namibia, 1.4 million tons was caught in 1968, but only 12 000 tons in 1980 (Fig. 2b).

Virtual population estimates of the spawner biomass of sardine off South Africa peaked at 0.63 million tons in 1961, falling to 0.03 million tons in 1977 (Fig. 3, Armstrong *et al.* 1983). Off Namibia, estimated overall sardine biomass exceeded 11 million tons in 1964, but only 0.05 million tons in 1979 (Fig. 4, Thomas 1986).

Acoustic surveys to estimate sardine abundance were initiated off South Africa in 1984 (Hampton 1987). The spawner biomass of sardine was then 0.03 million tons, but it increased steadily to 0.62 million

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Manuscript received: November 1996

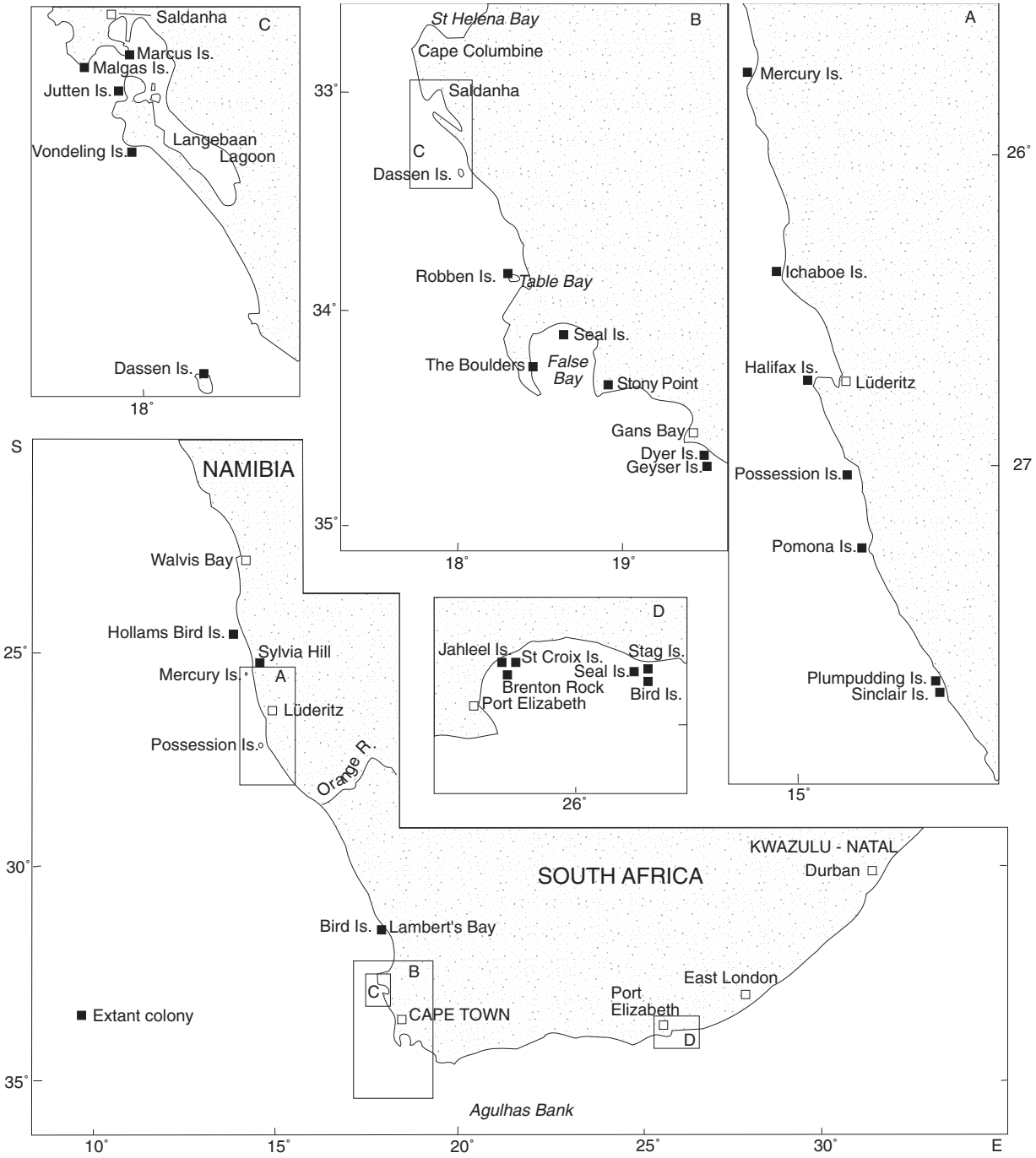

Fig. 1: The south-west coast of Africa, indicating extant colonies of African penguins and the localities mentioned in the text

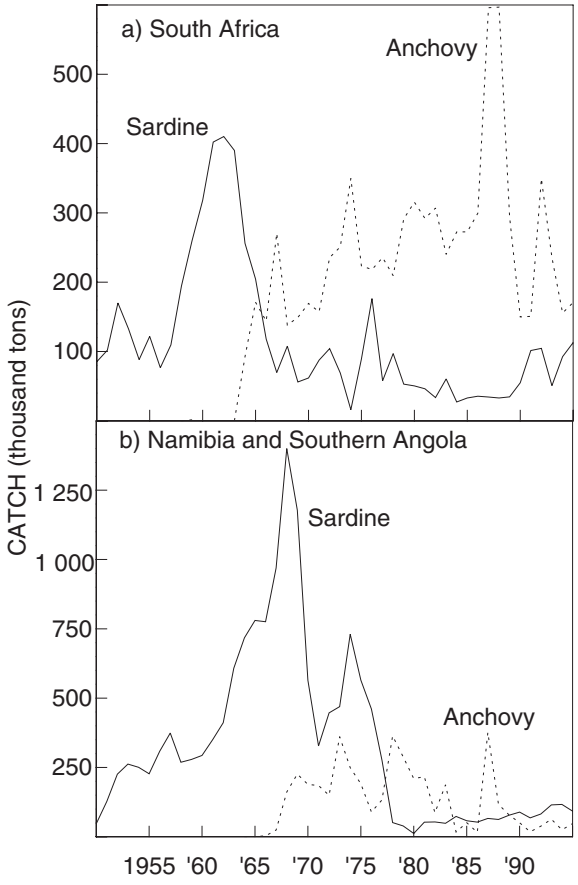

Fig. 2: Annual catches of sardine and anchovy off (a) South Africa and (b) Namibia and southern Angola, 1950–1995

tons by 1995 (Fig. 3, Hampton 1992). The increase is confirmed by the contribution of sardine to the diet of Cape gannets *Morus capensis* off western South Africa, with prevalence rising from < 10% by mass in each year between 1978 and 1984 to almost 60% by 1990 (Fig. 3, Crawford and Dyer 1995). A relatively strong sardine year-class off South Africa in 1983 (Berruti and Colclough 1987) led to subsequent growth of the sardine resource. Acoustic surveys for sardine have recently been undertaken off Namibia, where more than 0.5 million tons were recorded in both 1991 and 1992 (Boyer 1994).

Anchovy was first exploited by the southern African purse-seine fisheries in the 1960s. From September to December 1963, six boats off South Africa fished with a smaller-mesh net than had been used to catch sardine. They caught 300 tons of anchovy. In 1964, 48 South African boats fished throughout the year with small-mesh nets and caught 92 000 tons of anchovy. From 1965, all South African purse-seine boats were equipped with small-mesh nets (Newman *et al.* 1979). By 1966, anchovy contributed more than any other species to the South African purse-seine catch. This species continued to dominate the fishery for 30 years, up to and including 1995 (Fig. 2).

Off Namibia, small-mesh nets were introduced from 1963 to 1968, but they were only widely used after 1967 (Cram 1977, Schülein *et al.* 1978). Anchovy was first caught in 1964. Catches were small until 1968, when 0.16 million tons were landed. In 1978, when the catch was 0.36 million tons, anchovy became the most important contributor to the Namibian purse-seine fishery. This situation continued until 1984, when less than 17 000 tons of anchovy were caught. Poor catches continued in 1985 and 1986. In these three years, sardine dominated the landings. In 1987, the anchovy catch of 0.38 million tons off Namibia was the highest yet recorded there. Thereafter, catches rapidly plummeted and since 1989 have been <0.1 million tons annually (Fig. 2b). From 1990 to 1995, sardine regained dominance of the Namibian purse-seine catch.

Off South Africa, the spawner biomass of anchovy estimated acoustically was between 0.98 and 1.75 million tons from 1984 to 1988. It fell to about 0.5 million tons in 1989 and 1990, was above 1.5 million tons in 1991 and 1992, but fell again to <0.5 million tons in 1994 and 1995 and to <0.2 million tons in 1996 (Fig. 5, Hampton 1992).

In the 1950s, anchovy were probably scarce off South Africa. A large majority of fishermen (37 out of 45) held that anchovy increased in abundance after the mid 1950s. Most believed that the increase took place during the early 1960s (Crawford and Kriel 1985). In research catches of juvenile fish off western South Africa, anchovy contributed an annual average of 4% of total numbers of fish caught between 1955 and 1959. This rose to 30% between 1960 and 1965. Equivalent values for sardine were 25 and 10% (Crawford *et al.* 1987). An especially good research catch of juvenile anchovy was recorded in 1962 (Crawford *et al.* 1990a). The importance of anchovy as food for seabirds increased as well. From 1953 to 1956, anchovy formed 9–20% of the mass of the food eaten by Cape gannets off western South Africa (Davies 1955, 1956, Rand 1959), but from 1978 to 1988, it formed 37–64% of the diet (Berruti *et al.* 1993).

Off Namibia, anchovy was scarce in 1963 and 1964. Newman (1970, p. 12) commented of 1963: ". . . dur-

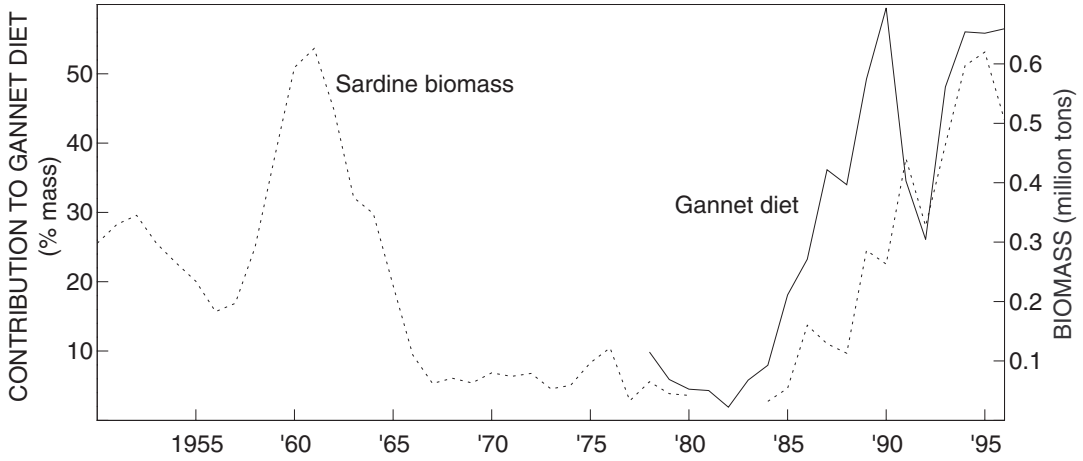

Fig. 3: Estimates of the biomass of sardine off South Africa (from Armstrong *et al.* 1985, Hampton 1992 updated), and the contribution of sardine to the diet of Cape gannets off western South Africa (from Crawford and Dyer 1995 updated), 1950–1996

ing this year the anchovy abundance was extremely low, and negligible catches were recorded". By 1964, 16 boats were searching for anchovy, their earnings being supplemented by the remainder of the fishing fleet. However, only 600 tons were caught, leading Thomas (1985) to conclude that the Namibian anchovy resource was then small. This pattern was reflected in the seabird diet. Between 1957 and 1959, anchovy contributed <2% to the diet of each of African penguins, Cape gannets and Cape cormorants *Phalacrocorax capensis* shot near Walvis Bay (Matthews 1961, Matthews and Berruti 1983). By contrast, from 1978 to 1982 anchovy formed 53% of the food of Cape gannets at Namibian islands south of Walvis Bay (Crawford *et al.* 1985). Therefore, off Namibia, anchovy was uncommon in the late 1950s.

To summarize, in the Benguela system, sardine was plentiful in the 1950s and 1960s. It started decreasing off South Africa in the mid 1960s and off Namibia in the early 1970s. In these regions, low levels of abundance were attained by the mid 1970s and early 1980s respectively. Sardine started increasing off South Africa in the early 1980s and were reasonably plentiful by 1995. Off Namibia, the sardine resource had recovered partially by 1991. By contrast, in the 1950s, anchovy were scarce off both South Africa and Namibia. The size of the resource increased off South Africa in the early 1960s and off Namibia from the mid 1960s. It remained abundant off Namibia until 1983. Except for 1987, when it was again temporarily plentiful, it has been scarce off Namibia since 1984. The high catches made off Namibia in 1987 may have been of fish from South Africa that were displaced northwards (Hewitson 1988, Cruickshank *et al.* 1990, Shannon *et al.* 1992). Off South Africa, anchovy were plentiful from 1965 until 1988. The spawner biomass fell to low levels in 1989 and 1990, recovered in 1991 and 1992, and then decreased again.

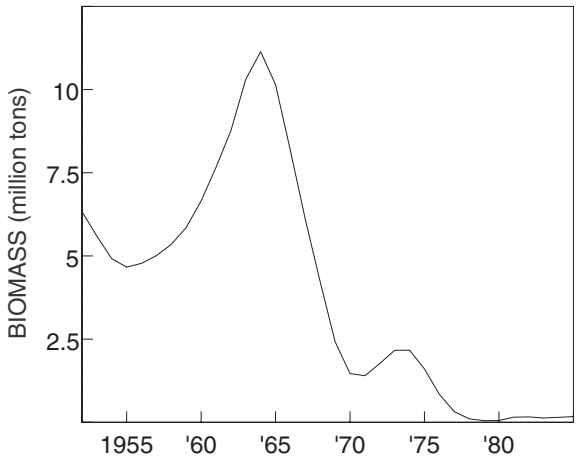

Fig. 4: Estimates of the biomass of sardine off Namibia, 1952–1985 (from Thomas 1985)

Fig. 5: Estimates of the biomass of anchovy off South Africa (from Hampton 1992 updated), and the contribution of anchovy to the diet of Cape gannets off western South Africa (from Crawford and Dyer 1995 updated), 1978–1996

Distribution

In the 1950s and 1960s, sardine were plentiful between Lüderitz and Table Bay, but as the resource collapsed the distribution contracted to the north off Namibia and to the south off South Africa (Lluch-Belda *et al.* 1989). This led to changes in the distribution of fishing effort (Crawford *et al.* 1987). In the 1950s, South African purse-seiners operated from Lambert's Bay to False Bay. In the 1960s and 1970s, they were forced to extend their range farther east and a processing factory was opened at Gans Bay. The Namibian fishery commenced in the vicinity of Walvis Bay. In 1964, a processing factory was opened at Lüderitz. As the Namibian sardine stock collapsed, fish became scarce in the vicinity of Lüderitz, resulting in the closure of the factory in 1974.

A contracted distribution of sardine may result from a decreased age composition of stocks that are at a low level of abundance. Off South Africa, young-of-the-year sardine recruit to nursery grounds north of Table Bay in autumn and winter. They later migrate southwards to the Agulhas Bank (Crawford 1980, 1981a). Sardine aged about one year frequently migrate eastwards, as far as the waters of KwaZulu-Natal (Armstrong *et al.* 1985). At about two years of age, sardine often are found once again north of Table Bay (Armstrong *et al.* 1987). In the 1950s, large sardine were readily available to purse-seine boats between Lambert's Bay and St Helena Bay from February until September (Crawford 1981a).

Off Namibia, the younger age-classes of sardine occur in the vicinity of, and to the north of, Walvis Bay (Crawford *et al.* 1987). It is the older fish that once extended farther south and were available to boats operating from Lüderitz.

Off South Africa, young-of-the-year anchovy have a similar distribution to sardine. These anchovy recruit to nursery areas north of Table Bay in autumn and winter and then migrate to the Agulhas Bank (Crawford 1981b). Older anchovy generally remain on the Agulhas Bank (Hampton 1987). Young-of-the-year sardine and anchovy often occur in mixed schools, but as they grow single-species schools are formed (Crawford 1980).

Off Namibia, most young-of-the-year anchovy recruit to the fishery in the vicinity of Walvis Bay in winter. Adults are caught farther north in autumn (Crawford *et al.* 1987).

In summary, when sardine abundance was at a high level, older fish were plentiful north of Table Bay and south of Walvis Bay. In a system dominated by anchovy, the only regular occurrence of anchovy and sardine between Lüderitz and Table Bay was of young-of-the-year fish that recruited to nursery areas and then migrated south. Older anchovy tend to remain on the western and central Agulhas Bank throughout the year, but sardine may migrate as far east as KwaZulu-Natal. Therefore, food is probably most consistently available to African penguins on the western Agulhas Bank when anchovy is dominant.

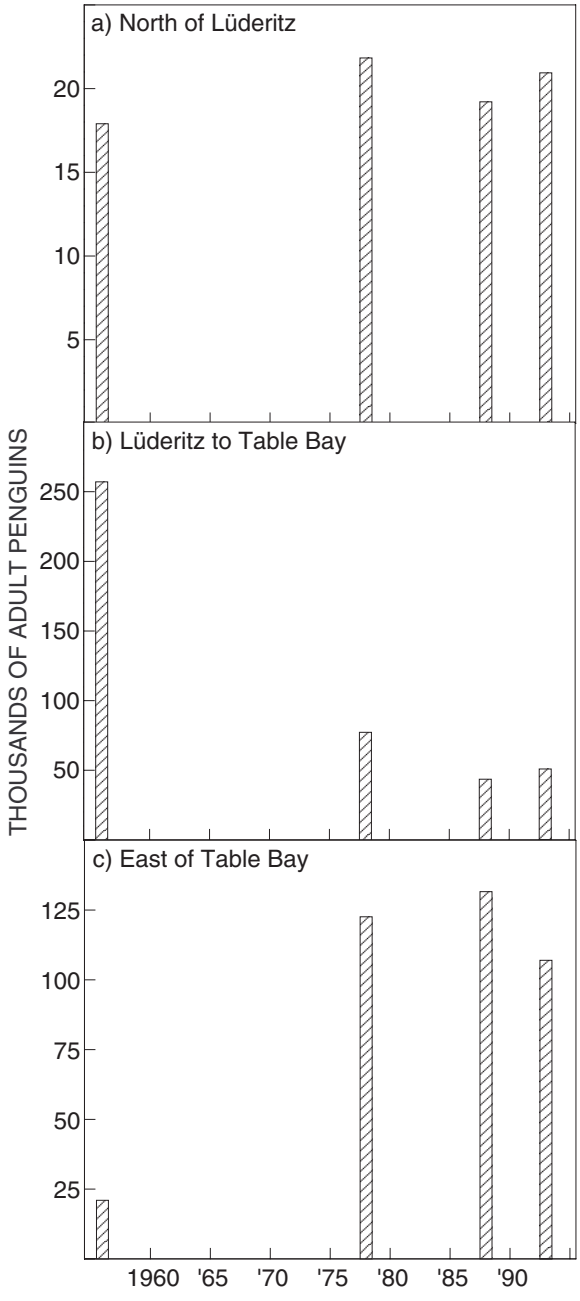

Fig. 6: Population of adult African penguins (a) north of Lüderitz, (b) between Lüderitz and Table Bay and (c) east of Table Bay for different periods during 1955–1995 (from Rand 1963a, b, Crawford *et al.* 1995a)

LONG-TERM TRENDS IN AFRICAN PENGUIN POPULATIONS

Changes in abundance and distribution

Trends in the population of African penguins have been documented by several authors (Frost *et al.* 1976, Crawford and Shelton 1981, Shelton *et al.* 1984, Crawford *et al.* 1990b, 1995a). In the 1950s, there were about 296 000 adult African penguins (Fig. 6, Rand 1963a, b). By the late 1970s, numbers had decreased to 222 000, by the late 1980s to 194 000 and by the early 1990s to 179 000 (Crawford *et al.* 1995a).

Between the 1950s and the late 1970s there were large decreases in numbers of African penguins at all colonies between Lüderitz and Table Bay (Shelton *et al.* 1984). Numbers at Mercury and Ichaboe islands north of Lüderitz and at Dyer Island south-east of Table Bay increased. The decreases between Lüderitz and Table Bay continued into the 1980s, but the increases north of Lüderitz and at Dyer Island stopped (Crawford *et al.* 1990b). Between 1982 and 1985 three new colonies were established in the vicinity of Table Bay (Broni 1982, Cooper 1985, Crawford *et al.* 1995b). After 1986, numbers of African penguins at Dyer Island decreased sharply, but colonies between Table Bay and Lüderitz stabilized. The colonies in Algoa Bay increased (Crawford *et al.* 1995a).

The result of these trends was that, whereas in 1956 some 87% of the breeding population was located between Lüderitz and Table Bay, by the late 1970s this region supported only 35% of the breeding population. By the late 1980s, the region supported only 22% of the adult population. In the early 1990s, 28% of the breeding population was between Lüderitz and Table Bay (Fig. 6).

In the 1950s, the region south-east of Table Bay supported only 7% of the overall breeding population. By the late 1970s, it contained 55% of the adult population. This proportion increased to 68% by the late 1980s and was 60% in the early 1990s (Fig. 6).

Localities north of Lüderitz had 6% of the breeding population in the 1950s, 10% in the 1970s and 1980s, and 12% in the early 1990s (Fig. 6).

RELATIONSHIP BETWEEN FISH REGIMES AND TRENDS OF AFRICAN PENGUINS

Transition from sardine to anchovy

The large downward trends of penguin numbers at

most breeding localities between Lüderitz and Table Bay between the 1950s and the 1980s suggest a common cause, such as food scarcity (Crawford *et al.* 1990b). It is likely that the shift from sardine to anchovy during the 1960s and 1970s resulted in a substantial decrease in food in this region.

At Possession Island, the African penguin population decreased by 99% between 1956 and 1986. This decrease was similar to what might have been expected from adult mortality had there been no recruitment of young adults (Cordes *et al.* in press). Breeding birds show strong fidelity to sites and mates are generally sedentary in the vicinity of islands where they breed and are unlikely to move between islands (Randall 1983, Randall *et al.* 1987, Crawford *et al.* 1995b). However, chicks rapidly disperse from natal colonies, often covering extensive distances (Randall *et al.* 1987). African penguins breeding for the first time may recruit in large numbers to colonies other than their natal island (Crawford *et al.* in press). There appears to have been minimal recruitment of breeding birds to the colony at Possession Island over a 30-year period. Either production and/or survival of young birds was low, or they emigrated to other colonies.

Contrasting the decrease in penguins between Lüderitz and Table Bay were increases at Dyer, Mercury and Ichaboe islands between the 1950s and the late 1970s (Shelton *et al.* 1984). The increase at Dyer Island between 1956 and 1967 would have necessitated a first-year survival of 0.88 in the absence of immigration (Shelton *et al.* 1984). Measurements of first-year survival, however, have ranged between 0.04 and 0.69 (Randall 1983, La Cock and Hänel 1987, La Cock *et al.* 1987). Therefore, a substantial immigration of first-time breeders to Dyer Island was likely in the 1960s.

African penguins have a protracted breeding season (Randall and Randall 1981). Off western South Africa it commences in January and continues until October (Crawford *et al.* 1995a). Birds then undergo their annual moult. For such an annual cycle, food must be available near breeding colonies throughout most of the year, especially from January to October. Anchovy are the main prey of penguins at Dyer Island (Duffy *et al.* 1985, Adams *et al.* in prep.). At Dyer Island during a regime of anchovy dominance, food should be available to penguins year-round, compared to the seasonal availability of young fish between Lüderitz and Table Bay that recruit to nursery areas before migrating southwards.

The increases in penguin numbers at Mercury and Ichaboe islands after the collapse of the Namibian sardine also may have resulted from immigration (Shelton *et al.* 1984). Penguins may have been attracted to these islands by a ready availability of pelagic goby *Sufflogobius bibarbatus*, which, like anchovy, are thought to have increased in abundance following the decrease of the Namibian sardine (Crawford *et al.* 1985). In 1980, the goby was important in the diet of African penguins at Mercury and Ichaboe islands, but scarce in the diet at Namibian islands south of Lüderitz (Crawford *et al.* 1985).

Transition from anchovy to sardine

Since the early 1980s, as the Benguela ecosystem reverted to a sardine regime, the regional trends in penguin populations evident when anchovy was dominant have reversed. Penguin numbers at Dyer Island have decreased, from 72 000 adults in the late 1970s to 27 000 in the early 1990s (Crawford *et al.* 1995a). Three new colonies were founded near Table Bay between 1982 and 1985 (see below). Numbers of penguins at colonies between Lüderitz and Table Bay stabilized, and at some localities may have increased (Crawford *et al.* 1995a).

At Dyer Island, the number of African penguins breeding in any year is significantly related to the spawner biomass of anchovy off South Africa (Adams *et al.* in prep.). This relationship suggests that, as the anchovy resource decreased, conditions for breeding became less favourable at Dyer Island. In February 1991, thousands of penguins abandoned nests at Dyer Island, probably as a result of food scarcity (Crawford and Dyer 1995). The decrease of the Dyer Island colony since the late 1970s can be modelled by assuming an annual adult survival of 0.93 and no recruitment of young breeders. Adult survival is probably between 0.88 and 0.96 (Randall 1983, Crawford *et al.* in press). Therefore, there probably has been little recruitment of breeders to Dyer Island since the late 1970s.

New African penguin colonies were established at Stony Point in 1982 (Broni 1982), Robben Island in 1983 (Shelton *et al.* 1984) and Boulders in 1985 (Cooper 1985). That these colonies were established at a time when the Benguela system began to shift from an anchovy regime to one dominated by sardine is of considerable interest. Except at Stony Point, where considerable numbers of birds are lost to mainland predators, the colonies are increasing (Crawford *et al.* 1995a). Growth of the Robben Island colony is being driven by immigration of young breeders; about 63% of the immigrants originated from Dyer Island (Crawford *et al.* in press). At Robben Island, the proportion of adults breeding is significantly related to spawner biomass of sardine off South Africa (Crawford *et al.* in press). Breeding success at Robben Island is significantly relat-

ed to spawner biomass of anchovy off South Africa, which has varied widely in recent years (Crawford and Dyer 1995).

In addition to Robben Island, four colonies between Lüderitz and Table Bay support more than 1 000 adult African penguins: Halifax, Possession, Jutten and Dassen islands. Numbers at Halifax Island are stable (Crawford *et al.* 1995a). At Possession Island, counts of breeding pairs approximately doubled between 1987 and 1995 (Cordes *et al.* in press). At Jutten and Dassen islands, the estimated populations increased by 28 and 11% respectively between the late 1980s and the early 1990s (Crawford *et al.* 1995a).

FISH REGIMES AND AFRICAN PENGUIN CONSERVATION

Following the switch in the 1960s from a sardine-based to an anchovy-based system, the number of African penguins breeding between Table Bay and Lüderitz decreased. Numbers of penguins breeding north of Lüderitz and east of Table Bay increased, but not sufficiently to balance the losses. Overall, the population of African penguins decreased by 25% between the 1950s and the late 1970s.

In the early 1980s, the Benguela system started reverting to one in which sardine was dominant and anchovy was at a lower level of abundance. The African penguin population at Dyer Island decreased rapidly, but new colonies were initiated in the vicinity of Table Bay and the decreases at many colonies between Table Bay and Lüderitz were halted. However, the net result was a 19% decrease in the overall African penguin population.

During a regime shift, the combined biomass of sardine and anchovy may be lower than when one of these species is dominant. The present transition from anchovy to sardine may not be complete and sardine may yet colonize to a greater extent the waters between Table Bay and Lüderitz. However, one question must be posed: if replacement of sardine by anchovy in the 1960s was a major factor in the decrease of the African penguin population then, why did recovery of the sardine in the 1980s not arrest the overall penguin decrease?

African penguins presumably have coped with many previous sardine-anchovy shifts, which off southern Africa appear to influence the distribution of food for penguins. A mechanism that may facilitate their ability to cope is the facility of first-time breeders to emigrate from natal colonies to those where forage fish are more available at the time when the young adults commence breeding (Crawford *et al.* 1995b, in press). Whereas flying birds have a greater foraging range, the breeding African penguin is dependent upon a ready availability of food near to colonies (Frost *et al.* 1976).

The failure of expanding colonies to have offset losses at decreasing colonies, both during the switch from sardine to anchovy and the later change from anchovy to sardine, more likely has resulted from inadequate recruitment of first-breeders to favourable breeding colonies than from decreased adult survival. Either the production of young by breeding pairs or the survival of immature birds has been insufficient.

In addition to the cyclic sardine-anchovy regime shifts, the Benguela system has been subject to long-term trends in other biotic properties during the 20th century. Commercial fisheries have greatly increased the fish harvest by man and the population of Cape fur seals *Arctocephalus pusillus pusillus* has been recovering from former decimation (Butterworth and Wickens 1990). Between 1930 and the 1980s, the annual take of fish and cephalopods by man and seals probably increased by about two million tons (Crawford *et al.* 1992). It is possible that this increased competition for food may have decreased reproductive success or juvenile survival of African penguins. At Robben Island, from 1989 to 1995, the number of chicks fledged annually per pair of African penguins averaged 0.47, with means varying between 0.32 and 0.59 (Crawford *et al.* in press).

What has been learned about the relationships of penguins to anchovy and sardine abundance in southern Africa may have relevance elsewhere. In Australia, the little penguin *Eudyptula minor*, which also feeds on sardine and anchovy *E. australis* (Montague and Cullen 1988) in a region where these fish are lightly exploited, has exhibited a much higher reproduction rate than exhibited by African penguins. Little penguins fledged a mean number of 0.84 chicks per pair per breeding season between 1968 and 1987 (Dann and Cullen 1990). In the Humboldt system, the Humboldt penguin *S. humboldti* has also experienced anchovy-sardine regime shifts (Lluch-Belda *et al.* 1989, 1992). Anchovy *E. ringens* was dominant in the 1960s, collapsed in the 1970s, but recovered in the late 1980s and early 1990s; sardine showed the opposite trend. There has been a long-term decrease in the population of Humboldt penguins, which is continuing (Croxall *et al.* 1996). As is the case with the African penguin, the Humboldt penguin appears unable to cope with the shifts in dominance between prey species in a system heavily exploited by man.

ACKNOWLEDGEMENTS

I am grateful to Prof. M. Cullen (Monash University, Australia) for valuable comments on an earlier draft of this paper, and to Mr I. Hampton, formerly Sea Fisheries for making available recent estimates of the biomass of sardine and anchovy off South Africa. Information was collected at islands under the control of Sea Fisheries of Namibia, Cape Nature Conservation, Eastern Cape Nature Conservation and National Parks Board of South Africa, to whom I am grateful for permission to undertake the research, and for transport to and accommodation at the islands. Transport was also provided by Sea Fisheries. This study was partly funded by the Sea Fishery Fund. This paper is a product of SCOR WG-98.

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